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The Structure of the Stomatogastric Neuromuscular System in Callinectes sapidus, Homarus americanus and Panulirus argus (Decapoda Crustacea)

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Phil. Trans. R. Soc. Lond. B 1974 **268**, 161-220
doi: 10.1098/rstb.1974.0024

THE STRUCTURE OF THE STOMATOGASTRIC NEUROMUSCULAR SYSTEM IN *CALLINECTES SAPIDUS*, *HOMARUS AMERICANUS* AND *PANULIRUS ARGUS* (DECAPODA CRUSTACEA)

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(*Communicated by H. G. Callan, F.R.S. – Received* 31 *May* 1973 – *Revised* 14 *November* 1973)

CONTENTS

	PAGE
INTRODUCTION	162
MATERIALS AND METHODS	163
GENERAL FORM OF THE FOREGUT	164
STOMACH OSSICLES	164
Classification of the stomach ossicles	165
Stomach ossicles of *Callinectes*	167
Stomach ossicles of *Homarus*	169
Stomach ossicles of *Panulirus*	171
STOMACH MUSCLES	173
Classification of the stomach muscles	173
Stomach muscles of *Callinectes*	175
Stomach muscles of *Homarus*	181
Stomach muscles of *Panulirus*	186
THE STOMATOGASTRIC NERVOUS SYSTEM	192
Classification of the stomatogastric nervous system	192
Stomatogastric nervous system of *Panulirus*	194
Stomatogastric nervous system of *Homarus*	201
Stomatogastric nervous system of *Callinectes*	207
DISCUSSION	214
Comments on the stomach muscles	214
Comments on the stomatogastric nervous system	215
REFERENCES	218

The stomatogastric nervous system of the reptantian Decapoda Crustacea, particularly the small isolated stomatogastric ganglion containing the 25–30 motor neurons that control the muscles of the gastric mill and the pyloric filter of the stomach, is an important preparation for research in comparative neurophysiology. Unfortunately there are no comprehensive descriptions of the neuromuscular system of the stomach in these animals. Therefore, since the stomatogastric motor neurons are identified by reference to the muscles they innervate, it has been difficult to identify neurons within or between species.

The most important features for classifying the muscles of the decapod stomach are the ossicles to which the muscles attach. In the latter part of the last century Mocquard demonstrated that the stomach ossicles of the decapods could be compared in different

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groups despite the large variations from group to group. A summary of Mocquard's (1883) classification scheme, with some modifications, is given. The scheme recognizes 33 ossicles in seven categories (cardiac gastric mill, I–VII; lateral supporting cardiac ossicles, VIII–XV; ossicles of the cardio-pyloric valve, XVI–XVIII; supporting ossicles of the dorsal pyloric stomach, XIX–XXI; supporting ossicles of the ventral pylorus and ampullae, XXII–XXVII; supra-ampullary ossicles, XXVIII–XXX; supporting ossicles of the lateral pylorus, XXXI–XXXIII). Where necessary, comments are then made on the ossicles of the three divergent species studied, the blue crab, *Callinectes sapidus* (Brachyura); the lobster, *Homarus americanus* (Macrura) and the spiny lobster *Panulirus argus* (Palinura). Most of the thirty-three ossicles are found in each of the species, but there are some major differences between species. *Callinectes*, for example, has the most complex ossicle system and *Panulirus* the most reduced.

A complete description of the stomach muscles of the three species is then presented. A new and flexible terminology is used in these descriptions. The stomach muscles are divided basically into five major groups by their location on the gut (cardiac sac, gastric mill, ventral cardiac, cardio-pyloric valve and pyloric). *Callinectes* has the most complex muscle system with 41 muscles and 51 muscle bundles, *Homarus* has 37 muscles and 49 muscle bundles, and *Panulirus* has 38 muscles but only 44 muscle bundles. Nevertheless it was clearly possible to identify homologous muscles in these species, at least thirty muscles being common to all three species. Most of the variation between species occurs in the intrinsic muscles (those confined to the stomach wall) of the gastric mill and the cardio-pyloric valve groups.

The gross anatomy of the stomatogastric nervous system is described for the three species. In the main the earlier terminology of Orlov was used but it was also convenient to classify the system into four broad groups (class 1, oesophageal motor neurons; class 2, sensory fibres; class 3, neurosecretory fibres; class 4, the stomatogastric ganglion and its associated input and output nerves). Again it was not difficult to identify the same gross nerve trunks in the three species. This was particularly true of the major axis of the stomatogastric ganglion system (stomatogastric nerve, stomatogastric ganglion, dorsal and lateral ventricular nerves, pyloric dilator nerve, and the pyloric nerve) of class 4 and of the general course of the postero-lateral nerve and posterior stomach nerve of class 2. Differences between the three species do occur, for example in the branching pattern in the pyloric region and the nature of the lateral nerves leaving the stomatogastric ganglion and dorsal ventricular nerve.

In *Panulirus* an almost complete description of the innervation of the stomach muscles by the individual stomatogastric ganglion motor neurons is also given. This description is partly based on physiological data published elsewhere. Where possible the description in terms of the motor neurons is also given for *Homarus* and *Callinectes*, but present physiological data are incomplete for these species. It should be noted that there is evidence that some homologous stomatogastric ganglion motor neurons travel along quite different nerve trunks in the different species. In *Homarus*, for example, the median ventricular nerve carries the axons of the ventricular dilator and lateral cardiac motor neurons, whereas in *Panulirus* this nerve carries the axons of the ventricular dilator and the inferior cardiac motor neurons.

In conclusion summary tables and diagrams are presented for the muscle and nervous anatomy, and it is suggested that the classification schemes presented here should provide the basis for consistent identification of the stomatogastric motor neurons throughout the reptantian decapods.

Introduction

Over the past century several papers have described the skeletal elements and musculature of the stomach of various decapod Crustacea (see, for example, Balss 1944). Among the earlier comparative writers, Mocquard (1883) excels in the number of species examined and the quality of his observations and illustrations. More recent papers describe the stomachs of single species, for example the lobster, *Homarus americanus* (Williams 1907); the crayfish, *Astacus fluviatilis* (Ringel 1924); the blue crab, *Callinectes sapidus* (Cochran 1935) and the rock lobster *Jasus lalandii* (Paterson 1968). These descriptions are not altogether complete, however, and ignore or are at slight variance with some of Mocquard's observations and with those of Nauck (1880). Accounts of the pyloric stomach musculature are particularly fragmentary so that the recognition of homologous muscles across major taxonomic groupings from published data is difficult or impossible.

We have become impressed with the need for reasonably accurate identification of the skeletal and muscular elements because of our interest in the comparative neurophysiology of the stomatogastric ganglion (Maynard 1966, 1969, 1972; Dando & Selverston 1972). The motor neurons of this ganglion are identified according to the muscle or muscles they innervate, and their intra-ganglionic connexions and output patterns are associated with the role such muscles play in producing stomach movements. Accordingly we must know the muscle anatomy of the species under study and, for comparative purposes, identify homologous muscles or muscle groups in members of different families or super-families.

This paper re-examines the stomachs of three divergent forms under current study, the lobster, *Homarus americanus* (Macrura); the spiny lobster, *Panulirus argus* (Palinura); and the blue crab, *Callinectes sapidus* (Brachyura). Our observations on the skeletal elements add little to those of Mocquard and serve primarily as a summary and an essential basis for the subsequent myoanatomy. Our observations on the stomach muscles are more complete than those published by Cochran, Williams, Ringel, or Paterson, and provide the basis for a consistent terminology among the three groups. We have attempted to utilize information about locus, general form, neighbouring ossicles or muscles, and muscle connexions, in interpreting homologies. There is clear indication, however, that muscles may shift origins and insertions on the stomach, that both muscles and ossicles may fuse, divide or disappear, and that the form of muscles and ossicles may vary greatly. Accordingly our interpretations will not always agree with those suggested by other authors, and must be considered subject to revision as more information, particularly about specific innervation, becomes available.

There is also apparently no published description of the complete anatomy of the nervous system innervating the stomach of any higher decapod (see, for example, Balss 1944; Bullock & Horridge 1965). The best of the available studies are those of Orlov (1926*a*, *b*, 1927, 1929) and Keim (1915) on *Astacus*, Allen (1894) on *Homarus*, and Mocquard on a wide variety of species. We have therefore given a gross description of the stomatogastric nervous system of the three species under study. Additionally in *Panulirus*, for which we have the most physiological data, we give an almost complete description of the innervation of the stomach muscles by the individual motor neurons of the stomatogastric ganglion. This has also been done, where it is possible, for *Homarus* and *Callinectes*.

Materials and methods

Dissections were made from fresh material, and from specimens preserved in formalin, alcohol, or Bouin's fixative. Some preparations were digested in KOH for the study of stomach ossicles. Intra-vital methylene blue techniques were used to stain nerves, or occasionally muscle fibres in fresh preparations. Freehand drawings were made with the aid of ruled paper, and a micrometer grid in the dissecting microscope used for examinations.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Spiny lobsters were collected at the Bermuda Biological Station, and most work on them was done there with fresh material. Maine lobsters were obtained alive from local fish suppliers in Ann Arbor, and living blue crabs were purchased from the Gulf Specimen Company, Panacea, Florida, or the Marine Biological Laboratory, Woods Hole, Mass., U.S.A.

General form of the foregut

The foregut of reptantian decapods is divided into three regions: the oesophagus, the cardiac stomach, and the pyloric stomach with its characteristic ventral ampullae. The oesophagus is a chitin-lined tube, often with longitudinal ridges, that opens into the cardiac stomach. The anterior portion of the cardiac stomach is a thin-walled, flexible chamber suited for the initial storage of ingested material. The pyloric stomach and posterior half of the cardiac stomach are strengthened and supported by articulating ossicles and plates – thickened calcified regions of the chitinous stomach lining. Some of the dorsal and lateral cardiac ossicles are toothed, forming a chewing apparatus or gastric mill. Much of the inner lining of the remainder of the pylorus and posterior cardium is equipped with various hairs, spines, and tubercles. These define passageways and form valves within the stomach (Williams 1907). The stomach is supported in place in the thorax and the ossicles are moved by a series of striated muscles under the control of nerves from the stomatogastric ganglion.

The general form of the stomach differs somewhat among the three groups examined here. In *Callinectes* (Brachyura) the oesophagus enters the anterior ventral border of the cardiac stomach. The anterior cardium expands laterally, and then angles inward at the level of the cardiac ossicles. The pyloric stomach turns sharply downward at the cardio-pyloric junction. Ossicles are well developed and elaborate. Mocquard considered the Brachyura to have the most complete complement of ossicles among the decapods. Two long tubular caeca originate at the dorsal, posterior border of the pylorus and extend forward over the dorsal pyloric stomach. In *Homarus* (Macrura), the oesophagus is located more ventrally, and the cardium tends to be more elongated than in the crab. The ossicles of the gastric mill are particularly well developed and strongly calcified. The ventral cardiac ossicles are also well developed, and are quite long. As in the Brachyura the pyloric stomach bends downward, but the linear distortion and bending of the pyloric ossicles suggests that the axis of the bend is more posterior and the radius of the bend larger than in the Brachyura. Also in comparison with the Brachyura, there are fewer pyloric ossicles. A single short caecum lies just above the dorsal ossicles of the posterior pylorus. In *Panulirus* (Palinura) the oesophagus is almost vertical and enters the cardium much more posteriorly than in either the crab or lobster. The ventral cardiac ossicles are thereby reduced in size. The pyloric stomach is essentially unbent and in line with the cardium. The number of pyloric ossicles tends to be reduced, but those remaining form extensive lateral calcified plates so that the pylorus appears to be more rigidly armoured than in the other two groups. A dorsal caecum is lacking.

The stomach ossicles

Figure 1 is a diagrammatic side view of the stomach ossicles of an idealized reptantian decapod. Figures 2–4 are similar views of the ossicles of the blue crab, *Callinectes*; the lobster *Homarus*; and the spiny lobster, *Panulirus*. It should be noted that, with the exception of some ossicles located in the midline, the ossicles are paired, with similar elements lying on each side of the gut.

Classification of the stomach ossicles

It is convenient to divide the stomach ossicles into seven categories. The terminology follows that of Mocquard (1883) with modifications suggested by Balss (1944) and Cochran (1935). For present purposes we recognize a total of 33 basic ossicles.

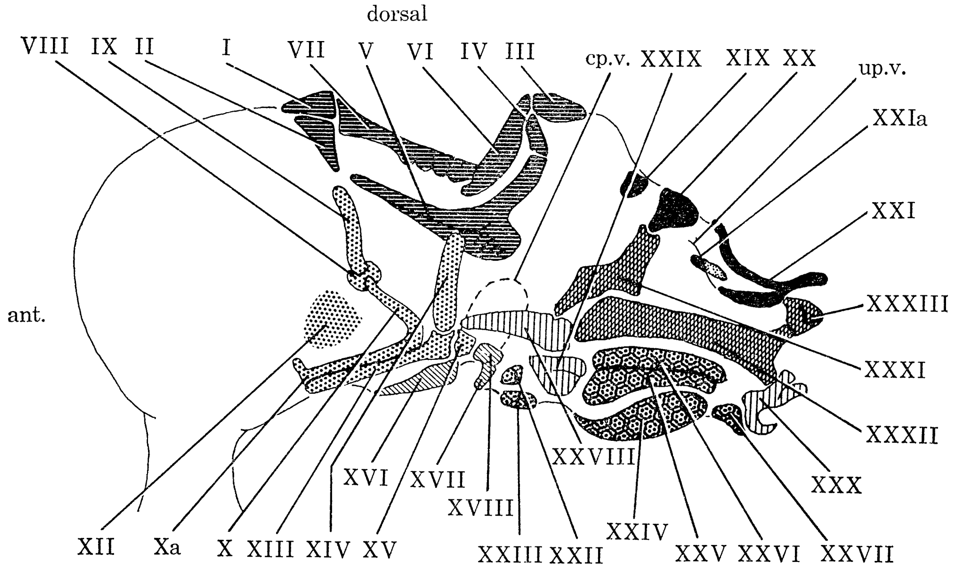

FIGURE 1. A diagrammatic lateral view of the stomach ossicles of an idealized reptantian decapod. Anterior is to the left and dorsal is uppermost in the figure. Full explanations of the numbering system (I–XXXIII) for the ossicles are given in the text below.

(i) *Cardiac gastric mill*

I	mesocardiac ossicle (one)
II	pterocardiac ossicle (one pair)
III	pyloric ossicle (one, sometimes paired)
IV	exopyloric ossicle (one pair)
V	zygocardiac ossicle (one pair, dentate)
VI	propyloric ossicle (one, dentate)
VII	urocardiac ossicle (one, dentate)

(ii) *Lateral supporting cardiac ossicles*

VIII	pectineal ossicle (one pair, dentate on inner side)
IX	prepectineal ossicle (one pair)
X	postpectineal ossicle (one pair)
Xa	‘quill’ of postpectineal ossicle found in some forms (one pair)
XI	anterior lateral cardiac plate (one pair) – not illustrated or considered in this paper
XII	posterior lateral cardiac plate (one pair)
XIII	inferior lateral cardiac ossicle (one pair)
XIV	subdentate ossicle (one pair)
XV	lateral cardio-pyloric ossicle (one pair)

(iii) *Ossicles of the cardio-pyloric valve*

The cardio-pyloric valve is a ventral invagination at the cardio-pyloric border. It partially closes the passageway between the two parts of the stomach, and thus limits access of food particles to the pyloric cavities. The valvular walls, or more frequently their borders at the point of invagination, are sometimes calcified, forming ossicles (Mocquard 1883). The lateral ossicles, here termed the cardio-pyloric ossicles and including both the auricle and bar of Mocquard, have apparently been confused sometimes with the anterior supra-ampullary ossicle or with the preampullary ossicle (Cochran 1935).

cp.v. cardio-pyloric valve
XVI anterior ossicle of cardio-pyloric valve (one) (posterior inferior cardiac ossicle)
XVII posterior ossicle of cardio-pyloric valve (one) (preanterior inferior pyloric ossicle)
XVIII lateral ossicle of cardio-pyloric valve (one pair) (cardio-pyloric auricular ossicle)

(iv) *Supporting ossicles of the dorsal pyloric stomach*

XIX anterior mesopyloric ossicle (usually one pair)
XX posterior mesopyloric ossicle (usually one)
XXI uropyloric ossicle (various, according to the extent of calcification and fusion, usually one or two midline pieces with one or two lateral pairs, often fused)
XXIa infra-uropyloric fragment (one pair). This represents a small calcified strip lying beneath the anterior half of the uropyloric fold. It is the site of muscle attachments. We are not sure whether this is best regarded as a portion of the uropyloric complex or as an isolated extension of one of the pleuro-ossicles (see below)
up.v. uropyloric fold

(v) *Supporting ossicles of the ventral pylorus and ampullae*

XXII preampullary ossicle (one pair)
XXIII anterior inferior pyloric ossicle (one)
XXIV inferior ampullary ossicle (one pair)
XXV ampullary roof ossicle, lower portion (one pair)
XXVI ampullary roof ossicle, upper portion (one pair). Mocquard did not recognize two portions of the ampullary roof. He also placed these ossicles in the next general group, supra-ampullary ossicles
XXVII posterior inferior pyloric ossicle (one)

(vi) *Supra-ampullary supporting ossicles*

XXVIII anterior supra-ampullary ossicle (one pair)
XXIX middle supra-ampullary ossicle (one pair)
XXX posterior supra-ampullary ossicle (one pair)

(vii) *Supporting ossicles of the lateral pylorus*

XXXI anterior pleuropyloric ossicle (one pair)
XXXII middle pleuropyloric ossicle (one pair)
XXXIII posterior pleuropyloric ossicle (one pair)

Stomach ossicles of Callinectes (*figure* 2)

Although Nauck (1880), Albert (1883), and Pearson (1908) have published on Brachyura, the most satisfactory descriptions of the brachyuran stomach were given by Mocquard (1883) and Cochran (1935).

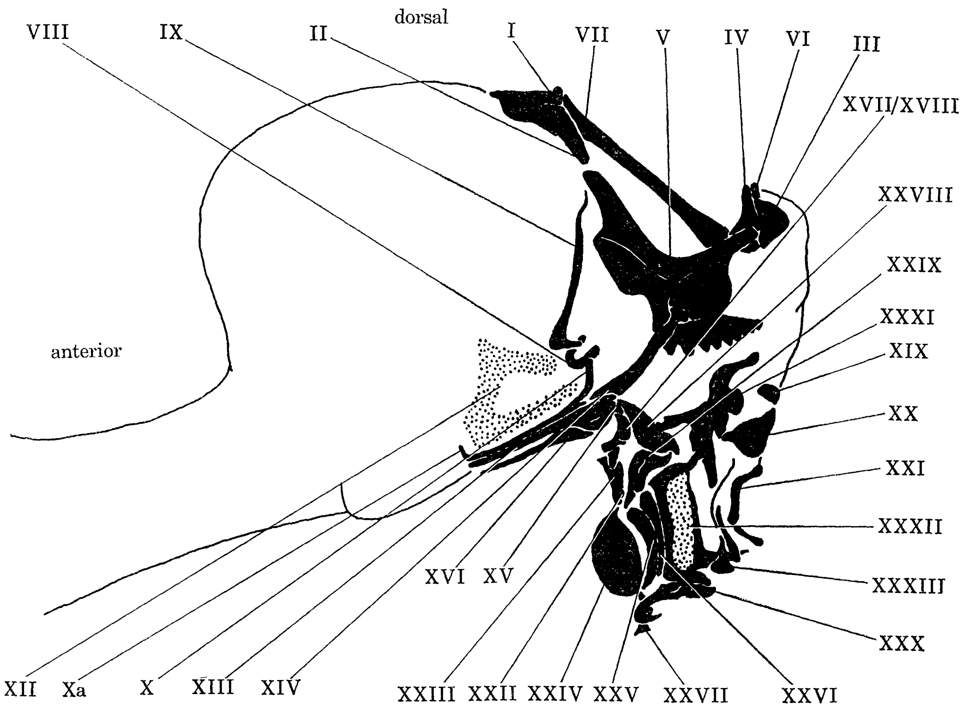

FIGURE 2. A diagrammatic lateral view of the stomach ossicles of *Callinectes sapidus*. Anterior is to the left and dorsal is uppermost.

(i) *Gastric mill*

Well described by Mocquard and Cochran.

(ii) *Lateral cardiac ossicles*

The posterior lateral cardiac plate (XII) is somewhat angular and often relatively well calcified. It is not as rigid as in the Palinura where it is essentially an ossicle, but it does serve as a point of attachment of several muscles. The lateral cardio-pyloric ossicle (XV) is more obvious in the crab than in either the lobster or spiny lobster. It lies on the inner side of the inferior lateral cardiac ossicle (XIII) with which it articulates.

(iii) *Cardio-pyloric valve*

The ossicles of the cardio-pyloric valve (cp.v.) often seem to be misunderstood. Cochran did not refer to the extensive descriptions of Mocquard and came to a number of misconceptions. Balss passed them over very lightly in his review.

Cochran completely overlooked the ossicle XVII, which forms the posterior margin of the valve, and confused the lateral ossicle of the valve (XVIII) with the anterior supra-ampullary ossicles (XXVIII). The lateral ossicles of the cp.v. (XVIII) extend forward along the lateral margins of the cardio-pyloric valve. They articulate with the lateral cardio-pyloric ossicle (XV) on each side and extend a process forward and upward into the valve, medial to the lateral ossicles and the posterior end of the inferior lateral cardiac ossicle (XIII). Posteriorly and medially the lateral ossicles of the cp.v. join, via slightly calcified chitin, with the posterior ossicle of the cardio-pyloric valve (XVII). Several intrinsic muscles originate at the lateral ossicle of the cp.v. (see below), among them some which Cochran mistakenly assigned to the anterior supra-ampullary ossicle (XXVIII) and the preampullary ossicle (XXII).

(iv) *Dorsal pyloric ossicles*

We have nothing to add to the accounts of these ossicles by Cochran and Mocquard. The infra-uropyloric fragment (XXIa) is sometimes not present.

(v) *Ventral pyloric ossicles and ampullae*

In most crabs a small, slightly calcified plate lies between the posterior ventral margin of the middle supra-ampullary ossicle (XXIX) and the anterior inferior pyloric ossicle (XXIII). This is the preampullary ossicle (XXII) as identified by Mocquard. Cochran confused it with the lateral ossicle of the cp.v. (XVIII) which lies forward of it. The ventral pyloric ossicles are unexceptional and generally have been described satisfactorily. In the crab, as in the other two species, we preferred to separate the roof of the ampullae into two parts, one which is perpendicular to the pyloric wall and concave dorsally (XXV) and one bordering its inner edge which tends to be more nearly parallel with the pyloric wall (XXVI). In the crab the latter ossicle is relatively narrow and tends to fuse with the ventral border of the middle pleuro-pyloric ossicle (XXXII).

(vi) *Supra-ampullary ossicles*

From Cochran's description of muscle attachments and her somewhat ambiguous figure (30), it is clear that she did not recognize the anterior supra-ampullary ossicle XXVIII as described by Mocquard, but rather applied the name to a portion of the lateral ossicle of cardio-pyloric valve (XVIII). We find that the anterior supra-ampullary ossicle (XXVIII) begins just medial to the lateral cardio-pyloric ossicle (XV), and, curving somewhat dorsally and medially, extends backward as an irregular plate which articulates with the ventral extension of the anterior pleuropyloric ossicle (XXXI). It is well calcified but does not seem to serve as the origin or insertion for any of the more superficial stomach muscles identified by Cochran. The middle supra-ampullary ossicle (XXIX) is well calcified, and relatively modest in size. As in all three species discussed in this paper, it carries a protrusion which serves as the origin of important lateral pyloric muscles. The posterior supra-ampullary ossicles (XXX) do not fuse with the posterior inferior pyloric ossicle (XXVII).

(vii) *Pleuropyloric ossicles*

The anterior pleuropyloric ossicle (XXXI) is an irregular, well calcified structure with anterior-posterior and dorsal-ventral extensions. The dorsal projection articulates with the posterior mesopyloric ossicle (XX), while the ventral extension articulates with the anterior supra-ampullary ossicle (XXVIII). A lateral protrusion at the central region of the ossicle serves as an attachment site for several lateral pyloric muscles. The middle pleuropyloric ossicle (XXXII) lies posterior and somewhat ventral to the anterior pleuropyloric ossicle. It provides the major lateral support of the pyloric stomach. In the crab, the ossicle is irregularly calcified, and an anterior dorsal knob is the site of muscle attachments. The ossicle articulates

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

or fuses ventrally with the upper ampullary roof ossicle (XXVI) and posteriorly with the posterior supra-ampullary ossicle (XXX) and the posterior pleuropyloric ossicle (XXXIII). Mocquard described the posterior pleuropyloric ossicle as a lateral, ear-like projection located just beneath and behind the uropyloric fold. Subsequent authors have failed either to figure it (Pearson 1908) or to identify it (Cochran 1935). In the crab, however, such a projection does occur. It is only slightly calcified, and is difficult to relate to other more medial or dorsal ossicles. In some instances it appears to connect with calcified chitin extending upward and forward under the uropyloric fold from the middle pleuropyloric ossicle (XXXII). We tentatively group the two calcified regions, the upward extension from the middle pleuropyloric ossicle and the ear-like projections, together as the posterior pleuropyloric ossicle (XXXIII).

Stomach ossicles of Homarus (*figure* 3)

Both Mocquard (1883) and Williams (1907) described ossicles in *Homarus*.

(i) *Cardiac gastric mill*

All of the ossicles are well calcified, and the mesocardiac (I) and pyloric (III) ossicles are unusually heavy. A lightly calcified, oval plate (IIIa) (Williams 1907) often occurs just ventral to the lateral, posterior border of the pyloric ossicle on either side.

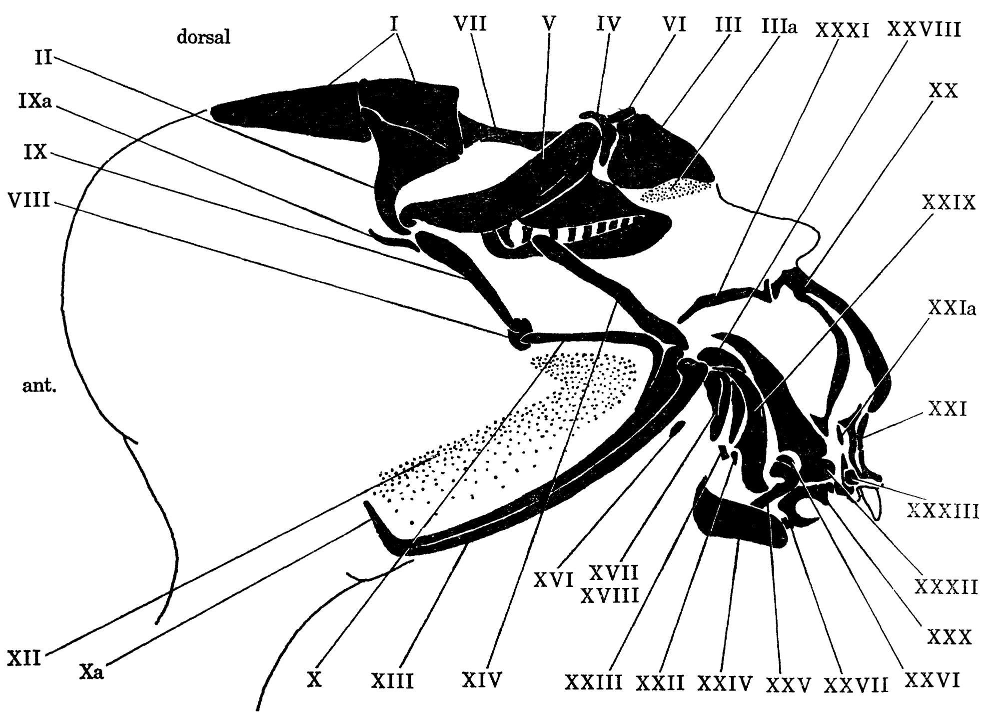

FIGURE 3. A diagrammatic lateral view of the stomach ossicles of *Homarus americanus*. Anterior is to the left and dorsal is uppermost.

(ii) *Lateral cardiac ossicles*

The lateral ossicles, particularly the inferior lateral cardiac ossicle (XIII) are well developed and heavily calcified. A small accessory prepectineal ossicle (IXa) extends forward from the upper end of the prepectineal ossicle and ventral to the pterocardiac ossicle. The postpectineal ossicle (X) often appears to be separated from the 'quill' segment (Xa) which parallels the inferior lateral cardiac ossicle (XIII). The lateral cardio-pyloric ossicles (XV) are not obvious; they may be entirely absent or may be represented by non-calcified chitin. The posterior lateral cardiac plate (XII) is generally not calcified and extends the length of the inferior cardio-pyloric ossicle.

(iii) *Cardio-pyloric valve*

The anterior ossicle of the cp.v. (XVI) is reduced to a small angular calcified plate. It is connected by ligaments to the auricular complex on each side. The posterior ossicle of the cardio-pyloric value (XVII) is a heavily calcified region in the midline. To each side, calcified bars extend forward along the inner wall of the valve. These form the base of the expanded, flap-like lateral ossicle of the cp.v. (XVIII) which extends outward from the posterior ossicle of the valve.

(iv) *Dorsal pyloric ossicles*

The anterior mesopyloric ossicles (XIX) are lacking. A heavily calcified fragment on either side articulates with the anterior pleuropyloric ossicle (XXXI) and represents part, if not all, of the posterior mesopyloric ossicle (XX). It is continuous with a thickened, often calcified fold of chitin which extends posteriorly parallel with the dorsal ridge on each side. There is also a thickening, and sometimes slight calcification, just lateral to the dorsal ridge. Both Mocquard and Ringel identified the folded ridge as part of the uropyloric ossicle (XXI) but Williams considered it homologous to the posterior mesopyloric ossicle of other forms. Our material is insufficient to resolve this difference. There is no question, however, that ossicles posterior to the fold and ridge are part of the uropyloric complex (XXI), and the outer edges of the uro-pyloric fold are characteristically calcified. There is also a small calcified strip beneath the anterior portion of the uropyloric fold, the infra-uropyloric fragment (XXIa).

(v) *Ventral pyloric ossicles and ampullae*

The preampullary ossicle (XXII) is poorly calcified and is located just laterally and slightly behind the anterior inferior pyloric ossicle (XXIII), which is reduced to a small, median, slightly calcified oval. The inferior ampullary ossicle (XXIV) is longer than it is wide, and its outer end is displaced posteriorly. The ossicles of the ampullary roof (XXV and XXVI) are also displaced backward, and reduced in size – particularly the upper portion (XXVI). The posterior inferior pyloric ossicle (XXVII) is strongly calcified.

(vi) *Supra-ampullary ossicles*

Both the anterior supra-ampullary ossicle (XXVIII) and the middle supra-ampullary ossicle (XXIX) are elongated and curve backward and downward. Neither are very strongly calcified, and the outer edge of the middle ossicle continues well back and over the anterior portion of the ampullae. The middle supra-ampullary ossicle is perhaps the most obvious of the pyloric ossicles in the lobster, and is much larger than in either the crab or spiny lobster. It provides extended sites for ventral attachments of lateral pyloric muscles. As in the crab the anterior ossicle does not appear to have attachment sites for superficial lateral pyloric muscles. The posterior supra-ampullary ossicles (XXX) are not fused with the posterior inferior pyloric ossicle (XXVII).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(vii) *Pleuropyloric ossicles*

The anterior pleuropyloric ossicle (XXXI) is a calcified bar articulating dorsally with the posterior mesopyloric ossicle (XX) and terminating ventrally in a chitinous fold somewhat anterior to the anterior supra-ampullary ossicle (XXVIII). The middle pleuropyloric ossicle (XXXII) is a flattened, calcified plate extending along the lower half of the lateral pylorus from the region of the anterior supra-ampullary ossicle posteriorly to the posterior supra-ampullary ossicles. It lacks the knobs and irregularities found in the homologous crab ossicle. As in the crab, the posterior pleuropyloric ossicle (XXXIII) occurs in two parts; one fairly well-calcified portion extends upward and forward from the posterior supra-ampullary ossicle (XXX) and the upper posterior corner of the middle pleuropyloric ossicle (XXXII) under the uropyloric fold, while the second, slightly calcified portion forms a lateral, ear-like projection just posterior to the fold.

Stomach ossicles of Panulirus (*figure* 4)

Mocquard (1883) provided the most complete figures and description of the ossicles of a palinurid. Of the three groups described here, the ossicles of the spiny lobster show the greatest departure from the brachyuran arrangement.

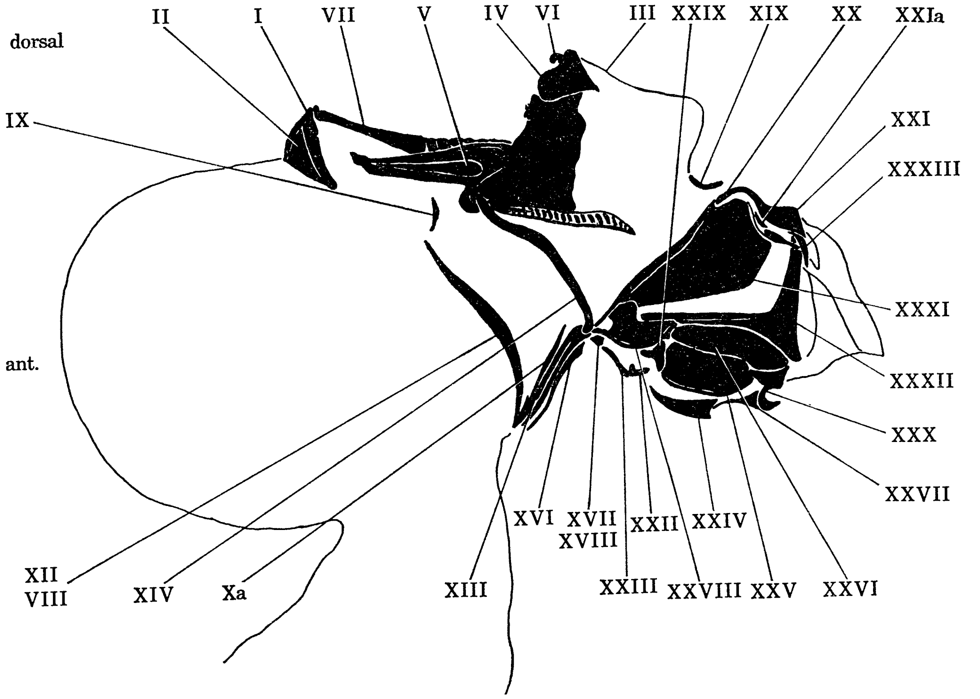

FIGURE 4. A diagrammatic lateral view of the stomach ossicles of *Panulirus argus*. Anterior is to the left and dorsal is uppermost.

(i) *Gastric mill ossicles*

The mesocardiac (I) and pterocardiac (II) ossicles are slightly calcified, and resemble those of *Callinectes* more than those of *Homarus*. The exopyloric (IV) and zygocardiac (V) ossicles are well developed and strongly calcified. It is possible that the lateral portion of the pyloric ossicle

(III) has fused with the exo-pyloric ossicle (IV), but we will follow Mocquard's interpretation and consider the more medial, essentially uncalcified region just behind the propyloric ossicle (VI) as the pyloric ossicle proper (III).

(ii) *Lateral cardiac ossicles*

Generally, the lateral cardiac ossicles are weak and reduced in the spiny lobster. The pectineal ossicle (VIII) with a single small tooth on the inner side is fused with the upper end of the posterior lateral cardiac ossicle (XII). This ossicle is formed from the old posterior lateral cardiac plate by folding and calcification. It appears to assume the function of the post-pectineal ossicle in the crab in providing muscle attachments and support for the pectineal tooth. The prepectineal ossicle (IX) is reduced to a small calcified fragment, and the post-pectineal ossicle itself (X) is lost, leaving the 'quill' (Xa) as a remnant. The inferior lateral cardiac ossicle (XIII) is present, but unlike the situation in the crab and *Homarus*, does not articulate directly with the elongate subdentate ossicle (XIV). The lateral cardio-pyloric ossicle (XV) seems to be lacking or greatly reduced, and possibly may fuse with the cardio-pyloric auricular ossicles (XVIII).

(iii) *Cardio-pyloric valve*

The anterior ossicle of the cp.v. (XVI) is well calcified with a medial spine projecting forward. Compared to the crab, the lateral ossicles of the cp.v. (XVIII) are small, but they are strongly calcified and are continuous medially with the posterior ossicle of the valve (XVII). The latter folds inward medial to the lateral ossicles and is continuous with the calcified walls of the valve invagination. The posterior ossicle of the valve (XVII) also articulates with the anterior inferior pyloric ossicle (XXIII).

(iv) *Dorsal pyloric stomach*

There are two obvious ossicle complexes along the mid-dorsal line. The most anterior is single, in the midline, and not heavily calcified. It forms the site of insertion of the most anterior of the dorsal pyloric dilators. The more posterior ossicle is more complex, having two laterally and anteriorly projecting horns, which form an arc above the anterior pleuropyloric ossicle (XXXI) on either side and articulate with the thickening ridge along the anterior margin of that ossicle. Mocquard named the most anterior of these ossicles the anterior mesopyloric ossicle (XIX). The more posterior was divided into lateral horns termed the posterior meso-pyloric ossicle (XX), and the remainder, the uropyloric ossicle (XXI). Mocquard considered the uropyloric ossicle reduced or absent in the palinurids. The exact homologies of the meso-pyloric ossicles in *Panulirus*, as in *Homarus*, are not clear, and their resolution will require a more complete comparative series than available here. In light of such uncertainties we shall follow the rule of priority and convenience, and identify the most anterior ossicle as the anterior mesopyloric ossicle (XIX) and the other complex, a combination of the posterior mesopyloric ossicle (XX) and the uropyloric ossicle (XXI). Although reduced, the uropyloric fold is present and its edges are well calcified. The infra-uropyloric fragment (XXIa) is also present.

(v) *Ventral pyloric ossicles and ampullae*

The preampullary ossicles (XXII) lie postero-laterally to the anterior inferior pyloric ossicle (XXIII). The latter ossicle forms a thick calcified medial plate which articulates anteriorly with the preanterior inferior pyloric ossicle (XVII). The inferior ampullary ossicle (XXIV) is unremarkable, but the ampullary roof ossicles (XXV and XXVI) are quite large and plate-like. Part of the posterior inferior pyloric ossicle (XXVII) appears to fuse with the posterior supra-ampullary ossicles (XXX) to form a continuous, heavy, calcified ventral arc. There is also a separate, more lightly calcified ossicle which extends from the inferior ampullary ossicle (XXIV) posteriorly to lie like a tongue just dorsal to the ventral arc. It is associated with the valvular structures at the opening from the pylorus into the midgut and may also be a portion of the posterior inferior pyloric ossicle (XXVII).

(vi) *Supra-ampullary ossicles*

The anterior supra-ampullary ossicle (XXVIII) is an irregular plate that articulates anteriorly with the inferior lateral cardiac ossicle (XIII) and dorsally borders on both the anterior (XXXI) and middle (XXXII) pleuropyloric ossicles. The middle supra-ampullary ossicle (XXIX) is reduced in size, and is most evident as a lateral calcified projection which is the site of lateral pyloric muscle attachments. The posterior supra-ampullary ossicles (XXX) are heavily calcified and are more ventrally situated in the posterior pylorus than in the *Callinectes* or *Homarus*. As described in a previous section they fuse across the ventral midline with the posterior inferior pyloric ossicle (XXVII).

(vii) *Pleuropyloric ossicles*

The anterior pleuroplyoric ossicle (XXXI) is a calcified plate with an anterior fold running from the posterior mesopyloric ossicle (XX) to the articulation of the anterior supra-ampullary ossicle (XXVIII) and the inferior lateral cardiac ossicle (XIII). The middle pleuropyloric ossicle (XXXII) runs as a heavily calcified ridge along the lower pylorus just above the upper ampullary roof ossicle (XXVI) and the anterior supra-ampullary ossicle (XXVIII). Posteriorly the ossicle expands and flattens, and continues upward in a projection that extends along the posterior pyloric margin to the uropyloric fold. Mocquard felt that the posterior pleuropyloric ossicle (XXXIII) was absent in palinurids, and certainly we did not find the ear-like projection present in the crab and *Homarus*. There is, however, a calcified region at the end of the dorsal middle pleuropyloric ossicle projection that is probably homologous with similar structures in the crab and *Homarus* and can be termed the posterior pleuropyloric ossicle (XXXIII).

Stomach muscles

Figures 5–7 are anterior, lateral and dorsal views of the stomach muscles of *Callinectes*. Figure 8 is a lateral view of the stomach muscles of *Homarus* and figures 9–11 present anterior, lateral and dorsal views of the muscles of *Panulirus*. As with the stomach ossicles the stomach muscles are typically paired with similar elements occurring on each side of the gut. For simplicity, however, the descriptions here usually refer only to the muscles on one side.

Classification of the stomach muscles

The stomach muscles are typically composed of parallel striated fibres running between origin and insertion on skeletal elements. The muscles spreading over the surface of the flexible chitin of the cardiac stomach depart somewhat from the type in that they may include branched elements which form a loose plexus or network of fibres. Earlier authors usually divided the stomach muscles into two groups: extrinsic muscles originating on the inner side of the thoracic skeleton and inserting on stomach ossicles or cuticle, and intrinsic muscles having both attachments on the stomach wall itself (Mocquard 1883; Cochran 1935; Balss 1944). We have found it useful to retain this distinction because the extrinsic muscles support the stomach in the thoracic cavity and act as dilators, but we have also considered individual stomach muscles as members of more functional groups. Such categories must be considered tentative until further information about the physiology of the stomach is available, but the following provisional classification seems to be useful:

1. muscles of the cardiac stomach c.
2. muscles of the gastric mill complex g.m.
3. muscles of the ventral cardiac ossicles c.v.
4. muscles of the cardio-pyloric valve cp.v.
5. muscles of the pylorus p.

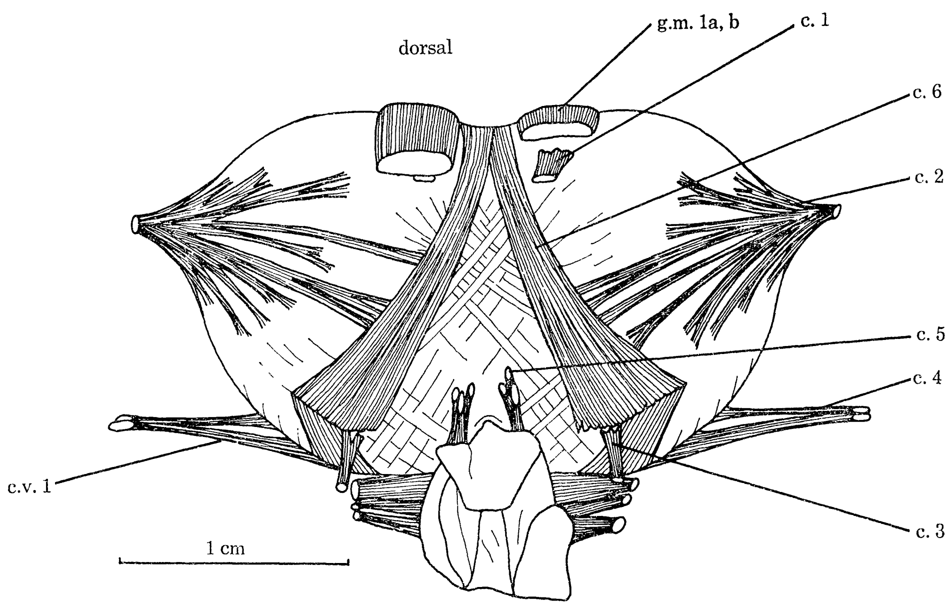

Figure 5. An anterior view of the stomach muscles of *Callinectes sapidus*. Dorsal is uppermost in the illustration. Full explanations of the muscle nomenclature are given in the text.

Individual muscles will be identified by a class code, e.g. c. for a cardiac stomach muscle; p. for a pyloric muscle, and numbers. Where function or anatomy are sufficiently similar to suggest a single structural unit, but separate bundles of fibres can be consistently recognized, the bundles will be identified by an individual letter. For example, g.m.1a represents the 'a' bundle of the first muscle of the gastric mill complex. There is an arbitrary component in this system of identification, because it depends upon the assignment of muscle bundles to an appropriate functional-structural class. This cannot always be certain because critical information about muscle function or innervation is occasionally lacking. It nevertheless is more useful than simple numbering or naming (see, for example, Cochran 1935) because of the large number of elements involved and the variations found between species. Where appropriate, previously published names for specific muscles will be used.

The muscles of the oesophagus are not properly stomach muscles, and we have not examined them in detail. For completeness, we recognize, as did Cochran, anterior, lateral and posterior oesophageal dilators and a number of circular oesophageal sphincters. Finer and more precise discrimination is possible and may become necessary as function and innervation become better understood.

Stomach muscles of Callinectes (*figures* 5–7, *table* 1)

Although Mocquard (1883) and Albert (1883) described stomach musculature in crabs, their accounts are not complete. Cochran (1935) provided the most adequate description of brachyuran cardiac musculature available, but still omitted a number of muscles (see table 1, pp. 212–13) and made several mistakes with respect to origins and insertions.

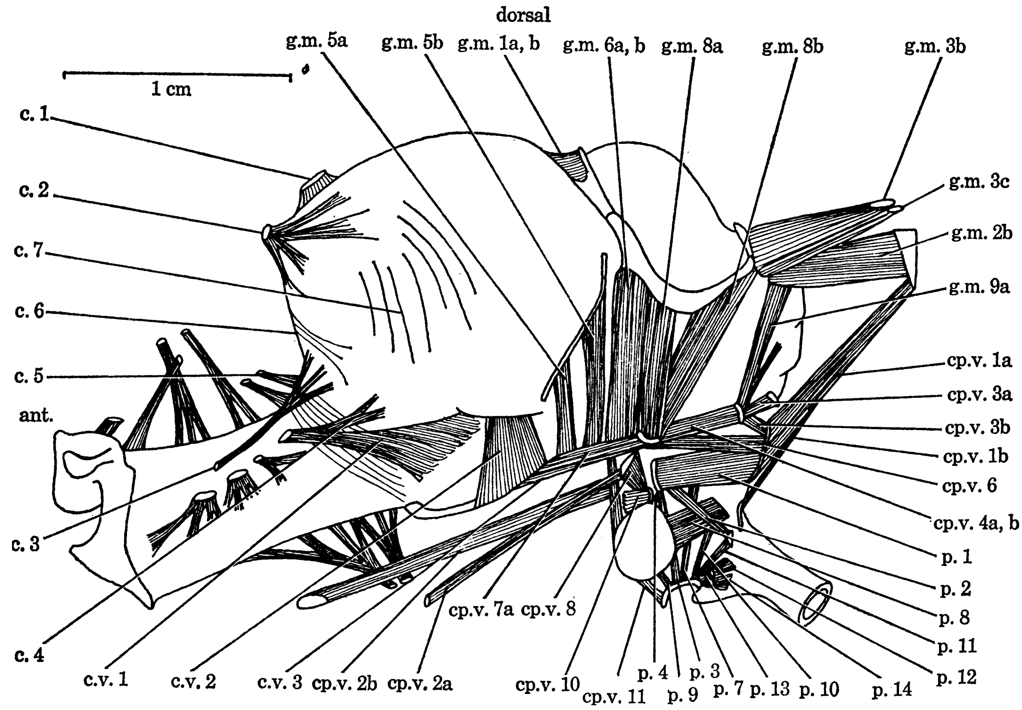

FIGURE 6. A lateral view of the stomach muscles of *Callinectes sapidus*. Anterior is to the left, and dorsal is uppermost.

(i) *Cardiac stomach*

The cuticular lining of the cardiac stomach is thin, flexible, and generally non-calcified. It forms a large bag opening off the oesophagus. Muscles attach both to the flexible cuticle and also to occasional calcified thickenings.

Extrinsic muscles. The extrinsic cardiac muscles run from the stomach wall to the anterior, antero-lateral and anterior ventral regions of the thoracic skeleton. They serve as dilators.

c. 1. These are a small pair of strap-like muscles lying just beneath the larger anterior gastric muscles g.m.1. Each originates with the respective g.m.1 on the 'cervical membrane' and inserts on the dorso-anterior portion of the non-calcified cardiac wall anterior to the mesocardiac ossicle (I). These muscles were not recognized by Cochran.

c. 2 (*anterior superior ventricle dilator* (*Cochran* 1935)). These muscles originate on the middle of the eye cup and, running medially and posteriorly, diverge to insert in a number of bundles on the anterior dorso-lateral margin of the cardium. They are very obvious, and are perhaps the most important of the cardiac dilators.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

c. 3. These muscles originate on the endoskeleton at the anterior-medial edge of the mandibular articulation, just anterior to origins of lateral oesophageal muscles. The muscles run, with only slight fanning of the bundles, dorsally and posteriorly to insert on the anterior ventral margin of the cardium lateral to the oesophagus on the medial edge of a slight thickening of the cardiac cuticle. These muscles were not recognized by Cochran.

c. 4 (*lateral anterior ventricle dilator*). These muscles originate with c.v.1 on the anterior-lateral wall of the prebranchial chamber and insert on the ventro-lateral cardium as it expands laterally above the oesophagus.

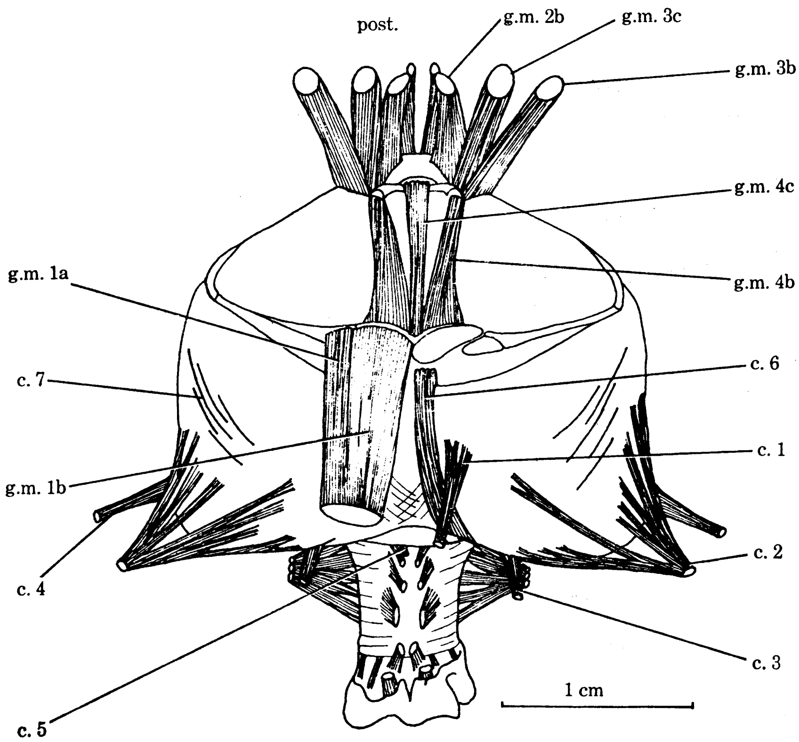

FIGURE 7. A dorsal view of the stomach muscles of *Callinectes sapidus*. Posterior is uppermost.

c. 5 (*anterior inferior ventricle dilator*). According to Cochran these muscles originate with the anterior oesophageal dilators on the epistome and insert medially on the anterior cardiac wall just above the oesophagus. We are uncertain whether they should be distinguished from the oesophageal dilators, but tentatively retain them in this group.

Intrinsic muscles. The intrinsic muscles of the cardiac stomach are represented by a layer of muscles running over the surface of the cardium and inserting on it. In some areas, parallel muscle bundles occur, but elsewhere the muscles intermesh in a plexus or are essentially absent. Cochran identified two muscle bands, the anterior mesial cardiac muscles (c.6, 213) and the anterior lateral cardiac muscles (c.7, 214). The former are much the larger, they originate on the mesocardiac ossicle (I) just anterior to insertions of the anterior gastric muscle (g.m.1), and running forward and downward over the surface of the stomach, form two bands which diverge laterally to insert on the cardiac wall near the insertion of c.3 on a cuticular thickening, the anterior lateral cardiac plate. We found less well-defined fibres, presumably belonging to the anterior lateral cardiac muscles (c.7) tending to run dorso-ventrally around the sides of the cardiac stomach and some to insert on the posterior lateral cardiac plate (XII). In addition to the above muscles, an extensive criss-crossing network of fibres pass over the anterior midline of the cardium.

(ii) *Gastric mill complex*

This group of muscles operates the ossicles of the gastric mill, and includes the largest of the gastric muscles. In addition to producing the primary grinding movements of the zygocardiac, propyloric, and urocardiac ossicles (muscles g.m.1–g.m.4), it also controls supporting ossicles which modify the angle of attack and ossicles which bear secondary teeth.

Extrinsic muscles. The extrinsic muscles are synergistic and pull the mesocardiac and pyloric ossicles apart. They are the most massive of the gastric muscles.

g.m.1a,b (*anterior gastric muscle*). This muscle originates in the dorsal midline on the 'cervical membrane', and passes backward. One bundle (a) inserts on the pterocardiac ossicle (II), while a second bundle (b) inserts more medially on the mesocardiac ossicle (I).

g.m.2b (*mesial posterior gastric muscle*). This muscle originates on paired apodemes projecting downward from the dorsal carapace just anterior to the cephalic groove. The dorsal pyloric dilators (see below) also originate on this apodeme below the gastric muscles. The gastric muscle runs forward to insert on the pyloric ossicle (III).

g.m.3b,c (*lateral posterior gastric muscle*). These muscles originate on the inner side of the dorsal carapace just anterior to the cephalic groove and lateral and anterior to the origin of the mesial posterior gastric muscle. On each side two muscle scars are visible from the outer carapace, one representing the lateral bundle (b) and one the medial bundle (c). The two bundles remain distinct as the muscle runs from its origins antero-ventrally and medially to insert, still as separate bundles, on the exopyloric ossicle (IV).

Intrinsic muscles. There are three sets of intrinsic muscles, one (g.m.4) is directly antagonistic to the gastric muscles, one (g.m.5–8) controls the angle and order of attack of the zygocardiac and accessory denticles, and one (g.m.9) may modify the movements of the pyloric and related ossicles.

g.m.4b,c (*cardio-pyloric muscle*). These muscles occur in two bundles. The paired lateral bundles (b) originate on the lateral region of the mesocardiac ossicle (I) and insert on the exopyloric ossicle (IV). The single median bundle (c) – which incidentally seems to be the only unpaired muscle in the stomach – originates in the middle of the posterior edge of the mesocardiac ossicle (I) and inserts on the propyloric ossicle (VI). These muscles draw the mesocardiac and pyloric ossicles together and thus directly antagonize the anterior and posterior gastric muscles. They are, however, quite small muscles.

g.m.5a,b (*lateral interior cardiac muscle*). These two flattened muscle bundles originate ventrally on the inferior lateral cardiac ossicle (XIII) and run dorsally to insert on the prepectineal ossicle (IX), one bundle (b) inserting above the other (a). Cochran figured only the longer, more posterior bundle. These muscles help control the denticle of the pectineal ossicle (VIII).

g.m.6a,b (*lateral interior cardiac muscle*). Most fibres of this flattened muscle belong to bundle g.m.6a which also originates on the inferior lateral cardiac ossicle (XIII) just posterior to muscle g.m.5b. A small fibre slip (g.m.6b) originates on the ventral portion of the subdentate ossicle (XIV). Both bundles insert along the anterior outer margin of the zygocardiac ossicle (V) and, together with g.m.8, control the zygocardiac denticles.

g.m.7. This small muscle does not occur in *Callinectes*.

g.m.8a,b (*lateral interior cardiac muscle*). This muscle, composed of at least two bundles, originates ventrally on the lateral ossicle of the cp.v. (XVIII) and inserts on the anterior (a) and posterior (b) portions of the zygocardiac ossicle (V). Cochran described this muscle (211*d*, *e*), but mistakenly considered it to originate from the anterior supra-ampullary ossicle (XXVIII).

g.m.9a (*lateral interior cardiac muscle*). This muscle originates on the anterior pleuropyloric ossicle (XXXI) and, according to Cochran, inserts on the pyloric and exopyloric ossicles behind the posterior gastric muscles. Our dissections generally showed the primary bundle inserting on the pyloric ossicle (III) with a small slip going to more posterior non-calcified cuticle anterior to ossicle XIX. We consider this muscle a member of the gastric mill complex because it is in a position to modify the movements of the pyloric ossicle during a gastric cycle, but it may also help control the anterior pyloric valves via its origin on the anterior pleuropyloric ossicle (XXXI).

(iii) *Ventral cardiac muscles*

These three muscles control the position of the inferior lateral cardiac ossicles (XIII), and thus the groove along the ventral cardiac stomach leading from the oesophagus to the cardio-pyloric valve.

Extrinsic muscle. c.v.1 (*lateral posterior ventricular dilator*). This muscle originates with c.4 on the anterior-lateral wall of the prebranchial chamber and, fanning out, runs medially and posteriorly to insert on the forward edge of the posterior lateral cardiac plate (XII).

Intrinsic muscles. c.v.2 (*lateral interior cardiac muscle*). This muscle originates on the upper edge of the posterior lateral cardiac plate (XII) posterior to c.v.1 and, spreading slightly, runs ventrally and medially in a thin sheet to insert along the forward portion of the inferior lateral cardiac ossicle (XIII).

c.v.3 (*posterior inferior cardiac muscle*). This muscle lies ventrally between the two inferior lateral cardiac ossicles (XIII). It originates as a thin sheet along the midline on the anterior projection of the posterior inferior cardiac ossicle (XVI) and the fibres then run laterally and anteriorly to insert on the lower inner margin of the inferior lateral cardiac ossicles (XIII).

(iv) *Cardio-pyloric valve*

The assignment of muscles to this group rather than the following is somewhat arbitrary. The major criterion used was whether a muscle's action had effect, whether direct or indirect, on the movement of the ossicles of the cardio-pyloric valve. Thus muscle cp.v.4 attaches directly to the cardio-pyloric auricular ossicle (XVIII) of the valve, while cp.v.3 is connected only indirectly through a junction common with cp.v.4 at the anterior pleuropyloric ossicle (XXXI). Tentatively, we assign both to this group, since cp.v.3 is in series with cp.v.4.

Extrinsic muscles. cp.v.1a,b (*anterior dorsal pyloric dilator*). These two muscle bundles originate together at the lower end of the apodeme projecting downward from the dorsal carapace just beneath the origin of the mesial posterior gastric muscle (g.m.2b). The anterior bundle (cp.v.1a), which is by far the largest, then travels downward and slightly anteriorly to insert on the posterior mesopyloric ossicle (XX), while the much thinner posterior bundle (cp.v.1b) inserts on the anterior portion of the uropyloric ossicle (XXI). Cochran mistakenly described the insertion of one of the bundles as the anterior pleuropyloric ossicle (XXXI), and thus confused anterior and posterior bundles in her numbering scheme.

cp.v.2a (*external inferior pyloric dilator*). This is a long, thin muscle with parallel fibres which originates just lateral to the posterior border of the oesophagus on the endopleurite of the first maxillary segment at the base of the major mandibular muscle, and inserts on a downward projection from the lateral ossicle of the cp.v. (XVIII), not the preampullary ossicle (XXII) as described by Cochran (see Mocquard).

cp.v.2b (*internal inferior pyloric dilator*). This muscle is very similar to the former except that it is longer. It originates beside the oesophagus on the mandibular apophysis just medial to the apodeme of the posterior mandibular adductor and, running backward and dorsally, inserts on the anterior inferior pyloric ossicle (XXIII).

The four pyloric dilator bundles are included in the cp.v. group although only one terminates directly on an ossicle of the cardio-pyloric valve, because all four receive the same innervation and function synergistically as antagonists to such muscles as cp.v.3 and cp.v.4 in addition to pyloric muscles.

Intrinsic muscles. cp.v.3a,b (*pyloric muscle* 216*l*, *k*). This muscle originates on the anterior pleuropyloric ossicle (XXXI) with g.m.9a, and travels dorsally in two diverging bundles, 3a to the anterior (XIX) and 3b to the posterior mesopyloric (XX) ossicle respectively. From anatomy alone, we cannot be sure of the precise function of these muscles but, since they are in line between cp.v.1 and cp.v.4, we assign them to the cardio-pyloric valve group.

cp.v.4a,b (*pyloric muscle* 216*a*). This muscle originates on the anterior pleuropyloric ossicle (XXXI), and runs antero-ventrally in two nearly parallel bundles (a few fibres of the anterior bundle may originate on the cuticle beneath the anterior pleuropyloric ossicle). The more dorsal anterior bundle (a) inserts on the lateral cardio-pyloric ossicle (XV), while the more posterior bundle (b) inserts on the lateral ossicle of the cp.v. (XVIII).

cp.v.5. This muscle is not present in *Callinectes*.

cp.v.6 (*pyloric muscle* 216*b*). This muscle originates on the posterior mesopyloric ossicle (XX), and runs antero-ventrally to insert on the lateral ossicle of cp.v. (XVIII).

cp.v.7a (*pyloric muscle* 216*n*). This muscle originates on the inferior lateral cardiac ossicle (XIII) on the ventral side of the stomach, and running posteriorly, inserts on the lateral ossicle of the cp.v. (XVIII).

cp.v.8 (*pyloric muscle* 216*i*). This short muscle was found only in *Callinectes*. It originates on the preampullary ossicle (XXII) and runs anteriorly to insert on the lateral ossicle of the cp.v. (XVIII).

cp.v.9. This muscle does not occur in *Callinectes*.

cp.v.10. This muscle originates on the inferior ampullary ossicle (XXIV) and inserts on the preampullary ossicle (XXII).

cp.v.11 (*pyloric muscle* 216*m*). This muscle originates on the posterior inferior pyloric ossicle (XXVII), and running as a thin band of fibres anteriorly and upward along the midline just under the ampullae, diverges to insert on either side of the anterior inferior pyloric ossicle (XXIII). This muscle is most clearly defined in *Callinectes*.

(v) *Pyloric muscles*

In our classification all the true pyloric muscles are intrinsic, originating and inserting on ossicles within the pylorus. In general they occur in two layers, an outer layer composed of muscles and bundles running primarily from the top to the bottom of the pylorus, and an inner layer (p.3, p.5, p.6, p.7) which also contains muscles running antero-posteriorly. The pyloric muscles are the most complex of the stomach muscles.

p.1 (*pyloric muscle* 216*c*). This muscle originates on the posterior mesopyloric ossicle (XX) and inserts on the middle supra-ampullary ossicle (XXIX). It is the most prominent of the pyloric muscles in *Callinectes*.

p.2 (*pyloric muscle* 216*d*). This muscle originates on the uropyloric ossicle (XXI) and runs forward as a small bundle of parallel fibres to insert on the middle supra-ampullary ossicle (XXIX) beneath muscle p.1.

p.3. This is a muscle of the inner layer, originating on the middle supra-ampullary ossicle (XXIX), and running backward to insert on the posterior supra-ampullary ossicle (XXX).

p.4 (*pyloric muscle* 216*j*). This is a short muscle, originating on the middle supra-ampullary ossicle (XXIX) and fanning downward and backward to insert on the inferior ampullary ossicle (XXIV).

p.5. This is a thin, inner muscle lying just above and medial to p.3. It apparently originates at the posterior edge of the anterior supra-ampullary ossicle (XXVIII) and proceeds backward to insert on the posterior margin of the middle pleuropyloric ossicle (XXXII), but it is less clearly differentiated than most other pyloric muscles.

p.6a. This inner muscle originates on an anterior projection of the middle pleuropyloric ossicle (XXXII), and fans backward and upward to insert beneath the uropyloric fold on the infra-uropyloric fragment (XXIa).

p.7 (*pyloric muscle* 216*f*). This muscle, with p.3, is one of the most prominent muscles of the inner layer. It originates on the anterior projection of the middle pleuropyloric ossicle (XXXII), and runs back as a bundle of parallel fibres, to insert on the posterior supra-ampullary ossicle (XXX).

p.8 (*pyloric muscle* 216*e*). This prominent muscle originates on the inferior ampullary ossicle (XXIV) at its lateral edge and runs upward to insert on the outer edge of the uropyloric fold.

p.9. This small muscle originates at the posterior edge of the inferior ampullary ossicle (XXIV) and runs backward to insert on the ventro-lateral margin of the posterior supra-ampullary ossicle (XXX).

p.10 (*pyloric muscle* 216*g*). This thin muscle originates on the inner side of the uropyloric fold behind p.6a and beneath p.8. It then runs downward and backward to insert on the posterior supra-ampullary ossicle (XXX).

p.11. This muscle originates on the outer edge of the uropyloric ossicle (XXI) just behind and beneath p.2, and then runs back and down to insert on the posterior supra-ampullary ossicle (XXX).

p.12. This short thin layer of muscle fibres originates along the posterior lateral margin of the uropyloric ossicle (XXI) and, running downward, inserts on a lateral ear-like projection of the posterior pleuropyloric ossicle (XXXIII).

p.13 (*pyloric muscle* 216*h*). This muscle originates as fibres spread along the projection of the posterior pleuropyloric ossicle (XXXIII) (termed the pyloric valve by Cochran) and then runs downward and forward to insert on the posterior supra-ampullary ossicle (XXX).

p.14. There are several thin muscle bundles which seem to bypass the posterior pleuropyloric projection, but rather run behind it from the uropyloric ossicle (XXI) to the posterior supra-ampullary ossicle (XXX).

Most of the 42 stomach muscles identified in the crab are common to the other two species examined, but figures 8–11 clearly show that there is considerable variation in form. Generally, the muscles in the crab do not form sheets or layers of fibres as often as in either the lobster or the spiny lobster. Rather the muscles occur as discrete, straplike bundles of parallel fibres.

Stomach muscles of Homarus (*figure* 8, *table* 1)

Mocquard (1883) and Williams (1907) provided the best descriptions of lobster stomach musculature. The work of Ringel (1924) on the crayfish is also relevant.

(i) *Cardiac stomach*

The lobster cardium does not spread as far laterally as that of the crab, and most of the extrinsic dilators tend to run anteriorly or antero-laterally. In addition there is a large oval of specialized epithelium on either side, the gastrolith field, where gastroliths form during the moult cycle.

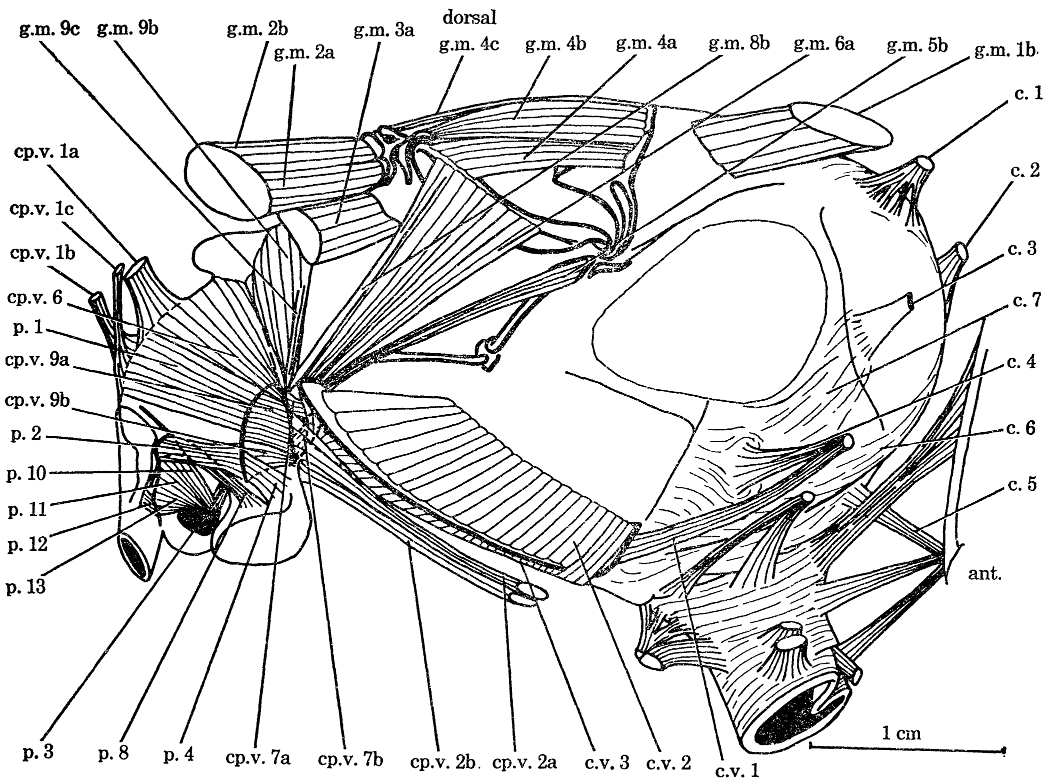

Figure 8. A lateral view of the stomach muscles of *Homarus americanus*. Anterior is to the right and dorsal is uppermost. Full explanations of the muscle nomenclature are in the text.

Extrinsic muscles. *c.1*. This muscle originates on the procephalic apophysis (Mocquard 1883) with the anterior gastric muscle (g.m.1) and passes backward spreading out below it to insert as a number of separate bundles on the anterior-dorsal wall. These muscles are relatively larger than their homologues in *Callinectes*, and are also larger than the next muscle pair, c.2.

c.2. These muscles originate at the ventro-lateral edge of the eye cup, and pass downwards and backwards to insert on the anterior wall of the cardiac stomach ventral to muscle c.1. In *Callinectes* the homologues are the dominant cardiac dilators and pull the stomach laterally, whereas here they are relatively small, terminating over a more limited area of the cardiac stomach and pulling the cardium forward and upward.

c.3. In the lobster this is apparently a strap-like ligament with very few if any contractile elements. It originates near the eye cup, just lateral to muscle c.2, and inserts on the anterior-lateral cardium just in front of the gastrolith field.

c.4. This muscle originates with the lateral posterior ventricle dilator (c.v.1) on the inner wall of the thorax slightly in front of the lateral adductor muscle of the mandible. It then passes medially to insert on the side of the cardium below the gastrolith field. It is somewhat larger than the homologous muscle in *Callinectes*.

c.5. This muscle originates in the midline on the epistome above the labrum. It passes backwards and upwards to insert on the anterior cardiac stomach just above the oesophageal junction on either side of the midline.

Intrinsic muscles. The muscular plexus of the cardium is less well developed than that of *Callinectes*; oriented muscle bands, particularly the anterior mesial cardiac muscles (c.6), are also smaller.

c.6. The fibres of c.6 originate near the insertions of the anterior gastric muscle (g.m.1) and then pass ventrally along the mid-anterior wall of the stomach. After passing below the insertions of muscles c.2 they spread to either side of the oesophagus along the ventro-lateral regions of the stomach where they terminate.

c.7. This band of fibres on either side is particularly obvious running from the insertion of muscle c.3 postero-ventrally to mingle with the terminating fibre bundles of c.6.

(ii) *Gastric mill complex*

The primary gastric mill muscles (muscles g.m.1–4) do not differ basically from those in *Callinectes*. The supporting muscles (g.m.5–9) on the other hand appear rather different. There are changes in orientation associated with differences in ossicle arrangement and there are fewer individual muscle bundles.

Extrinsic muscles. These are again the largest of the stomach muscles.

g.m.1b. This muscle originates on the procephalic apophysis behind the rostrum and passes back to insert on the anterior plate of the mesocardiac ossicle (I). Bundle g.m.1a is lacking.

g.m.2a,b. Bundle g.m.2b originates at the base of an apodeme situated on the inner side of the medial dorsal thoracic carapace close to the cervical groove as in *Callinectes*. The dorsal pyloric dilator (cp.v.1) also originates on this apodeme. The more lateral bundle, g.m.2a, originates laterally to the apodeme just anterior to the cephalic groove. Both bundles insert on the pyloric ossicle (III).

g.m.3a. This muscle originates lateral to g.m.2a on the inner side of the dorsal thoracic carapace between the bundles of the posterior adductor muscle of the mandible. There is only one muscle bundle, and this inserts on the zygocardiac ossicle (V), whereas g.m.3b,c in *Callinectes* insert on the exopyloric ossicle (IV).

Intrinsic muscles. *g.m.4a,b,c*. This muscle appears as a thin sheet of muscle fibres spanning the dorsal region between the anterior and posterior arches of the gastric mill. The tendency to form distinct bundles is less obvious than in *Callinectes*, but different origins and insertions permit discrimination of three bundles. Bundle g.m.4a originates on the pterocardiac ossicle (II) and inserts on the posterior dorsal arm of the zygocardiac ossicle (V). Bundle g.m.4b originates mostly on the mesocardiac ossicle (I) with a few lateral fibres originating on the pterocardiac ossicle (II) and inserts on the exopyloric ossicle (IV). Bundle g.m.4c, as in *Callinectes*, originates on the mesocardiac ossicle (I) and inserts on the propyloric ossicle (VI).

g.m.5b. This muscle is the smaller, more anterior and ventral of the two muscles on the side of the gastric mill in *Homarus*. It consists of a small bundle of fibres which originates on the posterior part of the inferior lateral cardiac ossicle (XIII) and runs antero-dorsally to insert on the dorsal part of the prepectineal ossicle (IX). This muscle is termed g.m.5b because g.m.5a in *Callinectes* inserts lower down on the prepectineal ossicle.

g.m.6a. This is the most prominent muscle of the lateral cardiac stomach. It originates as a narrow sheet of fibres at the posterior end of the inferior lateral cardiac ossicle (XIII) just behind g.m.5b. It then fans out, running antero-dorsally to insert along the dorsal lateral edge of the zygocardiac ossicle (V). The bundle of muscle fibres originating on the subdentate ossicle and termed g.m.6b in *Callinectes* does not occur in *Homarus*.

g.m.7. This muscle does not occur in *Homarus*. It is found only in *Panulirus*.

g.m.8b. This muscle, which is very prominent in *Callinectes*, is represented in *Homarus* only by a small group of fibres which lie at the posterior edge of g.m.6a. They originate on the lateral ossicle of the cardio-pyloric valve (XVIII) and insert on the posterior part of the zygocardiac ossicle (V). Bundle g.m.8a fibres inserting on the anterior part of ossicle V in *Callinectes* are not present here.

g.m.9a,b,c. In *Callinectes* g.m.9a is represented by a discrete muscle bundle; in *Homarus* the various bundles of g.m.9 form a sheet connecting the posterior arch of the gastric mill with the more ventral anterior pyloric and cardio-pyloric ossicles. Bundle g.m.9a consists of a small, thin sheet of muscle fibres which originate on the anterior pleuropyloric ossicle (XXXI) and insert mainly on the pyloric ossicle (III). They lie beneath g.m.9a and g.m.9c. A few muscle fibres which pass more posteriorly from the anterior pleuropyloric ossicle (XXXI) are considered remnants of cp.v.3b. Bundle g.m.9b forms the major bundle in *Homarus*, originating at the anterior end of the middle supra-ampullary ossicle (XXIX) and passing dorsally in a sheet of fibres to insert on the posterior margin of the pyloric ossicle (III). Bundle g.m.9c is represented by a small number of separate bundles of fibres which spread out over g.m.9b. They originate on the anterior edge of the lateral ossicle of the pyloric valve (XVIII) just behind fibres of g.m.8b and insert with g.m.9b on the pyloric ossicle (III).

(iii) *Ventral cardiac muscles*

Extrinsic muscle. c.v.1. This muscle is a narrow bundle of parallel fibres which originates with muscle c.4 on the lateral carapace. It does not fan out, as the homologous muscle does in *Callinectes*, and inserts on the quill of the postpectineal ossicle (Xa) at the anterior edge of the posterior lateral cardiac plate (XII).

Intrinsic muscles. c.v.2. This is the most prominent of the ventral cardiac muscles and differs from the homologous muscles in *Callinectes* and *Panulirus* in that it forms an extended sheet of fibres. It originates along the length of the upper edge of the posterior lateral cardiac plate (XII) and runs down to insert on the inferior lateral cardiac ossicle (XIII). A few of the most anterior muscle fibres may continue on past the ossicle (XIII) to meet similar fibres from the opposite side at the ventral midline and to insert there.

c.v.3. This muscle originates on the small posterior inferior cardiac ossicle (XVI) and also along the ventral midline anterior to the ossicle. It then fans out to insert along the inner edge of the inferior lateral cardiac ossicle (XIII).

(iv) *Cardio-pyloric valve*

Although the pyloric stomach is angled down from the cardiac stomach as it is in *Callinectes*, the bend in *Homarus* is longer and more posterior in position, and the lateral ossicle of the cardio-pyloric valve (XVIII) and the middle supra-ampullary ossicle (XXIX) are greatly expanded. In addition the posterior mesopyloric ossicle (XX) is elongated and the anterior mesopyloric ossicle (XIX) is missing. The muscles of this group consequently differ substantially from those of *Callinectes*. The absence of muscle cp.v.4 which in *Callinectes* connects the ventral ossicles XV and XVIII with ossicle XXXI, and the presence of cp.v.9 are particularly noticeable features.

Extrinsic muscles. cp.v.1a,b,c. The anterior dorsal pyloric dilator consists of three bundles. Two, cp.v.1a and cp.v.1b, originate together on the same apodeme as the mesial posterior gastric muscle (g.m.2), but more ventrally. Bundle cp.v.1c originates on a strand of muscle and elastic tissue connecting the posterior inner end of the apodeme with the pericardial septum. The larger anterior dilator bundle (cp.v.1a) inserts on the anterior portion of the posterior mesopyloric ossicle (XX). The smaller posterior bundles, cp.v.1b and c, insert more posteriorly on ossicle XX.

cp.v.2a,b. There are two inferior pyloric dilator bundles as in *Callinectes*. The bundles again consist of long parallel fibres, and in the mid-region of their course from the thoracic wall to the stomach come very close together to form essentially one muscle. At origin and insertion, however, they are separate. The larger external bundle, cp.v.2a, originates on the endophragmal skeleton at the back of the oesophagus and inserts on the lateral ossicle of the cardio-pyloric vale (XVIII). The internal dilator bundle (cp.v.2b) is longer. It originates on the mandible at its inner margin and inserts on the anterior inferior pyloric ossicle (XXIII).

Intrinsic muscles. cp.v.3b. This muscle consists of a few fibres which originate on the dorsal part of the anterior pleuropyloric ossicle (XXXI) and insert on the anterior region of the posterior mesopyloric ossicle (XX) beneath muscles cp.v.6 and p.1.

cp.v.4. This muscle is not found in *Homarus*.

cp.v.5. This muscle is not found in *Homarus*.

cp.v.6. As in *Callinectes*, this muscle originates on the antero-lateral edge of the posterior mesopyloric ossicle (XX) ventral to the insertion of the anterior pyloric dilator, cp.v.1a. It runs ventrally, parallel to and just above fibres of pyloric muscle p.1, to insert on the anterior part of the lateral ossicle of the cardio-pyloric valve (XVIII) just behind muscles g.m.8b and g.m.9c.

cp.v.7a,b. In *Homarus* this muscle is divided into two quite distinct bundles. Bundle cp.v.7a originates on the inner posterior edge of the inferior lateral cardiac ossicle (XIII) and runs backward and slightly upward to insert along the anterior lateral edge of the lateral ossicle of the cardio-pyloric valve (XVIII). Bundle cp.v.7b also originates on ossicle XIII, but more medially than muscle cp.v.7a. It inserts near the midline of the ossicle complex, perhaps closer to the ossicle XVII component than to ossicle XVIII.

cp.v.8. This muscle is lacking in *Homarus*.

cp.v.9a, b. The large space between the expanded lateral ossicle of the cardio-pyloric valve (XVIII) and the middle supra-ampullary ossicle (XXIX) which occurs in *Homarus* is spanned by this muscle sheet. The fibres of cp.v.9a originate along the anterior part of the lateral edge of ossicle XXIX and insert along most of the length of ossicle XVIII. The fibres of cp.v.9b originate just posterior and medial to those of cp.v.9a along the edge of the middle supra-ampullary ossicle (XXIX). They insert on the poorly calcified preampullary ossicle (XXII).

cp.v.10. This muscle is very small in *Homarus*, consisting of a thin sheet of muscle fibres which originate along the anterior medial region of the inferior ampullary ossicle (XXIV) and pass over the surface of the ossicle to insert on the ventral edge of the preampullary ossicle (XXII).

cp.v.11. Muscle fibres spanning the ampulla along the ventral midline are not found in *Homarus*.

(v) *Pyloric muscles*

The muscles of the pyloric region are generally sheet-like and not differentiated into such distinct bundles as found in *Callinectes*. There is a thin layer of muscle fibres covering the ampulla; these will not be described in detail.

p.1. This flat sheet of fibres forms the most prominent muscle of the pyloric stomach. It originates dorsally along the dorso-lateral edge of the posterior mesopyloric ossicle (XX) and passes antero-ventrally, narrowing to insert along the anterior half of the middle supra-ampullary ossicle (XXIX). The most anterior fibres of p.1 run parallel to and just beneath the thin layer of fibres of muscle cp.v.6.

p.2. This muscle consists of a distinct band of fibres running parallel with the most posterior portion of p.1. It originates on the antero-lateral edge of the uropyloric ossicle (XXI) and inserts on the posterior end of the middle supra-ampullary ossicle (XXIX).

p.3. In *Callinectes* this muscle is a discrete bundle of parallel fibres. In *Homarus* it takes the form of a fan-like sheet of muscle fibres embedded in connective tissue. The fibres originate along the posterior medial edge of the middle supra-ampullary ossicle (XXIX) and insert on the posterior supra-ampullary ossicle (XXX). This muscle is continuous with fibres of muscle p.7 which lie just dorsal to it (see below), resembling the situation in *Panulirus*.

p.4. This muscle, which is small in *Callinectes* and apparently lacking in *Panulirus*, is of reasonable size in *Homarus*. It originates on the posterior end of the middle supra-ampullary ossicle (XXIX) directly below muscle p.2 and passes downward to join the sheet of muscles which overlie the ventral and lateral ampullary region (ossicle XXIV).

p.5. This muscle is apparently lacking in *Homarus*.

p.6a,b. Bundle p.6a is a small flat sheet of fibres lying below muscle p.2 close to the pyloric wall. It originates on the middle pleuropyloric ossicle (XXXII) and fans upward to insert under the uropyloric fold in the region of the infra-uropyloric fragment (XXIa). It sometimes splits into an anterior and a posterior bundle. Bundle p.6b is a small slip which likewise originates on ossicle XXXII, but runs ventrally to insert on the inner edge of the middle supra-ampullary ossicle (XXIX).

p.7. In *Homarus* fibres of this muscle form the dorsal portion of the inner muscle sheet described under p.3. The p.7 fibres originate on the middle pleuropyloric ossicle (XXXII) and insert on the inner margin of the posterior supra-ampullary ossicle (XXX).

p.8. This muscle forms a distinct band of fibres which originate on the dorso-lateral part of the ampulla (the inferior ampullary ossicle, XXIV) and, passing dorsally beneath muscle p.2, insert on the uropyloric fold beneath the insertion of muscle p.2. Muscle p.8 in *Homarus* is not as large as in *Callinectes* or *Panulirus*, but it is a useful marker for the comparison of pyloric muscles in these three species.

p.9. This is a band of fibres which originate on the inferior ampullary ossicle (XXIV) at the tip of the ampulla and run to insert on the ventral part of the posterior supra-ampullary ossicle (XXX).

p.10. This muscle originates along the antero-lateral edge of the uropyloric ossicle (XXI) and passes downwards to insert on the posterior supra-ampullary ossicle (XXX). In some animals a small slip of muscle was also found running forward from the insertion of p.10 on the uropyloric ossicle to the lateral expanded region of the pyloric wall just anterior to the ossicle.

p.11. This muscle originates along the lateral edge of the uropyloric ossicle (XXI) just posterior to the insertion of p.10. Together with muscle p.10, it forms a single sheet of fibres which insert on the posterior supra-ampullary ossicle (XXX).

p.12. The posterior pleuropyloric ossicle (XXXIII) extends an ear-like projection just below the posterior end of the uropyloric ossicle. The thin sheet of fibres which comprise muscle p.12 originate on the surface of the gut and caecum which lie just above the uropyloric ossicle (XXI) and, passing ventrally, insert on the ear-like projection of ossicle XXXIII.

p.13. Just posterior to muscle p.11 and usually distinct from it, muscle p.13 originates on the ear-like projection of the posterior pleuropyloric ossicle (XXXIII) and passes ventrally to insert on the dorso-lateral edge of the posterior supra-ampullary ossicle (XXX).

p.14. No fibres homologous to p.14 of *Callinectes* have been observed in *Homarus*.

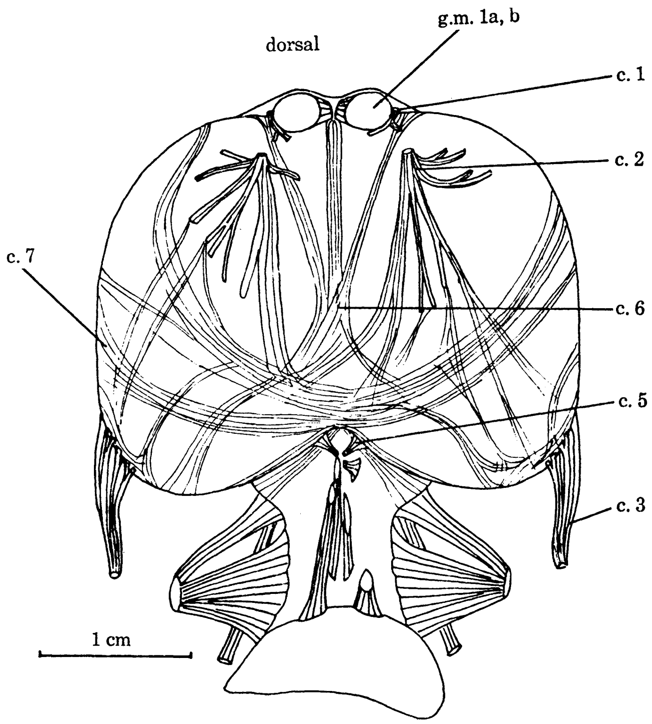

FIGURE 9. An anterior view of the stomach muscles of *Panulirus argus*. Dorsal is uppermost. Full explanations of the muscle nomenclature are in the text.

Stomach muscles of Panulirus (*figures* 9–11, *table* 1)

Mocquard (1883) described the major gastric muscles of a related genus, *Palinurus*. Paterson (1968) gave a short description of the stomach muscles of the rock lobster *Jasus*. Many of the muscles of *Panulirus* differ significantly from those of either *Callinectes* or *Homarus*.

(i) *Cardiac stomach*

Relative to the size of the pyloric stomach the cardium of the spiny lobster is intermediate between those of the crab and lobster. The ventro-lateral intrinsic musculature is well developed.

Extrinsic muscles. c.1. This muscle, which is smaller than that in *Homarus*, originates with muscle g.m.1 on the procephalic apophysis. It passes back to insert on the anterior dorsal wall of the cardium below g.m.1.

c.2. This muscle is slightly larger than muscle c.1. It originates on the ventral edge of the eye socket and inserts ventro-laterally to c.1 on the cardium. As in *Homarus* this muscle in *Panulirus* is much smaller than the homologue in *Callinectes*.

c.3. This muscle originates as a narrow bundle of fibres on the inner carapace slightly anterior and lateral to the mandible. The muscle fans out as it passes medially and slightly posteriorly to insert on the ventro-lateral region of the cardium. This is the largest of the cardiac muscles in *Panulirus*. Its identification as a c.3 rather than c.4 may be subject to reconsideration when further information about innervation is available.

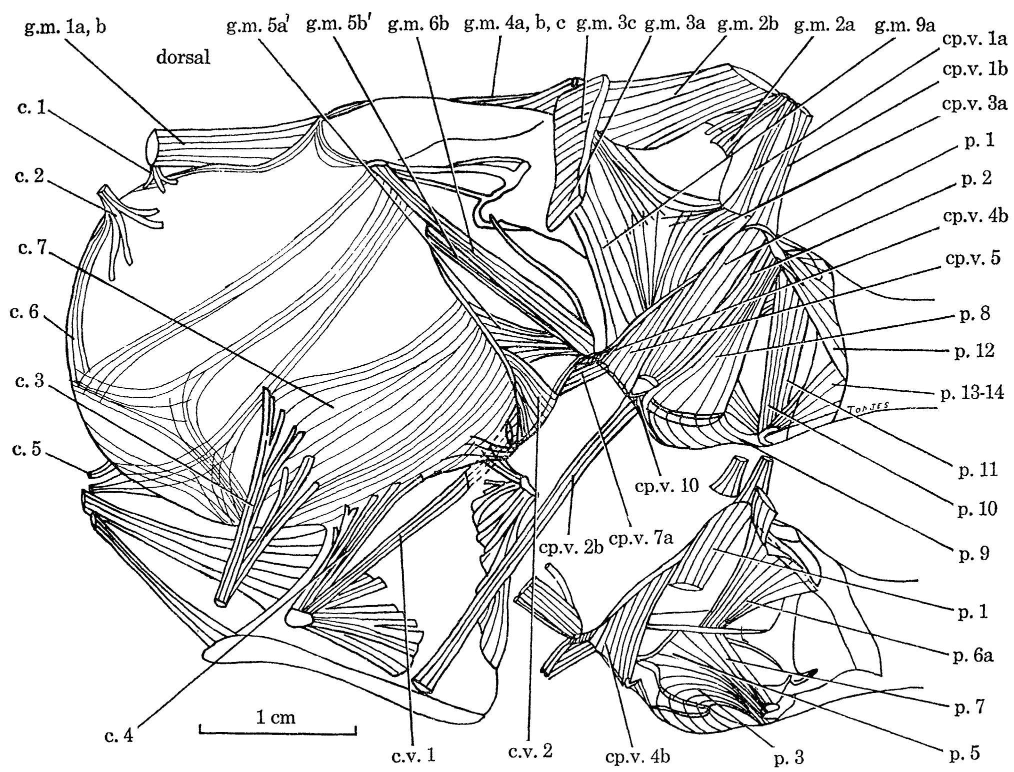

FIGURE 10. A lateral view of the stomach muscles of *Panulirus argus*. Anterior is to the left and dorsal is uppermost. The inset (lower right) shows the inner layer of pyloric muscles.

c.4. Muscle c.4 originates medial and ventral to muscle c.3 on the carapace close to the anterior edge of the mandible. It passes back along the same route as muscle c.3 and inserts ventral to that muscle on the cardium close to the oesophageal junction. Muscle c.v.1 originates just above muscle c.4.

c.5. This originates in the midline on the epistome and passes back to insert on the anterior region of the cardium very close to the junction with the oesophagus.

Intrinsic muscles. The cardiac sac in *Panulirus* is partially covered with a layer of muscle fibres as in *Callinectes*. The anterior mesial cardiac muscle (c.6) is not large in *Panulirus* but small groups of fibres do run forward and downwards over the cardium from the mesocardiac ossicle (I). The meshwork of fibres is particularly evident on the anterior midline of the cardium, and the lateral cardiac muscle (c.7) is well developed in the region between ossicle XII, where it inserts, and the insertion of muscle c.3.

(ii) *Gastric mill complex*

The primary muscles of the gastric mill (g.m.1–4) in *Panulirus* are basically similar to those in *Callinectes* and *Homarus*. The arrangement of the lateral gastric mill, however, is quite different in *Panulirus*. The whole region is relatively shorter, the posterior lateral cardiac plate (XII) largely replaces the prepectineal ossicle (IX) as the anterior border of the lateral gastric mill, and the subdentate ossicle (XIV) articulates with the cardio-pyloric valve in a different manner. As in *Homarus* the supporting muscles (g.m.5–9) are oriented diagonally rather than vertically, and as there are fewer separate bundles (muscle g.m.8 is entirely absent) the arrangement appears simpler than in *Callinectes*.

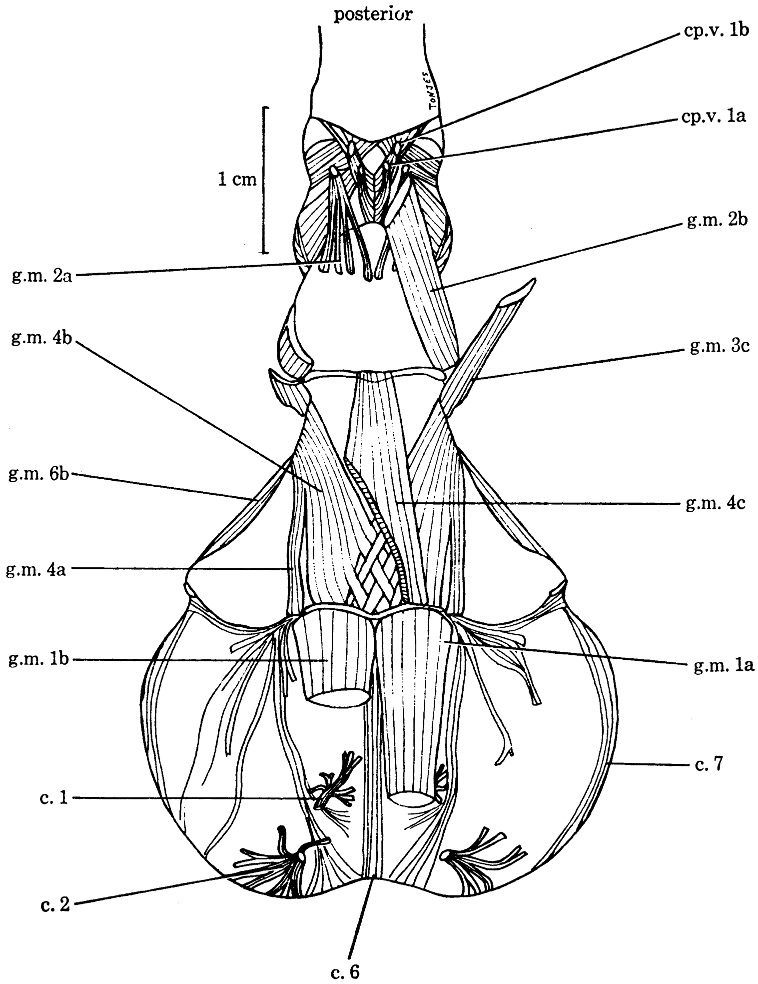

FIGURE 11. A dorsal view of the stomach muscles of *Panulirus argus*. Posterior is uppermost.

Extrinsic muscles. g.m.1a,b. This muscle originates on the procephalic apophysis and passes back to insert on the anterior arch of the gastric mill. Bundle g.m.1a inserts on the medial portion of the pterocardiac ossicle (II) and is relatively small. It is not obviously separate from bundle g.m.1b which inserts on the mesocardiac ossicle (I).

g.m.2a,b. The mesial posterior gastric muscle (g.m.2b) originates with the dorsal pyloric dilator (cp.v1) on the apodeme extending downward from the inner edge of the dorsal carapace just anterior to the cephalic groove as in *Callinectes* and *Homarus*. The fibres of this large bundle pass forward and downward from their origin to insert partially along the medial edge of the exopyloric ossicle (IV) but mostly on the lateral edge of the region of the pyloric ossicle (III). Muscle g.m.2a presumably is represented by a smaller group of separate fibres which likewise originate on the apodeme but which insert medially and posterior to g.m.2b on the pyloric ossicle (III). A bundle with this particular course has been identified only in *Panulirus*.

g.m.3a,c. The lateral posterior gastric muscle (g.m.3) originates on the inner side of the dorsal carapace lateral to muscle g.m.2 and between the origin of bundles of the posterior adductor muscle of the mandible. Muscle g.m.3, which is strap-like in cross section, then passes medially and anteriorly. A small medial bundle of fibres (g.m.3c) inserts on the exopyloric ossicle (IV) while the larger ventro-lateral bundle (g.m.3a) inserts on the posterior ventral region of the zygocardiac ossicle (V). As with muscle g.m.1, the two bundles are not separated as in *Callinectes* and are identified only by their separate insertions.

Intrinsic muscles. g.m.4a,b,c. These muscles, particularly g.m.4c, appear to be thicker and larger in *Panulirus* than in either *Homarus* or *Callinectes* but they still remain relatively thin sheets. Bundle g.m.4a originates mostly along the medial posterior edge of the pterocardiac ossicle (II) but a few fibres also originate at the lateral posterior margin of the mesocardiac ossicle (I). It inserts on the anterior dorsal angle of the posterior arch of the zygocardiac ossicle (V). This is the smallest of the three bundles of muscle g.m.4. Bundle g.m.4b originates along the posterior margin of the mesocardiac ossicle (I) largely under the origin of bundle g.m.4c. Fibres of bundle g.m.4b originate on both sides of the midline; accordingly near their origin there is some intermingling of fibres from the bundle g.m.4b on each side of the stomach. Bundle g.m.4b inserts on the anterior edge of the exopyloric ossicle (IV). Bundle g.m.4c originates along the mesocardiac ossicle above the origin of bundle g.m.4b. The fibres then come together to insert at the midline on the propyloric ossicle (VI).

g.m.5a′,b′. This muscle has attachments in *Panulirus* differing slightly from those found in *Callinectes* and *Homarus*, but it is clearly homologous. The prime (′) indicates the altered attachments. Bundle g.m.5a′ is flat and sheet-like. It originates on the base of the subdentate ossicle (XIV), not ossicle XIII as in *Callinectes* and *Homarus*, and inserts along the posterior edge of ossicle XII (posterior lateral cardiac plate) above muscle cv.2. Bundle g.m.5b′ is a separate bundle of parallel fibres which lie beneath muscle g.m.6b (see below). It originates on the base of the subdentate ossicle (XIV) and inserts on the reduced prepectineal ossicle (IX).

g.m.6b. In *Panulirus* bundle g.m.6a, which is the major lateral muscle of the gastric mill in both *Callinectes* and *Homarus*, is lacking and its place is taken by muscle g.m.6b. As in *Callinectes*, muscle g.m.6b originates on the base of the subdentate ossicle (XIV) and inserts on the anterior tip of the zygocardiac ossicle (V).

g.m.7. This small muscle occurs only in *Panulirus*. It originates on the dorsal part of the inferior lateral cardiac ossicle (XIII) and inserts on the lower part of the subdentate ossicle (XIV). The presence of this muscle no doubt is associated with the loose articulation of the subdentate ossicle with ossicle XIII and the cardio-pyloric valve.

g.m.8. This muscle, which is very prominent in *Callinectes*, is not found in *Panulirus*.

g.m.9a. This thin sheet of fibres is quite unlike the homologous muscle in either *Callinectes* or *Homarus*. At the posterior border it is continuous with fibres which are considered homologous with muscle cp.v.3a. Muscle g.m.9a originates along the length of the anterior edge of the anterior pleuropyloric ossicle (XXXI) and running forward and dorsally inserts along the ventral margin of the pyloric ossicle (III) and the posterior margin of the exopyloric ossicle (IV). Some fibres along the dorsal edge of the muscle sheet appear to originate on ossicle III and to insert on the anterior mesopyloric ossicle (XIX).

(iii) *Ventral cardiac muscles*

Extrinsic muscle. c.v.1. This muscle consists of a long bundle of fibres which originate just above muscle c.4 near the anterior edge of the mandible and insert at the base of the posterior lateral cardiac plate (XII).

Intrinsic muscles. c.v.2. This sheet-like muscle originates along the ventral portion of the posterior lateral cardiac plate (XII) ventral to and slightly overlapping the insertion of muscle g.m.5a′. It inserts along the ventral edge of the anterior half of the inferior lateral cardiac ossicle (XIII).

c.v.3. As in *Callinectes* and *Homarus* this muscle originates on the posterior inferior cardiac ossicle (XVI) and runs laterally in a sheet of fibres to insert on the inferior lateral cardiac ossicle (XIII).

(iv) *Cardio-pyloric valve*

The pyloric stomach is not bent downward as much as in *Callinectes* and *Homarus* and, as mentioned previously, the subdentate ossicle does not articulate closely with the ossicles forming the cardio-pyloric valve. The number of muscles is significantly reduced, and the form of those present differs markedly from those in *Callinectes* and *Homarus*.

Extrinsic muscles. cp.v.1a,b. As in *Callinectes* and *Homarus*, the two bundles of the anterior dorsal pyloric dilator muscle originate together with muscle g.m.2 on the same dorsal apodeme. The anterior bundle (cp.v.1a) inserts on the anterior mesopyloric ossicle (XIX) rather than the posterior mesopyloric ossicle (XX) as in the other two species. This insertion may provide some support for the argument that the first dorsal pyloric ossicle should be considered the posterior mesopyloric ossicle in *Panulirus*, but more information is required before a firm decision can be reached. Meanwhile we retain Mocquard's identification as indicated in the section on stomach ossicles. The more posterior bundle (cp.v.1b) is slightly larger and inserts on the lateral horns of the posterior mesopyloric ossicle (XX). This contrasts with *Callinectes* where the anterior bundle is the largest and the much smaller posterior bundle inserts on the uropyloric ossicle (XXI).

cp.v.2b. A major difference between the muscle systems of *Panulirus* and of the other two species examined here is the absence of the external inferior pyloric dilator (cp.v.2a) in the spiny lobster. In *Panulirus* the remaining bundle cp.v.2b originates at the inner edge of the mandible and passes backward as a very long bundle of parallel fibres to insert on the anterior inferior pyloric ossicle (XXIII).

Intrinsic muscles. cp.v.3a. As described above under muscle g.m.9a, the fibres of this muscle form the posterior portion of a sheet of muscle lying on the surface of the stomach between the insertions of the posterior gastric muscles and the pyloric region. The fibres involved originate on ossicle XXXI and insert on ossicle XIX.

cp.v.4b. Since the lateral cardio-pyloric ossicle (XV) is apparently reduced or absent in *Panulirus*, muscle bundle cp.v.4a is lacking. Bundle cp.v.4b originates along the ventral, posterior margin of the anterior edge of the anterior pleuropyloric ossicle (XXXI) and runs ventrally to insert on the lateral ossicle of the cardio-pyloric valve (XVIII). This bundle of fibres forms the anterior portion of a thick sheet of fibres running ventrally from ossicle XXXI. The posterior portion of the sheet is formed from muscle cp.v.5, see below.

cp.v.5. This muscle occurs only in *Panulirus*. It originates on the anterior pleuropyloric ossicle (XXXI) dorsal to the fibres of cp.v.4b, and inserts ventrally along the side of the anterior inferior pyloric ossicle (XXIII). Together with cp.v.4 it forms one functional group.

cp.v.6. This muscle does not occur in *Panulirus*.

cp.v.7a. This muscle originates on the inferior lateral cardiac ossicle (XIII) and runs to the lateral edge of the lateral ossicle of the cardio-pyloric valve (XVIII) as in *Callinectes*. It is of interest to compare the situation in *Panulirus*, where only two muscles (cp.v.4 and cp.v.7) attach to ossicle XVIII, with that in *Callinectes* and *Homarus* where six do so.

cp.v.8. This muscle is found only in *Callinectes*.

cp.v.9. This muscle is found only in *Homarus*.

cp.v.10. Fibres of this muscle originate in the muscle sheet covering the inferior ampullary ossicle (XXIV) and running forward insert on the preampullary ossicle (XXII).

cp.v.11. This muscle, composed of a clearly defined bundle of fibres spanning the ampulla, is found only in *Callinectes*.

(v) *Pyloric muscles*

The ossicles of the pylorus of *Panulirus* form a much stouter, simpler structure than in *Callinectes* and the muscles are less well differentiated into distinct bundles. Caeca are lacking and the connexion of the pylorus with the hind gut is somewhat different from that in both *Callinectes* and *Homarus*. As with *Homarus*, the complex sheet of fibres which covers the ampulla is not described in detail.

p.1. This muscle originates on the lateral horn of the posterior mesopyloric ossicle (XX) and passing ventrally, inserts on the middle supra-ampullary ossicle (XXIX).

p.2. This muscle lies just behind and parallel with muscle p.1. It originates posteriorly to muscle p.1 on the posterior mesopyloric-uropyloric complex (XX–XXI) and inserts on the middle supra-ampullary ossicle (XXIX). Muscle p.2 does not cross over muscle p.8 as it does in *Callinectes* and *Homarus*.

p.3. The inner layer of pyloric muscles is not clearly differentiated into bundles as in *Callinectes* and, to a lesser extent, in *Homarus*. The horizontal fibres forming muscle p.3 along the ventral half of the pylorus above the ampulla are embedded in connective tissue, not easily dissected, and apparently combine with fibres of muscles p.5 and p.7 to form a continuous fan-shaped muscle mass which inserts on the posterior supra-ampullary ossicle (XXX). Those fibres originating on the middle supra-ampullary ossicle (XXIX) and the lower ampullary roof ossicle (XXV) are considered to belong to muscle p.3.

p.4. This muscle is not found in *Panulirus*.

p.5. In *Panulirus* this muscle is represented by the few fibres of the muscle mass described above under muscle p.3 which appear to originate on the anterior supra-ampullary ossicle (XXVIII).

p.6a. Fibres of this muscle run medial to muscles p.2 and p.8 close to the pylorus wall. Again this inner muscle is not easily located because of the connective tissue which invests the region. The fibres originate on the dorsal border of the middle pleuropyloric ossicle (XXXII) and fan dorsally to insert beneath the uropyloric fold in the region of the infra-uropyloric fragment (XXIa).

p.7. The fibres of muscle p.7 originate on the lower edge of the dorsal border of the middle pleuropyloric ossicle (XXXII) and insert on the posterior supra-ampullary ossicle (XXX). They form the dorsal border of the muscle mass described under muscle p.3.

p.8. This is the most prominent of the pyloric muscles in *Panulirus*. It originates as a broad sheet of fibres along the lateral edge of the ampullary roof ossicle (XXV) and narrows as it passes dorsally to insert on the edge of the uropyloric fold just behind the insertion of muscle p.2. Sometimes a few of the most anterior fibres of the muscle appear to originate more ventrally than the edge of the ampulla, perhaps among the ampullary muscle layers.

p.9. This thin, sheet-like muscle originates on the inferior ampullary ossicle (XXIV) and inserts on the ventro-lateral margin of the posterior supra-ampullary ossicle (XXX).

p.10. This muscle lies posterior to muscle p.8. It originates on the lateral edge of the uropyloric fold and inserts on the posterior supra-ampullary ossicle (XXX).

p.11. Immediately posterior to muscle p.10 is a second smaller, but distinct bundle of vertical fibres which we consider to be homologous with muscle p.11 in *Callinectes* where it forms a separate bundle. It originates along the ventro-lateral edge of the uropyloric ossicle (XXI) and inserts on the posterior supra-ampullary ossicle (XXX).

p.12. The last two muscles of the pyloric stomach of *Panulirus* do not obviously fit the categories set up for *Callinectes*. Dorsally there is a sheet of muscle fibres which insert on the posterior lateral edge of the uropyloric ossicle (XXI) and fan posteriorly and ventrally to attach along the dorso-lateral edge of the intestinal tube. A similar muscle sheet fans posteriorly from the posterior supra-ampullary ossicle (XXX) to insert along the ventro-lateral margin of the intestine. It is possible that the dorsal muscle sheet is homologous with muscle p.12 in *Callinectes* which originates on the uropyloric ossicle (XXI) and inserts on the posterior pleuropyloric ossicle (XXXIII) while the ventral muscle sheet may be homologous with muscles p.13 and p.14. In *Callinectes* these latter originate on the posterior pleuropyloric ossicle (XXXIII) and the uropyloric ossicle (XXI) respectively and insert on ossicle XXX. If the above identifications are correct, then we may presume that the great variation in form is associated with the absence of intestinal caeca and the lateral ear-like projection of the posterior pleuropyloric ossicle in *Panulirus*, and with the rather different kind of connexion between the pyloric stomach and the intestinal tube.

p.13. See above discussion.

p.14. See above discussion.

The stomatogastric nervous system

Figure 12 is a lateral view of the foregut of *Panulirus* to show the stomatogastric nervous system. Figures 13–15 are anterior, lateral and dorsal views of the foregut of *Homarus* to show the nervous system, and figure 16 is a lateral view of the foregut of *Callinectes*. Although most of the stomatogastric nerves are paired there can be considerable variation in the detailed branching of the nerves on either side of the gut.

Classification of the stomatogastric nervous system

There are essentially four classes of nerves involved in the innervation of the muscles and wall of the oesophagus and stomach. One group contains motor fibres originating in the ganglia of the ventral nerve cord (commissural and sub-oesophageal ganglia and possibly the median oesophageal ganglion), which innervate the oesophageal muscles and perhaps some of the anterior cardiac muscles. A second group of nerves primarily contains sensory fibres originating from sensory cells on the stomach and oesophagus and passing to the ventral ganglia. The nature and distribution of sensory cells will not be considered here. It will be the subject of another communication (Dando & Maynard 1974).

A third, rather small group of nerves contains mostly neurosecretory fibres which ramify in the region of the oesophagus and lower stomach. The fourth group of nerves contains motor fibres which originate in the stomatogastric ganglion and pass outward to the stomach muscles. The nerves which carry interneuron axons linking the stomatogastric ganglion with the oesophageal ganglion and the rest of the central nervous system are also included in this group. In some places nerves may carry more than one kind of fibre in reasonable numbers or nerves from more than one group may anastomose to varying degrees. While all nerves, therefore, do not fall clearly into one of the four groups, and the classification must be considered rather loose, it nevertheless remains useful in emphasizing the divergent origins and functions of the nerve fibres ramifying over the decapod stomach. In this paper we are particularly concerned with the identification and description of nerves belonging to the fourth group, nerves carrying fibres which originate in neuron somata in the stomatogastric ganglion. Little attention will be given to the innervation of the oesophagus, the labrum, and the mouth area in general (Orlov 1926*a*, *b*; Laverack & Dando 1968; Dando & Laverack 1969; Moulins, Dando & Laverack 1970).

In previous sections on ossicles and muscles approximately equal attention has been given to each of the three species, starting with *Callinectes* in each case because the ossicles and muscles of the crab are the most highly differentiated. In this section, the order of presentation will be reversed: first *Panulirus argus*, then *Homarus americanus*, and finally *Callinectes sapidus*. We do this because our data on stomach innervation, both physiological and anatomical, are most complete for *Panulirus*, less so for *Homarus*, and least for *Callinectes*.

In describing ossicles and muscles we attempted to give homologous structures the same name in each of the three species. Accordingly muscles or muscle bundles having the same designation in *Callinectes*, *Homarus*, and *Panulirus* may be considered probable homologues. In naming the nerves, we depart from this procedure, and similar designations in the three species will not always imply homologous nerves. This is necessary because in so far as innervation is concerned, the basic homologous structure is the nerve fibre itself, not the channel or nerve it travels in, and there is direct evidence that homologous nerve fibres innervating homologous muscles may travel in quite different nerves in different species. The median ventricular nerve (m.v.n.) in *Homarus* and *Panulirus* serves as one example. In both species (see figures 12, 14 below) it branches from the dorsal ventricular nerve (d.v.n.) and travels laterally just anterior to the pterocardiac ossicle (sometimes it is double in *Panulirus*). In both species it usually contains only two nerve fibres and these originate in the stomatogastric ganglion. One of these fibres innervates the same muscle c.v.1 in the two species. The second fibre innervates quite different muscles: in *Panulirus*, muscle c.v.2; in *Homarus*, muscles g.m.5 and g.m.6. It is thus inappropriate to consider the entire medial ventricular nerve in *Panulirus* homologous with that in *Homarus* when only half of the contained fibres are similar.

Although it is dangerous to homologize among the secondary stomatogastric nerves, the major neural pattern of the fourth group is similar in each of the three species examined. The stomatogastric ganglion (st.g.) is located on the mid-dorsal, anterior region of the cardium within the lumen of the anterior aorta at the expansion known as the cor frontale (Maynard 1961). A single major nerve, the stomatogastric nerve (st.n.), runs anteriorly from the ganglion, leaving the dorsal aorta and passing ventrally along the front of the cardium to the oesophagus. There it unites with paired lateral nerves, the superior oesophageal nerves (s.o.n.) from the commissural ganglia (c.g.), and continues ventrally for a very short distance as a central trunk. A single median nerve originating in the brain, the inferior ventricular nerve (i.v.n.), joins this trunk just ventral to the junction with the superior oesophageal nerves, and the trunk, after continuing slightly further ventrally, eventually terminates by dividing into the paired inferior oesophageal nerves (i.o.n.) which pass to the commissural ganglia. Several cell bodies are located along the median trunk connecting the superior and inferior oesophageal nerves, the degree of consolidation and the location varying with the species. This region is accordingly considered the oesophageal ganglion (o.g.).

In none of the species were we able to find a dorsal nerve from the brain to the stomatogastric nerve as reported in crayfish by Lemoine (1868). This agrees with Mocquard's observations on a number of other species and leads to the conclusion that the primary, if not only, interneurons mediating interaction between the stomatogastric ganglion and the central nervous system travel along the stomatogastric nerve.

The major motor nerve leaving the stomatogastric ganglion is the unpaired dorsal ventricular nerve (d.v.n.). Originating at the posterior end of the ganglion, this nerve exits from the dorsal aorta through the ventral wall of the blood vessel and passes on backward to divide into the paired lateral ventricular nerves (l.v.n.) at some point between the anterior and posterior arches of the gastric mill. The lateral ventricular nerve on each side angles ventro-laterally and posteriorly to the insertion of the ventral border of the lateral posterior gastric muscles (muscle g.m.3). At about this point it anastomoses with the posterior stomach nerve (p.s.n.), and then continues back to branch, variously supplying posterior and lateral gastric mill muscles, muscles of the cardio-pyloric valve, and pyloric muscles.

Other nerves leaving the stomatogastric ganglion and branches from the stomatogastric nerve, the dorsal ventricular nerve, or the lateral ventricular nerves differ somewhat among the three species. The nature of branching from the oesophageal ganglion and the superior and inferior oesophageal nerves also varies.

Stomatogastric nervous system of Panulirus (*figure* 12, *table* 2)

(i) *Class* 1, *motor fibres to oesophageal muscles*

Fibres innervating oesophageal muscles appear to travel in small nerves originating in the commissural ganglia, or branching from the oesophageal and posterior oesophageal nerves. These nerves have not been examined in detail, and have not been named.

(ii) *Class* 2, *sensory fibres*

There are two major nerve systems belonging to this group, that of the postero-lateral nerve (pl.n.) and that of the posterior stomach nerve (p.s.n.). The postero-lateral nerve as described by Mocquard (1883) has been termed the posterior inferior ventricular nerve by Keim (1915), Orlov (1926*a*, *b*), and Balss (1944) and the posterior stomach nerve by Bullock & Horridge (1965). It is formed from the fusion of the dorsal posterior oesophageal nerve (d.-p.o.n.) and the ventral posterior oesophageal nerve (v.-p.o.n.) anterior to the insertion of muscle c.v.1 at the forward end of the lateral cardiac ossicle (XII). The dorsal posterior oesophageal nerve in turn arises from the superior oesophageal nerve shortly after it leaves the anterior portion of the commissural ganglion. The ventral posterior oesophageal nerve arises from the posterior portion of the commissural ganglion. In addition to giving off branches carrying sensory fibres from the stomach, oesophagus and mouth region, the d.-p.o.n. and v.-p.o.n. carry some motor axons to the oesophageal muscles, and a single motor axon to each of muscles c.3 and c.4. The origin of these motor axons (C.D.$_{1-2}$) innervating the stomach musculature is unknown.

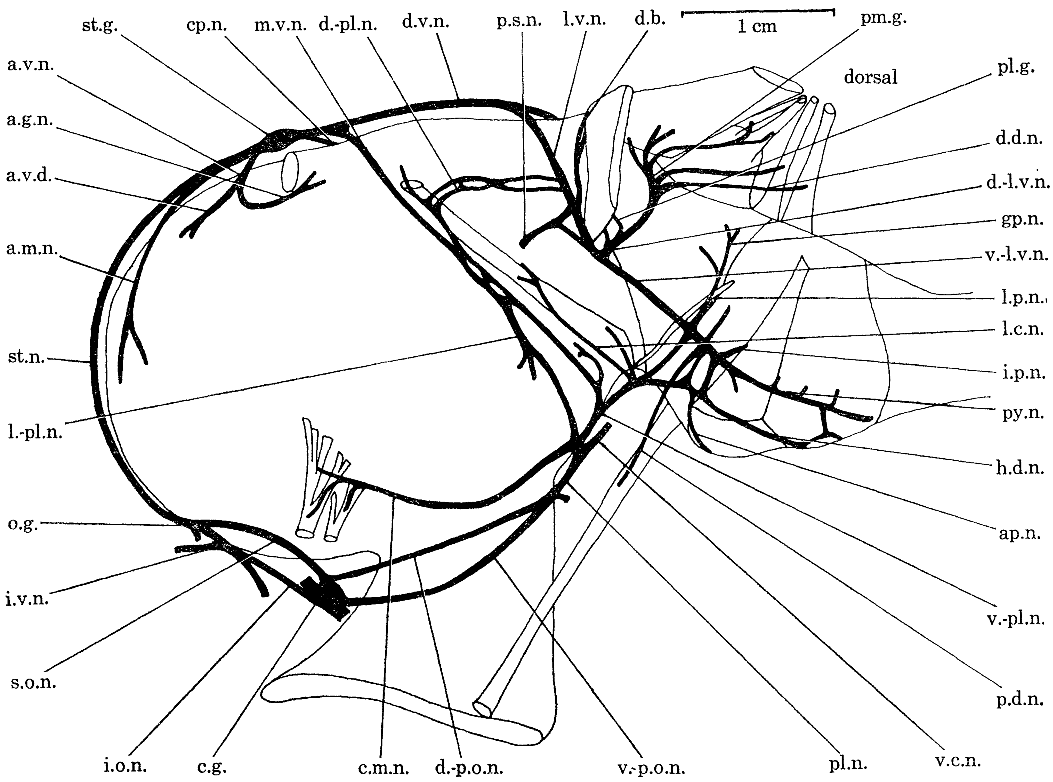

FIGURE 12. A lateral view of the foregut of *Panulirus argus* to show the stomatogastric nervous system. Anterior is to the left and dorsal is uppermost. Full details of the nomenclature of the nerves are in the text and nomenclature key.

After sending a branch or branches to the posterior oesophageal muscles, the postero-lateral nerve continues along the ventral side of the stomach to the insertion of muscle c.v.1. There it appears to split into several branches and to anastomose with the median ventricular nerve (m.v.n.), a motor nerve from the stomatogastric ganglion (class 4). The pattern of branching and anastomosis is somewhat variable. The most ventral branch, the ventral cardiac branch (v.c.n.), is usually small, often occurring as a bundle of small fibres. It leaves the pl.n. just anterior to the anastomosis, and passes medially and ventrally to the ventral surface of the cardiac stomach. It carries the axons of sensory cells located in the ventral cardiac gutter.

The middle branch, or small group of branches, the ventral branch of the posterior lateral nerve (v.-pl.n.), anastomoses with the portion of the m.v.n. which often passes beneath muscle c.v.2 and then, after m.v.n. turns dorsally, continues along the ventral cardium to anastomose briefly with the lateral cardiac nerve (l.c.n.) and sometimes other nerves of class 4 in the region of the cardio-pyloric valve. Some fibres from v.-pl.n. may eventually enter the ventral branch of the lateral ventricular nerve (v.-l.v.n.). The majority of fibres in the v.-pl.n. however, continue backward above the ampulla to form the hepatopancreas duct nerve (h.d.n.) which runs to the duct of the hepatopancreas. This nerve contains the axons of sensory cells located on the duct and initial segment of the hindgut, and rarely (if ever) motor axons from the ventral branch of the lateral ventricular nerve (v.-l.v.n.). The anatomy of the nerve near the duct is unclear, but some branches anastomose with the posterior region of the pyloric nerve (py.n) while others appear to extend onto the hindgut.

The third, most dorsal trunk (or group of trunks) of the pl.n. turns upward at muscle c.v.2 and runs dorsally as the lateral branch of the postero-lateral nerve (l.-pl.n.). It travels parallel to and usually slightly anterior to m.v.n.; often there are anastomoses between the two nerves. A number of small side branches leave the l.-pl.n., ramifying over the lateral cardiac muscles or running forward to the cardiac sac in the region of muscle c.7. Many of these branches contain sensory cells. At the region of the insertion of muscle g.m.6b, the l.-pl.n. often splits into a number of small irregular branches. Some of these run medially to the pterocardiac (II) and mesocardiac (I) ossicles and contain axons from sensory cells located in the region of the ossicles. Most of the branches turn posteriorly, however, recombining to form the dorsal branch of the postero-lateral nerve (d.-pl.n.) which eventually anastomoses with the lateral ventricular nerve (l.v.n.) and the posterior stomach nerve (p.s.n.) (Dando & Laverack 1969) near the insertion of the lateral gastric muscle (g.m.3).

The central portions of the posterior stomach nerve have been described for several European species (*Homarus vulgaris*, *Palinurus vulgaris*, and *Cancer pagurus*) by Dando & Laverack and need not be reconsidered here. In *Panulirus*, the segment of the p.s.n. ramifying over the stomach often divides into several branches just before it forms the complex anastomoses with the d.-pl.n. and the l.v.n. at the most ventral margin of the insertion of muscle g.m.3. Some of the fibres of the p.s.n. may enter the l.v.n., but many continue on past in small nerve branches which ramify along the posterior arch of the gastric mill. Characteristically there is a dorsal branch (d.b.) which travels medially along the anterior edge of the insertions of muscles g.m.2 and 3 and eventually joins with a similar branch from the opposite side. Smaller nerve twigs leave the d.b. and run posteriorly, particularly near the midline, among the muscles of the gastric mill and over the pyloric ossicle (III). Often such branches appear to carry motor axons from the cells of the stomatogastric ganglion (class 4) but the exact pattern seems to be rather variable and it is our impression that small processes from sensory elements predominate.

(iii) *Class* 3, *neurosecretory fibres*

In *Panulirus* we did not observe neurosecretory fibres as in *Homarus* and *Callinectes*. Methylene blue staining revealed a plexus of fine nerve fibres spreading over the sheath of the stomatogastric and superior oesophageal nerves near their point of junction. This configuration is similar to the pericardial organs in crabs and the situation in *Homarus* (see below) where such fibres contain dense granules characteristic of neurosecretory elements. Possibly the ramifications in *Panulirus* also contain such granules but we have not investigated the matter further.

(iv) *Class* 4, *stomatogastric ganglion system*

The stomatogastric ganglion is the chief motor centre for nerves to the stomach muscles. In *Panulirus* it appears as an oval swelling about 1 mm long in an animal weighing 1–1.5 kg. The ganglion lies in the dorsal aorta on the ventral wall between the anterior gastric muscles (g.m.1) and just behind the posterior basal ocular muscles (Baumann 1917), which pass through the lumen of the artery as a part of the cor frontale (Maynard 1961). The ganglion is usually bordered on either side by a pad of fatty tissue within the aortic lumen. The unpaired stomatogastric nerve (st.n.) which brings in the major presynaptic axons runs forward from the ganglion and immediately passes ventrally through the wall of the artery. The unpaired dorsal ventricular nerve (d.v.n.) which carries out postsynaptic axons, passes backward from the ganglion, remaining within the aorta for several millimetres before also passing out through the ventral wall. The d.v.n., however, then remains bound to the outside of the ventral wall of the artery for a further distance, often up to the origin of the two lateral ventricular nerves (l.v.n.). Other nerves originating in the ganglion will be considered below.

The cell bodies of non-sensory neurons in the ganglion are located primarily on the dorsal half of the oval. A few, perhaps 3–6, occur scattered on the ventral side. Most, if not all (Orlov 1927), appear to be monopolar, sending initial processes toward the centre of the ganglion where they ramify to form a central neuropile region before passing out as axons to the stomach muscles. All motor neurons innervate muscles on both sides of the stomach, and accordingly all axons eventually divide into at least two major branches. Sometimes such branching occurs within the ganglion, and where anterior and posterior muscles are also innervated by the same neuron, as many as three axons from a single cell (GM neurons, for example) may leave the ganglion (see, for example, Orlov 1927; Maynard 1972). Sensory neuron somata are known to occur in the stomatogastric ganglion in *Homarus* (Allen 1894) and crayfish (Orlov 1926*a*, *b*; Larimer & Kennedy 1966). Similar cells have been observed just posterior to the ganglion cell mass, near the origin of the cardio-pyloric nerve in *Panulirus*. It seems probable that such cells may occasionally lie more forward among the rest of the neuron somata. Such variability in the location of two sensory cell bodies could account for the observation that in somata counts made from serial sections from 13 *Panulirus*, two ganglia had 30 cells, seven had 29, and four had 28.

In animals weighing 1–1.5 kg, cell bodies in a typical fixed (Bouin) and sectioned ganglion ranged in length from 40 to 100 μm. Most lay in the 70–100 μm range, but five were above 100 μm, and three were below 50 μm. The location of cell bodies on the surface of the ganglion is variable and although a given type of neuron may be expected to occur in a specific quadrant, precise localization such as that found in the cardiac ganglion or the abdominal ganglion (Otsuka, Kravitz & Potter 1966) has not been observed.

Most of the neurons of the ganglion have been identified according to the muscle or muscles they innervate. Identity has been established through a combination of physiological and anatomical techniques which include simultaneous electrical recording from various points on a given neuron and its axon, methylene blue staining, and selected stimulus-recording experiments. In some instances, as with the gastric mill (GM) and lateral gastric (LG), elements can be assigned to a defined group, but differentiation of separate neurons within that group has not been established.

Table 2 (p. 216) lists motor neurons whose cell bodies lie in the stomatogastric ganglion. The first and second columns give the name and initial proposed for each element according to the muscle it innervates. The third column gives the locus of the cell body and the fourth column gives the nerve (or nerves) by which the axon leaves the stomatogastric ganglion. The fifth and sixth columns give respectively the muscles definitely and probably innervated. The number of identified motor neurons with somata in the ganglion is 23. Together with two presumed sensory cells and one non-sensory non-motor neuron, identified (as yet) only by its electrophysiological response, this leaves a maximum of four unidentified elements in the ganglion. Perhaps they include one or more of the three additional neurons indicated in the table. Although the latter innervate muscles of the anterior and ventral cardiac stomach, the location of their somata is unknown.

Once it leaves the aorta the stomatogastric nerve (st.n.) runs antero-ventrally from the stomatogastric ganglion along the front of the cardiac stomach, with almost no branches until it joins with the superior oesophageal nerves (s.o.n.). Just before this junction there are sometimes small branches to the anterior oesophageal muscles. After the junction the central trunk continues ventrally to be shortly joined by the inferior ventricular nerve (i.v.n.). The latter angles upward again to pass between the anterior basal ocular muscles near their ventral insertion and then enters the tritocerebrum of the brain. It appears to contain 8 nerve fibres (Dando & Selverston 1972). In many preparations a few small branches leave the central trunk as it continues ventrally to terminate in the paired inferior oesophageal nerves (i.o.n.). The detailed branching pattern of the superior and inferior oesophageal nerves was not documented. In *Panulirus*, neurons belonging to the oesophageal ganglion (o.g.) are scattered along the more ventral segment of the central trunk.

The stomatogastric nerve is mixed, containing both sensory axons travelling from the stomach toward the ventral ganglia of the c.n.s. and interneuron axons connecting the ganglion with the brain and other c.n.s. ganglia. It also contains a few non-sensory axons (at least two) which carry activity from the stomatogastric ganglion toward the c.n.s. and oesophageal and ventral cardiac muscles. The axon of the anterior median neuron (A.M.) does not run in the stomatogastric nerve in *Panulirus*.

One unpaired and one paired motor nerve leave the anterior half of the stomatogastric ganglion. The unpaired anterior median nerve (a.m.n.) usually arises from the ganglion ventrolaterally near the origin of the stomatogastric nerve. Sometimes it springs from the stomatogastric nerve slightly anterior to the ganglion. It then passes through the wall of the aorta and travels ventrally along the anterior cardiac stomach. It branches extensively among the intrinsic surface muscles of the cardiac stomach where it terminates. The anterior median nerve carries a single motor axon, that of the anterior median neuron (A.M.).

The paired anterior ventricular nerves (a.v.n.) leave the ganglion antero-laterally, one on each side. After passing through the arterial wall each divides into several branches. The exact pattern varies, but characteristically there is always at least one branch (sometimes two), the anterior ventricular dilator branch (a.v.d.), which travels forward to ramify among extrinsic cardiac muscles c.1 and c.2. The other branches travel more posteriorly and laterally as the anterior gastric nerve (a.g.n.) to terminate on the anterior gastric muscle (g.m.1). There is a medial and a lateral gastric branch (or branches). At least five axons (according to methylene blue staining) run in the a.v.n. as it leaves the artery; one of these (A.D. neuron) runs into the a.v.d. and innervates the cardiac muscles; the remaining four ($G.M._{1-4}$) run in the branches of a.g.n. innervating the anterior gastric muscle (g.m.1). These four G.M. neurons also innervate the major mesial posterior gastric muscle (g.m.2) as described below.

In *Panulirus* there are two primary unpaired and one primary paired motor nerves originating at the posterior half of the stomatogastric ganglion. In addition there are one or two smaller variable branches which carry sensory fibres from the anterior gastric arch, and perhaps the cardio-pyloric muscle (g.m.4).

The cardio-pyloric nerve (c.p.n.) is the smallest of the unpaired nerves. It arises ventrally near the origin of the dorsal ventricular nerve and the paired median ventricular nerves (see below). It passes through the ventral arterial wall and, running posteriorly, branches extensively over the cardio-pyloric muscle where it ends. This nerve carries only one motor axon, that of the cardio-pyloric neuron (CP.). Frequently other small nerves also leave the ganglion with the c.p.n. Where examined with methylene blue staining these always appear to contain sensory fibres, and sometimes bipolar sensory cell bodies can be detected near their origin (Orlov 1926*a*, *b*; Larimer & Kennedy 1966).

The paired median ventricular nerve (m.v.n.) arises on either side at the posterior end of the ganglion, and passes laterally through the arterial wall. Sometimes it originates as twin roots on each side that come together only after leaving the aorta. The nerve travels laterally over the dorsal stomach to the margin of the pterocardiac ossicle (II) near the upper insertion of muscle g.m.6b. It then turns ventrally, running beside and often anastomosing with the lateral branches of the postero-lateral nerve (l.-pl.n.). Upon reaching muscle c.v.2, if not before, the nerve splits into two branches, one ramifying over and terminating on muscle c.v.2, and the other turning forward to run beneath (usually) muscle c.v.2 to anastomose with the postero-lateral sensory nerve (pl.n.). The nerve then leaves the anastomosis to run along muscle c.v.1 and send small branches into it. About half-way along a large branch, the cardiac branch of the median ventricular nerve (c.m.n.) leaves and runs forward and laterally to terminate in muscle c.3. Two stomatogastric ganglion motor axons run in m.v.n.; the ventricular dilator (V.D.) which innervates muscle c.v.1 and the inferior cardiac (I.C.) which innervates muscle c.v.2. When the two axons leave the ganglion in separate roots, the more posterior root often carries the V.D. axon innervating muscle c.v.1. Additionally at the ventral anastomosis, the axon of the first cardiac dilator ($C.D._1$) turns from the pl.n. into the m.v.n. and continues on to muscle c.3 in the cardiac branch of m.v.n.

The unpaired dorsal ventricular nerve (d.v.n.) emerges from the posterior end of the stomatogastric ganglion, and after running through layers of connective tissue eventually leaves the ventral wall of the artery. Anterior to the posterior gastric arch, it splits into two major branches, the paired lateral ventricular nerves (l.v.n.) which angle postero-laterally to the most ventral point of insertion of the lateral posterior gastric muscle (g.m.3). There the l.v.n. anastomoses, as described, with d.-pl.n. and p.s.n. Just behind the muscle insertion, l.v.n. splits into two or more major branches. Typically there is a single dorsal branch of the lateral ventricular nerve (d.-l.v.n.) and a single ventral branch (v.-l.v.n.), but this is variable, and the dorsal branch may split immediately into smaller nerves.

In the preparation figured (figure 12) there is a single dorsal branch (d.-l.v.n.). Shortly after its origin several small branches, the postero-lateral gastric branches (pl.g.), leave to run along the posterior margin of muscle g.m.3. They carry branches of axons from the two lateral gastric neurons ($L.G._{1-2}$) which innervate g.m.3. The dorsal branch (d.-l.v.n.) then continues upward behind muscle g.m.3 until it splits into several branches. One branch typically goes anteriorly to the region between the lateral (g.m.3) and mesial (g.m.2) posterior gastric muscles. Another branch (or branches), the postero-median gastric branch (pm.g.), ramifies over the more dorsal, posterior side of muscle g.m.2b and also muscle g.m.2a. At this point, the pm.g. usually contains axon branches from the gastric mill neurons ($G.M._{1-4}$) which also innervate the anterior gastric muscle (g.m.1) (see above). Often there is a smaller nerve which travels posteriorly to end among the dorsal pyloric dilators (cp.v.1). This is the dorsal dilator nerve (d.d.n.), but it can also arise more posteriorly as a branch from the ventral branch of the lateral ventricular nerve (see below). The d.d.n. carries two axon branches from the pyloric dilator neurons ($P.D._{1-2}$), which also innervate the ventral pyloric dilators (cp.v.2) via a separate nerve (see below).

The ventral branch of the lateral ventricular nerve (v.-l.v.n.) passes backward over the surface of muscle g.m.9, giving off small branches to it, until it reaches the anterior margin of ossicle XXXI. The dorsal dilator branch (d.d.n.) sometimes emerges separately from v.-l.v.n. in this region. At ossicle XXXI, v.-l.v.n. gives off several major branches. One, the lateral cardiac branch of the ventral trunk (l.c.n.) runs downward along the edge of the ossicle toward the cardio-pyloric valve. It may anastomose with the ventral branch of the posterior lateral nerve (v.-pl.n.) in the region of the origin of muscle g.m.6b, but then turns antero-dorsally, dividing into several branches to run up along the forward edge of muscle g.m.6. These carry the axon branches of the lateral cardiac neuron (L.C.) that innervates muscles g.m.5 and g.m.6. It is probable that some branches from l.c.n. also run to muscle g.m.7. Certainly small branches run from l.c.n. near its origin to the underlying muscles cp.v.4 and cp.v.5. A second major branch (or branches) runs dorsally from the v.-l.v.n. This branch, the gastro-pyloric nerve (gp.n.), characteristically ramifies over the more dorsal surface of the gastro-pyloric muscle (g.m.9). The gp.n. carries the axon of the gastro-pyloric neuron (G.P.) which innervates the muscle sheet, g.m.9 and cp.v.3. Sometimes the d.d.n. emerges this far posteriorly, and combines with the initial section of gp.n. as it runs dorsally to muscle cp.v.1. In addition to these motor nerve branches, two large sensory cells having dendrites which spread over muscle g.m.9 are situated in the v.-l.v.n. near ossicle XXXI. Their axons apparently enter the v.-l.v.n., but have not been traced further.

As the v.-l.v.n. continues posteriorly over ossicle XXXI, it gives off several small twigs, lateral pyloric branches (l.p.n.), which run to the underlying muscles cp.v.4 and cp.v.5 and contain branches of the axon of the lateral pyloric neuron (L.P.). It also gives rise to two or sometimes three major, ventrally directed branches which tend to anastomose with one another and with the v.-p.l.n. before separating into an anterior pyloric dilator nerve (p.d.n.) which runs along and innervates the ventral pyloric dilator muscle (cp.v.2) and a more posterior ampullary nerve (ap.n.) which runs medially and posteriorly over the ventral surface of the ampulla. The p.d.n. contains the ventral axonal branches of the two P.D. neurons. The fibre content of the ap.n. has not been examined in detail, but it contains axonal branches from at least some PY. neurons. The hepatopancreas duct nerve (h.d.n.) originates at the anastomosis with v.-pl.n. and runs without obvious branching over the top of the ampulla to the duct of the hepatopancreas where it may again anastomose with branches of the pyloric motor nerves. Some of the axons in the h.d.n. originate in sensory cells located on the hepatopancreatic duct and the initial segment of the hindgut.

After giving rise to the above major branches, the v.-l.v.n. becomes the pyloric nerve (py.n.) and continues posteriorly across the surface of the pyloric muscles slightly above the ampulla. At this level the py.n. contains axons of eight pyloric neurons ($PY._{1-8}$) according to methylene blue-stained material. Just before it reaches the anterior border of muscle p.8, the py.n. gives off a major branch, the internal pyloric branch (i.p.n.) which dives beneath muscle p.8 and presumably innervates the interior layer of pyloric muscles (p.3, p.5, p.6, p.7, p.9). The i.p.n. contains four axons. Two of these are branches from axons of pyloric neurons which continue posteriorly in the py.n., and two are axons of pyloric neurons ($PY._{3,4}$) which do not send branches into the posterior py.n. After giving off the i.p.n., therefore, the py.n. contains six pyloric neuron axons. As it passes backward, the py.n. gives off small branches to the various pyloric muscles. As evident from table 2, these muscles characteristically have multiple innervation (Maynard & Atwood 1969). A small nerve branch often links the py.n. and h.d.n. near the termination of the stomach. Branches of the pyloric nerve running over p.10, p.11, and p.13 also appear to innervate p.12 and p.14, but it is not clear whether any fibres reach the midgut.

Stomatogastric nervous system of Homarus (*figures* 13, 14, 15)

Mocquard (1883) gave a reasonable description of the major nerves in *Homarus vulgaris*. Allen (1894) gave a detailed account of the commissural ganglia and oesophageal nerves of *Homarus vulgaris*, Maynard (1966) figured the major nerves arising from the stomatogastric ganglion of *Homarus americanus* and E. Maynard (1971) has described the fine structure of the stomatogastric ganglion in the same species. Unfortunately at this time we do not have the detailed physiological data on *Homarus* which was used to supplement anatomical observations in *Panulirus*. Thus we are limited to a grosser description, and can only indicate the major similarities and differences between the innervation in *Panulirus* and *Homarus*.

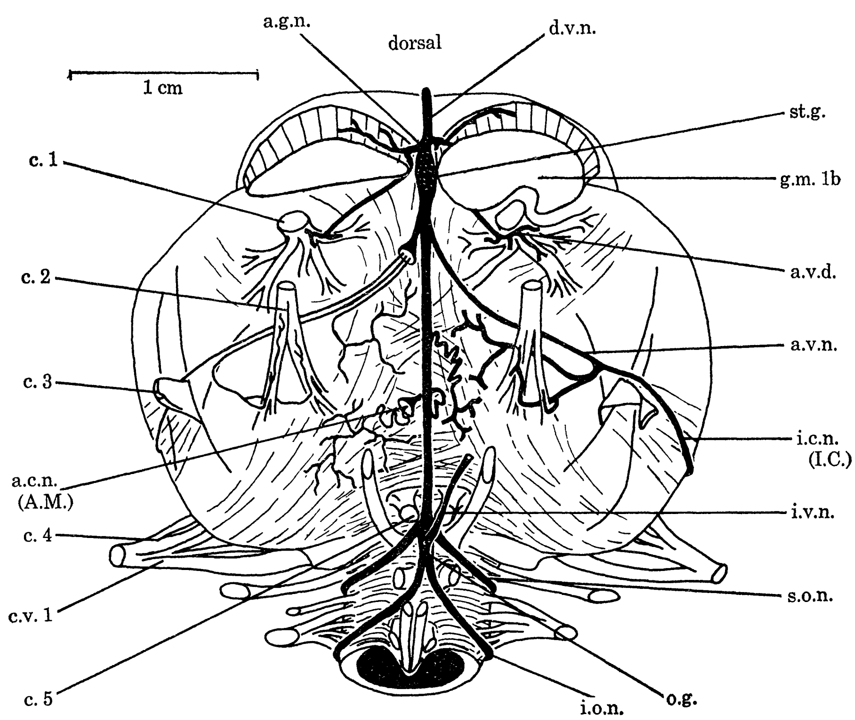

FIGURE 13. An anterior view of the foregut of *Homarus americanus* to show the stomatogastric nervous system. Note that some of the individual motor axons (A.M., I.C.) are illustrated here. Dorsal is uppermost. Full details of the nomenclature for the nerves are in the text and key.

(i) *Class* 1, *motor fibres to oesophageal muscles*

The oesophageal muscles appear to be innervated mainly by branches of nerves originating in the commissural ganglia. These have not been examined in detail.

(ii) *Class* 2, *sensory fibres*

The postero-lateral nerve (pl.n.) does not obviously originate, as in *Panulirus*, from a fusion of the dorsal posterior oesophageal branch (d.-p.o.n.) of the superior oesophageal nerve (s.o.n.)

and the ventral posterior oesophageal nerve (v.-p.o.n.). Rather, most of the fibres of the pl.n. come from the d.-p.o.n. alone. The v.-p.o.n. seems to contain mostly motor fibres to the oesophageal muscles and, although there are one or two points of anastomosis, exchange of fibres appears to be minimal. Just before the pl.n. anastomoses with the class 4 median ventricular nerve (m.v.n.) at the anterior border of ossicle Xa, it gives off a ventrally directed branch which should probably be considered the ventral cardiac branch (v.c.n.) that runs to the gutter along ossicle XIII. Some branches from the v.-p.o.n. may also extend into this region. After anastomosing with m.v.n., the fused pl.n.-m.v.n. continues posteriorly beneath muscle c.v.2.

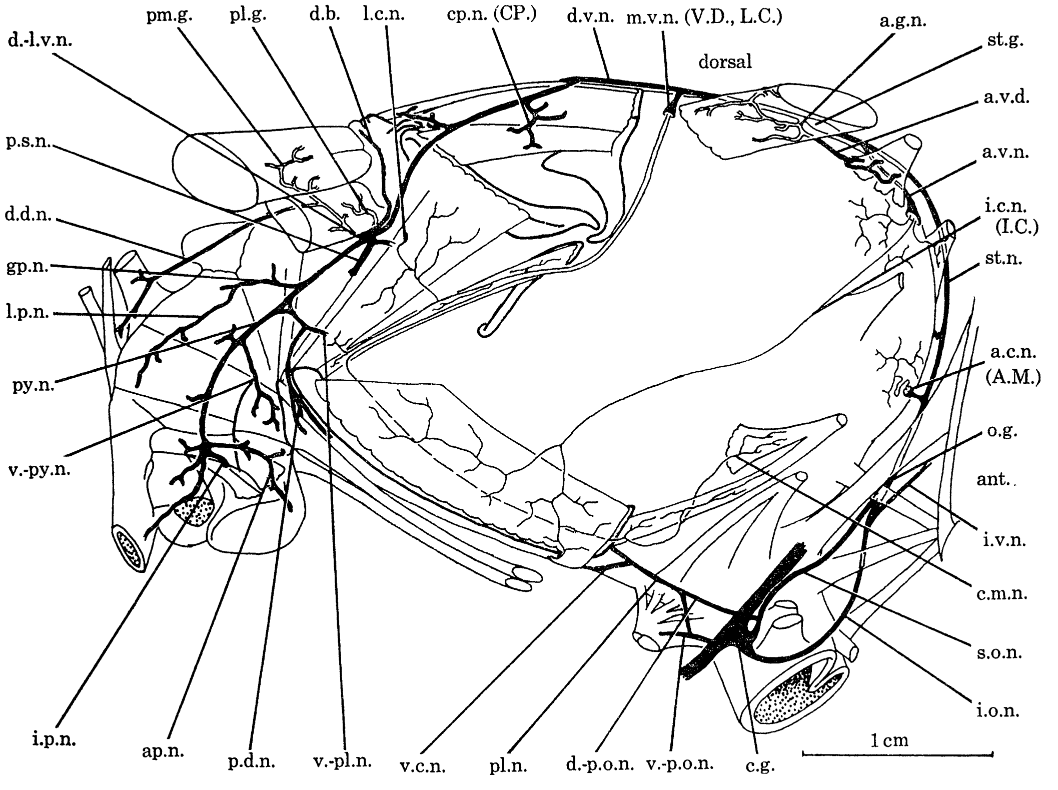

FIGURE 14. A lateral view of the foregut of *Homarus americanus* to show the stomatogastric nervous system. Anterior is to the right and dorsal is uppermost. Note that some of the individual motor axons (A.M., I.C., V.D., L.C.) are illustrated here and that some nerves (for example, a.g.n.) are shown in transparency.

At the posterior end of muscle c.v.2, the m.v.n. turns dorsally along muscle g.m.5 while a small ventral branch of the postero-lateral nerve (v.-pl.n.) continues posteriorly to eventually anastomose with the ventral branch of the lateral ventricular nerve (v.-l.v.n.), or sometimes with the pyloric dilator nerve (p.d.n.), in the pyloric region. A separate lateral branch of the pl.n. seems to be lacking in *Homarus*, and we presume that the anastomosis with the m.v.n. is complete and that in it fibres from the pl.n. run dorsally toward the region of the anterior and posterior gastric mill ossicles. An anastomosis, between the lateral cardiac nerve (l.c.n.) which runs over the lateral cardiac muscles (g.m.5, 6 and 8) and the m.v.n., could provide a pathway for postero-lateral sensory fibres to reach the posterior gastric arch as in *Panulirus*. More dorsally, nerve branches containing fine fibres extend forward from m.v.n. above the gastrolith field. In general, sensory fibres in *Homarus* appear more prone to run in the nerves containing motor axons from the stomatogastric ganglion than in *Panulirus*, and less likely to form separate, parallel nerves. The hepatopancreas duct nerve is apparently not clearly differentiated in *Homarus*. Presumably fibres homologous to those it carries in *Panulirus* run beside or within the pyloric nerve in *Homarus*.

The second major sensory nerve, the posterior stomach nerve (p.s.n.), is exactly like that described in *Homarus vulgaris* by Dando & Laverack. As in *Panulirus* it anastomoses with the lateral ventricular nerve (l.v.n.) at the insertion of the lateral posterior gastric muscle (g.m.3), and fibres from it pass into a number of other nerves in the region. A dorsal branch running upward in front of the posterior gastric muscles (g.m.2, 3) toward the midline is also present.

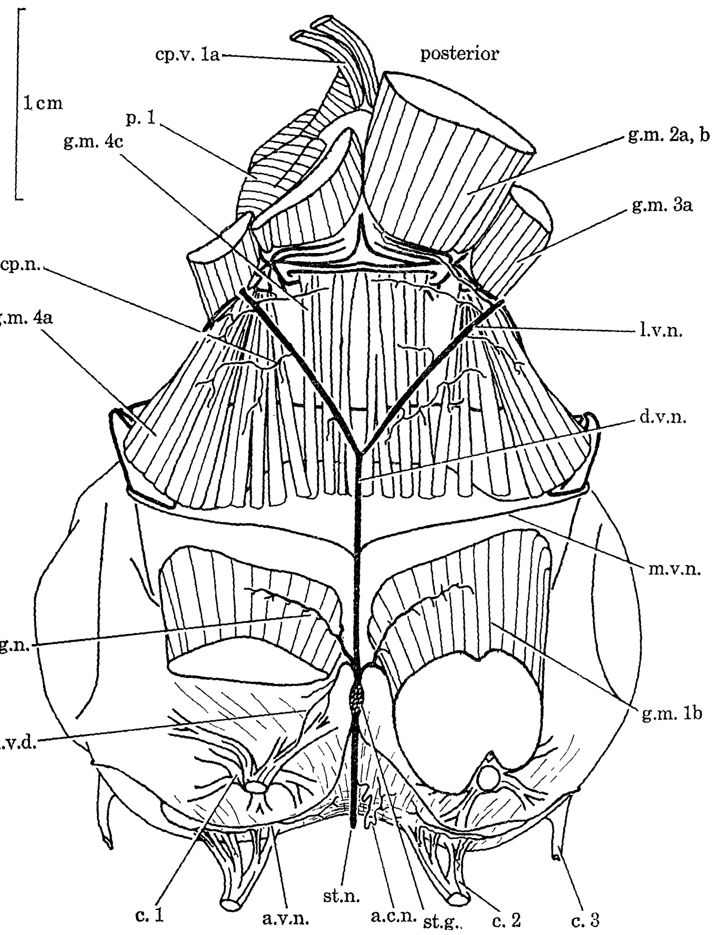

FIGURE 15. A dorsal view of the foregut of *Homarus americanus* to show the stomatogastric nervous system. Posterior is uppermost.

(iii) *Class* 3, *neurosecretory fibres*

The surface of the major nerves in the region of the oesophageal ganglion is covered with a dense, branching network of fine fibres. These closely resemble the configuration of branching neurosecretory terminals in the pericardial organs of Crustacea (Alexandrowicz 1953; Maynard 1961). As in the pericardial organs (Maynard & Maynard 1962) they contain accumulations of dense granules generally considered indicative of neurosecretory material. Orlov (1929) figures similar ramifications in *Astacus*. The neurosecretory ramifications clearly originate from fibres in the core of the nerves involved, and pass in numerous bundles to the surface to lie among the superficial layers of neural connective tissue. The principal nerves involved in *Homarus* include the ventral portion of the stomatogastric nerve just dorsal to its junction with the superior oesophageal nerves, the ventral portion of the inferior ventricular nerve, the superior and inferior oesophageal nerves together with many of their branches, and the central trunk containing the oesophageal ganglion. The location of the cell bodies of the neurons involved is unknown.

(iv) *Class* 4, *stomatogastric ganglion system*

In *Homarus* the stomatogastric ganglion is spindle-shaped, and more elongate than in *Panulirus*. It is about 1 mm long in a 500 g lobster. Just anterior to the ganglion the central core of axons in the stomatogastric nerve passes upward toward the surface of the thick connective tissue neural sheath as it enters the ganglion, and just posterior to the ganglion the emerging dorsal ventricular nerve axons dive back into a similar sheath. The ganglion, therefore, lies on a cushion of connective tissue that is contiguous with the thick inner perineural sheaths of the major afferent and efferent nerves, and in this differs from both *Panulirus* and *Callinectes*. *Homarus* also differs from *Panulirus* in that both the stomatogastric nerve and dorsal ventricular nerve tend to run for longer distances within the lumen of the anterior aorta. At intervals straps of connective tissue bind them to the ventral wall of the aorta.

With the exception of a bipolar sensory cell normally located at the posterior end of the ganglion (Allen 1894; Orlov 1926*a*, *b*; Larimer & Kennedy 1966), the neurons of the ganglion appear to be monopolar. They are located in a rind covering the dorsal half of the ganglion (E. Maynard 1971). None have been observed below the dorsal or dorso-lateral surface within the neuropile, or on the ventral side between the neuropile and the connective tissue cushion. Cell counts from two serially-sectioned ganglia gave 31 and 32 cell bodies in the ganglion plus one soma belonging to the bipolar sensory cell. In the second series, there was also a small neuron soma about 0.4 mm anterior to the ganglion, possibly a second sensory element.

In lobsters weighing about 500 g cell bodies ranged from 40 to 90 μm in maximum diameter, but most seemed to lie within the 50–60 μm range. Since sufficient physiological information is lacking, identification of ganglion neurons according to muscles innervated is not as complete in *Homarus* as in *Panulirus*. Elements which have been identified include the anterior median neuron (A.M.), the cardio-pyloric neuron (CP.), the lateral cardiac neuron (L.C.), the ventricular dilator neuron (V.D.), the inferior cardiac neuron (I.C.), and two pyloric dilator neurons (P.D.). Undoubtedly others will be recognized as physiological evidence accumulates.

Anterior to the ganglion, the stomatogastric nerve turns ventrally, passes through the wall of the artery, and runs down the midline of the anterior cardiac stomach. After leaving the aorta, and in contrast to *Panulirus*, it gives off several small unpaired nerves which branch among the intrinsic muscle layer of the cardium (muscles c.6 and c.7). These normally contain axon branches of a single neuron, the anterior median neuron (A.M.) and are termed the anterior cardiac branches (a.c.n.). Just above the oesophagus the stomatogastric nerve (st.n.) is joined by the paired superior oesophageal nerves (s.o.n.). The combined trunk continues ventrally, being joined first by the unpaired inferior ventricular nerve (i.v.n.) from the brain, and then terminating in a slight swelling containing an accumulation of nerve cell bodies, the oesophageal ganglion (o.g.) and a division into the paired inferior oesophageal nerves (i.o.n.) and other smaller, more median nerves which ramify among the oesophageal musculature and the area surrounding the mouth (Allen 1894; Laverack & Dando 1968).

Homarus differs from *Panulirus* in that the cells of the oesophageal ganglion tend to be more coalesced, forming a knot-like accumulation (Allen 1894), and branches of the axon of the anterior median neuron (A.M.) run almost the entire length of the stomatogastric nerve, some turning back and passing into the anterior cardiac nerves (a.c.n.) just dorsal to the junction with the s.o.n.

In *Homarus* there are two and sometimes three pairs of 'anterior' motor nerves. Of these only the first pair, the anterior ventricular nerves (a.v.n.) originate in front of the ganglion; the remainder emerge from the side or just behind the ganglion (Maynard 1966). The single unpaired anterior median nerve (a.m.n.) present in *Panulirus* is lacking in *Homarus*, and the axon it carries runs instead in the stomatogastric and anterior cardiac nerves (see above).

Each anterior ventricular nerve (a.v.n.) arises from the stomatogastric nerve shortly after it leaves the stomatogastric ganglion. After passing through the walls of the aorta, the nerve splits into three branches, each carrying a branch of a single motor axon. One nerve terminates among the fibres of the dilator muscle c.2; a second terminates dorso-laterally among the intrinsic cardiac muscles and its axon is presumably a branch of the anterior median neuron (A.M.); the third inferior cardiac branch (i.c.n.) continues laterally and ventrally around the cardiac stomach. It carries a single axon from the inferior cardiac neuron (I.C.) and terminates on muscle c.v.2. This contrasts with *Panulirus* where the I.C. axon runs in the median ventricular nerve (m.v.n.).

The paired anterior ventricular dilator nerve (a.v.d.) arises sometimes as a branch of the anterior gastric nerve (a.g.n.) and sometimes directly from the dorsal ventricular nerve (d.v.n.) just behind the stomatogastric ganglion (st.g.). It is a small nerve and innervates the cardiac dilator muscle, c.1.

The paired anterior gastric nerve (a.g.n.) arises from the dorsal ventricular nerve (d.v.n.) shortly after it leaves the ganglion, sometimes just behind the origin of the a.v.d. After passing through the aortic wall, the nerve divides into branches which innervate the anterior gastric muscle, g.m.1. In methylene blue preparations as many as nine axons can be identified in the basal region of the a.g.n. One or more of these certainly represents dendritic branches of the sensory neuron (or neurons) found in the stomatogastric ganglion (Allen 1894; Orlov 1926*a*, *b*; Larimer & Kennedy 1966). The remaining fibres are presumably motor, thus it seems more neurons innervate the anterior gastric muscles in *Homarus* than in *Panulirus*.

In *Homarus* only one primary posterior nerve, the unpaired dorsal ventricular nerve (d.v.n.), originates at the posterior end of the ganglion (excepting the a.g.n. and a.v.d.). The dorsal ventricular nerve (d.v.n.) passes backward in the aorta from the stomatogastric ganglion (st.g.). At the level of the insertion of the anterior gastric muscles, it gives off a pair of small lateral nerves, the median ventricular nerves (m.v.n.), which run laterally over the dorsal surface of the mesocardiac ossicle (I) toward the junction of the zygocardiac (V) and pterocardiac ossicles (II). The nerve then runs ventrally along the forward edge of muscle g.m.5 almost to the posterior end of the inferior lateral cardiac ossicle (XIII). As it passes ventrally, it gives off twigs which terminate in muscles g.m.5 and g.m.6. The branches to the latter muscle often originate along the lateral cardiac nerve (l.c.n.) which connects the m.v.n. with the lateral ventricular nerve (l.v.n.) about halfway down muscle g.m.5. Just above ossicle XIII, a small branch, the v.-pl.n., turns posteriorly (see above) while the main trunk of the m.v.n., now certainly anastomosing with the pl.n., turns forward to run parallel with ossicle XIII beneath muscle g.m.2. At the insertion of muscle c.v.1, the m.v.n. and the pl.n. separate, the former arborizing along the fibres of muscle c.v.1, which it innervates, and then sending a secondary branch, the cardiac branch (c.m.n.), to muscle c.4, while the latter (p.l.n.) continues forward eventually to terminate, via two roots, in the commissural ganglia (see above, sensory nerves). At its origin the m.v.n. contains two axons. One of these, the lateral cardiac neuron (L.C.), innervates muscles g.m.5, g.m.6 and g.m.8, and in some instances apparently c.v.3. The other fibre, the ventral dilator neuron (V.D.), continues forward to innervate muscle c.v.1. The difficulties of homologizing the medial ventricular nerves in *Homarus* and *Panulirus* have been discussed at the beginning of this general section (see above).

After passing through the ventral wall of the aorta, the dorsal ventricular nerve (d.v.n.) eventually terminates above the cardio-pyloric muscles (g.m.4) by dividing into the paired lateral ventricular nerves (l.v.n.). At this point, fibre counts of methylene blue-stained preparations indicate that there are at least 18 large fibres which branch to enter each l.v.n. As the l.v.n. runs postero-laterally toward the insertion of the lateral posterior gastric muscles (g.m.3), it gives off various small branches which terminate on muscles g.m.4. These are the cardio-pyloric branches (cp.n.), and carry axon branches of the cardio-pyloric neuron (CP.). In *Panulirus* branches of the homologous neuron run in an unpaired nerve of the same name which originates separately at the posterior end of the stomatogastric ganglion.

At the base of the lateral posterior gastric muscle (g.m.3) each lateral ventricular nerve (l.v.n.) is joined by the posterior stomach nerve (p.s.n.) (Dando & Laverack 1969). The form of the anastomosis is variable and often quite complex, frequently differing significantly on the two sides of the same animal. Nevertheless, there are characteristic features. A branch (the dorsal branch, d.b.), carrying mostly small fibres from the p.s.n. typically leaves the anastomosis and passes medially over the posterior arch of the gastric mill just anterior to the insertion of the posterior gastric muscles. Another relatively small branch passes forward over the lateral cardiac muscle to form the lateral cardiac nerve (l.c.n.) joining the median and lateral ventricular nerves (see above). Some of the fibres entering the l.c.n. from the l.v.n.-p.s.n. anastomosis are small and obviously sensory, but there is also at least one larger axonal branch which apparently innervates muscles g.m.6b and g.m.8b. The exact configuration of the anastomosis and the branches to the muscles arising from the l.c.n. is rather variable.

Just behind the lateral posterior gastric muscle (g.m.3) the l.v.n. divides into a ventral branch (v.-l.v.n.) and a dorsal branch (d.-l.v.n.). The dorsal branch of the lateral ventricular nerve immediately gives off a short branching nerve (or nerves) which innervates muscle g.m.3; these are the postero-lateral gastric branches (pl.g.). The dorsal branch then continues medially and dorsally, sometimes giving off small branches until it typically divides into a postero-median gastric branch (pm.g.) innervating postero-gastric muscles, and a posteriorly directed dorsal dilator branch (d.d.n.) which contains the two pyloric dilator (P.D.) axons that innervate the anterior dorsal pyloric dilator muscle (cp.v.1).

The ventral branch of the lateral ventricular nerve (v.-l.v.n.) passes postero-ventrally toward muscle g.m.9, where it gives off a dorsally directed branch, the gastro-pyloric nerve (gp.n.) near the anterior edge of muscle g.m.9. This branch runs over the surface of muscles g.m.9, cp.v.6 and p.1 dorsal to, and generally parallel with, the posterior extension of v.–l.v.n., the pyloric nerve (py.n.). The gp.n. gives off branches to the muscles it passes over, and posterior to the edge of muscle g.m.9 can be considered the lateral pyloric branch (l.p.n.). Just beyond the origin of gp.n., an antero-ventral branch leaves the v.-l.v.n. and shortly separates into two further branches. The most anterior of these is the ventral branch of the postero-lateral nerve (v.-pl.n.) which forms the most ventral anastomosis between the m.v.n. and l.v.n. The more posterior branch can be called the pyloric dilator nerve (p.d.n.) because it carries the two axons which innervate the inferior pyloric dilator muscles, cp.v.2, but it may also carry other fibres which innervate muscles cp.v.7. or c.v.3. After the origin of the p.d.n. and v.-pl.n., the v.-l.v.n. becomes the pyloric nerve (py.n.), and continues posteriorly over the surface of the pyloric muscles. A ventral branch, v.-py.n., passes downward to muscle cp.v.9a which it innervates. At the level of muscle p.2, another ventral branch runs downward over muscles p.4 and cp.v.9b and after giving off branches to these continues over the ventro-lateral surface of the ampulla. This is the ampullary nerve (ap.n.). Just behind the ampullary nerve the py.n. gives off a medially directed branch which passes inward behind the posterior margin of muscle p.2 and beneath muscle p.8. This is the internal pyloric branch (i.p.n.). Unnamed branches run from the py.n. to the various pyloric muscles, and a major branch passes posteriorly over the hepatopancreatic duct. Although this apparently continues on over the midgut to join the intestinal network, we have no evidence that motor fibres from the pyloric nerve reach so far posteriorly.

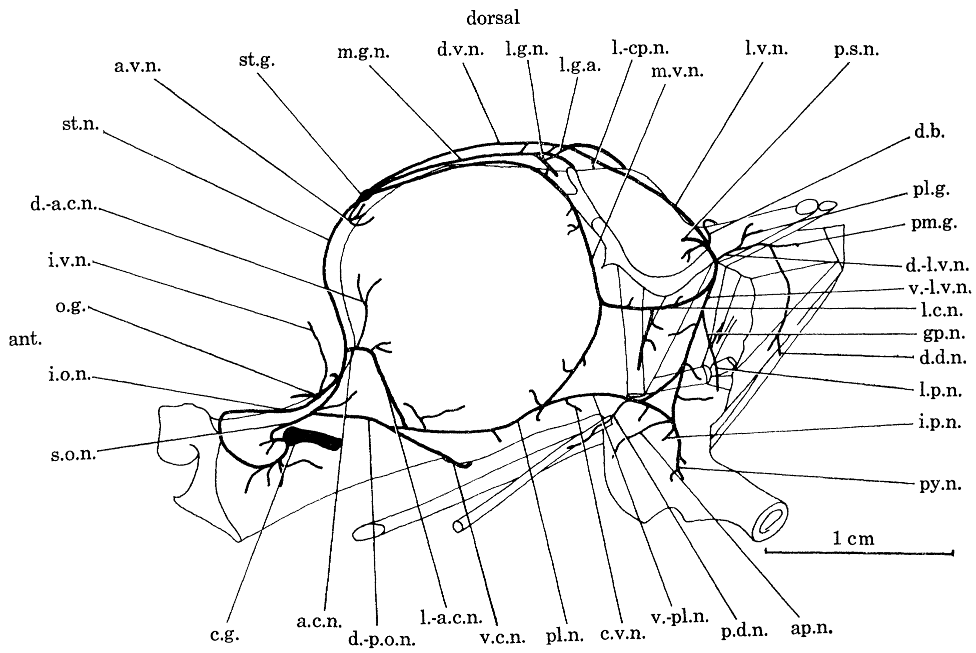

FIGURE 16. A lateral view of the foregut of *Callinectes sapidus* to show the stomatogastric nervous system. Anterior is to the left and dorsal is uppermost. Full details of the nomenclature for the nerves are in the text and key.

Stomatogastric nervous system of Callinectes (*figure* 16)

Mocquard (1883) described some of the nerves innervating the brachyuran stomach and Pearson (1908) gave a general description of the larger stomach nerves in *Cancer pagurus*. Heath (1941) figured nerves in the kelp crab *Pugettia producta* and Dando & Laverack (1969) also discuss stomach nerves in *Cancer pagurus*. As with *Homarus*, however, a comprehensive description of the crab stomatogastric nervous system is lacking. The detailed comments on the system in *Cancer pagurus* are derived from a separate physiological investigation (Dando, Chanussot & Nagy 1974).

(i) *Class* 1, *motor fibres to oesophageal muscles*

Most of the oesophageal muscles appear to be innervated by fibres originating in the commissural ganglia and running to the muscles in relatively short nerves. Some of the anterior oesophageal dilators, however, are innervated by nerve branches arising from the region of the oesophageal ganglion. These nerves have not been named.

(ii) *Class* 2, *sensory fibres*

As in *Panulirus* and *Homarus* there are two primary nerves carrying fibres from sensory cells on the stomach to the CNS, one, the posterior stomach nerve (p.s.n.), runs to the thoracic nerve mass and has been adequately described by Heath and Dando & Laverack, the other, the postero-lateral nerve (pl.n.), runs toward the commissural ganglion.

The configuration of oesophageal nerves in *Callinectes* differs somewhat from that in *Panulirus* and *Homarus*. The ventral posterior oesophageal nerve (v.-p.o.n.) seems to be completely separate from the dorsal posterior oesophageal branch (d.-p.o.n.) and anastomoses between the two are apparently lacking or very rare. As in *Homarus*, the d.-p.o.n. originates from the superior oesophageal nerve (s.o.n.) well along its course, and passes backward over the lateral surface of the oesophagus. The d.-p.o.n. gives off small branches to oesophageal muscles, and then a major branch, the ventral cardiac branch (v.c.n.), to the ventral cardiac gutter. Slightly posterior to the v.c.n. origin, the d.-p.o.n. anastomoses with the lateral branch of the anterior cardiac nerve (l.-a.c.n.) (see below) and becomes the postero-lateral nerve. Sensory fibres from the pl.n. therefore must first traverse both the d.-p.o.n. and s.o.n. before reaching the commissural ganglion.

After a very short length, the pl.n. anastomoses with the class 4 nerve, the median ventricular nerve (m.v.n.) at the point it sends branches to muscle c.v.1. The two nerves fuse and continue posteriorly above the muscles c.v.2 and g.m.5 and 6. At the forward edge of muscle c.v.2 a small branch runs ventrally toward the anterior end of ossicle XIII. Branches are given off to muscle c.v.2, and then the median ventricular nerve (m.v.n.) turns dorsally, undoubtedly carrying some sensory fibres of the pl.n. with it. The remainder of the pl.n. continues posteriorly as the ventral branch (v.-pl.n.) eventually to anastomose briefly with the pyloric dilator nerve (p.d.n.) and then continues backward over the pyloric muscles to join with the pyloric nerve (py.n.) and finally reach the hepatopancreatic duct. A distinct hepatopancreatic duct nerve was not found. A small ventral branch arising just after the origin of the v.-pl.n. runs toward muscles c.v.3 and cp.v.7, and presumably represents a class 4 rather than a class 2 nerve. It is sufficiently distinct to receive a name, and may be termed the cardiac valve branch (c.v.n.).

Sensory fibres in the m.v.n. running dorsally undoubtedly reach the posterior gastric mill region in the lateral cardiac nerve (l.c.n.), while others leave the m.v.n. in small anterior nerves at the level of the lateral edge of the pterocardiac ossicle (II). In many respects the configuration of the pl.n. and its branches over the stomach in *Callinectes* resembles that in *Homarus* in that anastomoses and fusion with nerves of class 4 are prominent. In all three species examined, however, the general distribution of the sensory elements over the cardiac and pyloric stomachs is very similar, the major difference being whether or not sensory fibres run in the same connective tissue sheaths as the stomatogastric motor elements.

(iii) *Class* 3, *neurosecretory fibres*

Surface plexuses of fine nerve fibres are not obvious in the region of the oesophageal ganglion and the origin of the stomatogastric nerve. Rather, an accumulation of neural elements containing small granules which make them appear opaque bluish-white often occurs at a swelling of the anterior cardiac nerve (a.c.n.) where it gives off the major lateral and dorsal branches (l.-a.c.n. and d.-a.c.n., respectively) as well as smaller branches to muscle c.7. It is likely that this represents the neurohaemal organ in crabs. The location of the neuron somata whose processes supply it is unknown.

(iv) *Class* 4, *stomatogastric ganglion system*

As in *Homarus* and *Panulirus* the stomatogastric ganglion (st.g.) is located in the lumen of the cor frontale of the anterior aorta. It tends to be more anterior than in the other two genera, and the stomatogastric nerve is relatively shorter.

The form of the ganglion is characteristic. Fibres from the stomatogastric nerve lead into a flattened, almond-shaped neuropile. The somata of the stomatogastric ganglion neurons are arranged in a cresent around the sides and back of the neuropile rather than on top as in *Homarus* and *Panulirus*. We have not made sections of the ganglion, but we have the impression that the layer of cell bodies is essentially one cell thick, certainly not commonly more than two, and that neuron somata are generally absent directly above or below the neuropile. We have not counted the number or measured the diameters of the neurons in the ganglion.

The unpaired stomatogastric nerve (st.n.) passes forward from the ganglion, leaves the aorta through its ventral wall, and runs without branching down the midline of the cardiac stomach to the oesophagus. There, just above the junction of the stomach and oesophagus, a pair of side branches, the anterior cardiac nerves (a.c.n.), pass laterally to the stomach wall. The stomatogastric nerve then continues for a short distance before giving rise to the paired superior oesophageal nerves (s.o.n.) which connect with the commissural ganglia (c.g.). Again a short trunk continues and this gives rise to a small nerve innervating the anterior oesophageal muscles. Then the unpaired inferior ventricular nerve (i.v.n.) leaves to pass to the brain, and just below it the trunk swells slightly to accommodate the accumulation of cell bodies forming the oesophageal ganglion (o.g.). The trunk terminates in the paired inferior oesophageal nerves (i.o.n.) which also pass to the commissural ganglia.

The anterior cardiac nerves (a.c.n.) differ somewhat from the single anterior median nerve in *Panulirus*, and the multiple branched anterior cardiac nerve in *Homarus*. They appear to contain, however, the axon of the A.M. neuron which in each species innervates the muscles of the cardiac stomach. In the crab they apparently also carry neurosecretory fibres, and perhaps sensory fibres and other motor axons. After passing directly laterally and giving off small branches, the a.c.n. enlarge slightly (see above) and give rise to a dorso-medially directed branch, d.-a.c.n., which ramifies over the anterior, median, and dorsal portion of the cardium, and to a lateral branch (l.-a.c.n.) which eventually anastomoses with the dorsal posterior oesophageal nerve (d.-p.o.n.) to form the postero-lateral nerve (pl.n.). In addition, smaller branches originate at this point, notably some which ramify among the fibres of muscle c.7.

One paired motor nerve, the anterior ventricular nerve (a.v.n.), leaves the anterior half of the stomatogastric ganglion. Its fibres generally originate at the level of the most anterior cell bodies in the ganglion and pass laterally through the wall of the blood vessel. The a.v.n. then divides, sending one branch to the cardiac dilator muscle c.1, and the other to the ventral side of the anterior gastric muscles, g.m.1. We have not yet determined the innervation of muscle c.2.

The a.v.n. in *Callinectes* is similar to that in *Panulirus* because it carries axons supplying muscles c.1 and g.m.1, but it differs from that in *Homarus* because it contains these but does not contain the axons of neurons A.M. and I.C.

The configuration of the posterior motor nerves is more complex and variable in *Callinectes* than in the two other genera examined here. A typical instance will be described, but the number and form of the anastomosing trunks in the midline just behind the ganglion can vary greatly. There are essentially two unpaired and one pair of nerves arising from the posterior end of the stomatogastric ganglion.

The paired nerve is the median ventricular nerve (m.v.n.) which originates on either side of the ganglion as the most lateral of the posterior trunks. After leaving the aorta, the m.v.n. turns laterally to run over the upper surface of the posterior portion of the anterior gastric muscles, g.m.1. There it may or may not anastomose with the lateral gastric nerve (l.g.n.) (see below). In any case, no motor fibres are exchanged at the anastomosis and the m.v.n. continues laterally just anterior to the pterocardiac ossicle (II). At the outer edge of the ossicle it may give off small branches which run forward over the anterior gastric arch or over the lateral cardium and which presumably carry sensory fibres (see above). The main portion of the m.v.n. turns downward and slightly backward along the zygocardiac ossicle (V). At the level of muscle g.m.6, m.v.n. turns sharply downward and after a short distance gives off a major branch, the lateral cardiac nerve (l.c.n.) which passes backward over the lateral cardiac muscles. After giving off scattered small branches to muscle g.m.6 and a major ventral branch along muscle g.m.8, the l.c.n. eventually joins with the ventral branch of the lateral ventricular nerve (v.-l.v.n.). Below the junction with l.c.n., m.v.n. gives off small branches to muscle g.m.5 as it continues ventrally and anteriorly to the posterior edge of muscle c.v.2. There the ventral branch of the postero-lateral nerve (v.-pl.n.) separates to continue posteriorly (see above) while the m.v.n., now fused with fibres of pl.n., passes forward over muscle c.v.2, which it innervates. The m.v.n. eventually terminates in ramifications over muscle c.v.1. (In the crab *Cancer pagurus* the m.v.n. carries only two motor axons from the stomatogastric ganglion. These are presumably V.D. and I.C. as in *Panulirus* because the L.C. neuron is definitely not included.)

The larger and more dorsal of the unpaired posterior nerves leaving the stomatogastric ganglion is the dorsal ventricular nerve (d.v.n.). It passes backward from the ganglion, leaves the blood vessel on the ventral side, and continues to the posterior margin of the mesocardiac ossicle (I). It gives off no side branches, but along its course there may be one or more small anastomoses with the underlying median gastric nerve (m.g.n.). At the level of ossicle I, the d.v.n. divides into two branches, the lateral ventricular nerves (l.v.n.) which pass postero-laterally over the cardio-pyloric muscles (g.m.4) to the lateral margin of the posterior gastric arch. There are three small nerves which leave l.v.n. and ramify over the cardio-pyloric muscles, these are the median and lateral cardio-pyloric nerves (m.-cp.n. and l.-cp.n.) innervating muscles g.m.4c and 4b respectively. There are characteristically two additional lateral anastomoses between the gastric and ventricular nerve complexes. These run from the lateral gastric nerve (l.g.n.) (see below) on each side shortly after its origin to either the d.v.n. or l.v.n. near the latter's origin. These anastomoses, together with the one indicated above between d.v.n. and m.g.n. can be termed lateral gastro-ventricular anastomoses (gv.a.).

The other unpaired posterior nerve is the median gastric nerve (m.g.n.). It is of smaller diameter than the d.v.n. and usually originates beneath it. It passes backwards, parallel with d.v.n. and, like it, emerges through the ventral wall of the aorta. The m.g.n. then divides into two major branches, the lateral gastric nerves (l.g.n.), which pass laterally. At the point of branching there may be a small junction with the d.v.n. and another small unnamed branch may pass ventrally between the anterior gastric muscles. Shortly after its origin, each l.g.n. gives off a large, posterior branch, the lateral gastro-ventricular anastomosis (g.v.a.) which passes directly to the l.v.n., or sometimes the trunk of the d.v.n. The l.g.n. then continues laterally over the anterior gastric muscle (g.m.1), sending a number of branches to it. Sometimes the l.g.n. or one of its branches anastomoses briefly with the m.v.n. (see above) at this level.

The median gastric nerve does not occur as such in either *Homarus* or *Panulirus*. It presumably resembles cp.n. in *Panulirus*, and the lateral gastric nerves of *Callinectes* are presumably similar to the anterior gastric nerves of *Homarus*. In some species of crab anastomoses do not occur between the ventricular and gastric nerve complexes, and the cardio-pyloric muscles (g.m.4) are innervated by posteriorly directed branches from the median or lateral gastric nerves. It seems likely therefore, that in *Callinectes* the median gastric nerve may often carry the axon of the CP. neuron which innervates muscle g.m.4 and also axons of G.M. neurons which innervate muscle g.m.1. (This is certainly true of the crab *Cancer pagurus*.)

When the lateral ventricular nerves (l.v.n.) reach the insertion of the lateral posterior gastric muscles (g.m.3) at the outer edge of the posterior gastric arch, they anastomose with the posterior stomach nerve (p.s.n.) (see, for example, Dando & Laverack 1969). As in other species the configuration of the anastomosis is variable. Characteristically a large dorsal branch (d.b.) runs medially along the posterior gastric arch just anterior to the insertions of the posterior gastric muscles (g.m.2 and 3), and after giving off posteriorly directed side branches joins with the similar nerve from the opposite side. Another smaller branch, also carrying sensory fibres from the p.s.n., runs laterally and anteriorly along the upper surface of the zygocardiac ossicle (V). Just behind the l.v.n.-p.s.n. anastomosis, the l.v.n. can be considered to divide into a dorsal and a ventral branch (d.-l.v.n. and v.-l.v.n. respectively). The dorsal branch in turn often divides immediately into postero-median gastric and postero-lateral gastric branches (pm.g. and pl.g. respectively) which ramify over the posterior surfaces of the posterior gastric muscles (g.m.2 and 3). Often there is also a rather long branch, the dorsal dilator branch (d.d.n.), which runs from the d.-l.v.n. to the anterior dorsal pyloric dilators (cp.v.1) which it innervates; in *Cancer pagurus* as in *Scylla* (Maynard 1969) this carries the axons of two small and two large pyloric dilator (P.D.) motor neurons. Sometimes the pm.g. and pl.g. seem to originate directly from the v.-l.v.n., and the short d.-l.v.n. is essentially absent.

Shortly after its origin, the v.-l.v.n. gives off a major branch running forward over muscles g.m.8 and 6. This is the lateral cardiac nerve (l.c.n.) which runs to the m.v.n. (in *Cancer pagurus* this carries the axon of the lateral cardiac L.C. motor neuron from the l.v.n. to muscles g.m.5b, 6 and 8a). A major branch often leaves the l.c.n. between muscles g.m.8a and 8b and turns ventrally toward the cardio-pyloric valve region. After giving off the l.c.n., the v.-l.v.n. continues toward the pyloric region. Several smaller branches run forward to muscle g.m.8b, and a larger branch, the gastro-pyloric nerve (gp.n.) leaves to travel toward muscle g.m.9 and the dorsal pyloric region. There it ramifies over muscle g.m.9 and sends other branches, the lateral pyloric branches (l.p.n.), to muscles cp.v.3, cp.v.6, and eventually p.1. Upon reaching muscles cp.v.4 and 6, the v.-l.v.n. gives off small branches to them and then divides into the dorsal pyloric nerve (py.n.) and the ventral pyloric dilator nerve (p.d.n.) which terminates on the

TABLE 1. SUMMARY OF THE STOMACH MUSCLES†

muscle	origin	insertion	Cochran no.	*Callinectes*	*Homarus*	*Panulirus*
cardiac muscles						
extrinsic						
c.1	e	sw	—	×	×	×
c.2	e	sw	200	×	×	×
c.3	e	sw	—	×	×	×
c.4	e	sw	202	×	×	×
c.5	e	sw	201	×	×	×
intrinsic						
c.6	I	sw, XI	213	×	×	×
c.7	sw	sw, XII	214	×	×	×
gastric mill complex						
extrinsic						
g.m.1a	e	II	—	×		×
b	e	I	197	×	×	×
g.m.2a	e	III	—		×	×
b	{e	III	198	×	×	× }
	e	IV	—			× }
g.m.3a	e	V	—		×	×
b	e	IV	199*a*	×		
c	e	IV	199*b*	×		×
intrinsic						
g.m.4a	{II	V	—		×	× }
	I	V	—			× }
b	{I	IV	210*b*	×	×	× }
	II	IV	—		×	}
c	I	VI	210*a*	×	×	×
g.m.5a	{XIII	IX	—	×		}
a′	XIV	XII	—			× }
b	{XIII	IX	211*b*	×	×	}
b′	XIV	IX	—			× }
g.m.6a	XIII	V	211*c*	×	×	
b	XIV	V	—	×		×
g.m.7	XIII	XIV	—	0	0	×
g.m.8a	XVIII	V	211*d*	×		0
b	XVIII	V	211*e*	×	×	0
g.m.9a	{XXXI	III	211*f*	×	×	× }
	XXXI	IV	211*g*			× }
b	XXIX	III	—		×	
c	XVIII	III	—		×	
ventral cardiac muscles						
extrinsic						
c.v.1	{e	XII	203	×		× }
	e	Xa	—		×	}
intrinsic						
c.v.2	XII	XIII	211*a*	×	×	×
c.v.3	XVI	XIII	212	×	×	×
cardio-pyloric valve muscles						
extrinsic						
cp.v.1a	{e	XIX	—			× }
	e	XX	204*a*	×	×	}
b	{e	XX	—		×	× }
	e	XXI	204*b*	×		}
c	e	XX	—		×	
cp.v.2a	e	XVIII	205*a*	×	×	
b	e	XXIII	205*b*	×	×	×

Table 1 (*cont.*)

muscle	origin	insertion	Cochran no.	*Callinectes*	*Homarus*	*Panulirus*
cardio-pyloric valve muscles						
intrinsic						
cp.v.3a	XXXI	XIX	216*l*	×		×
b	XXXI	XX	216*k*	×	×	
cp.v.4a	XXXI	XV	216*a*	×	0	
b	XXXI	XVIII	—	×	0	×
cp.v.5	XXXI	XXIII	—	0	0	×
cp.v.6	XX	XVIII	216*b*	×	×	0
cp.v.7a	XIII	XVIII	216*n*	×	×	×
b	XIII	XVII	—		×	
cp.v.8	XXII	XVIII	216*i*	×	0	0
cp.v.9a	XXIX	XVIII	—	0	×	0
b	XXIX	XXII	—	0	×	0
cp.v.10	XXIV	XXII	—	×	×	×
cp.v.11	XXVII	XXIII	216*m*	×	0	0
pyloric muscles						
p.1	XX	XXIX	216*c*	×	×	×
p.2	XXI	XXIX	216*d*	×	×	×
p.3	{XXIX	XXX	—	×	×	× }
	{XXV	XXX	—			× }
p.4	XXIX	XXIV	216*j*	×	×	0
p.5	{XXVIII	XXXII	—	×	0	}
	{XXVIII	XXX	—		0	× }
p.6a	XXXII	XXIa	—	×	×	×
b	XXXII	XXIX	—		×	
p.7	XXXII	XXX	216*f*	×	×	×
p.8	{XXIV	u-p	216*e*	×	×	}
	{XXV	u-p	—			× }
p.9	XXIV	XXX	—	×	×	×
p.10	{u-p	XXX	216*g*	×		× }
	{XXI	XXX	—		×	}
p.11	XXI	XXX	—	×	×	×
p.12	XXI	XXXIII	—	×	×	× ?
p.13	XXXIII	XXX	216*h*	×	×	× ?
p.14	XXI	XXX	—	×	0	× ?

† The old terminology of cardiac and pyloric stomach is illogical but we prefer to retain it because for our purpose there is no compelling need for a new terminology, and any change would certainly cause confusion.

Columns 1 and 4 identify the muscle and muscle bundle according to our numerical scheme and the numerical scheme of Cochran. Columns 2 and 3 give the origin and insertion of all bundles. The abbreviation e indicates an extrinsic muscle attachment, sw indicates an attachment to the stomach wall but not to an ossicle and u-p indicates an attachment to the uropyloric fold. For each species an × indicates the presence of the muscle or muscle bundle. Muscle bundles with the same designation but slightly different attachments are shown by the combining parentheses. A blank space indicates that a bundle is not present and an 0 indicates the absence of an entire muscle.

inferior pyloric dilator muscles (cp.v.2). Near its origin the p.d.n. may also contain fibres which innervate muscles g.m.8 or cp.v.8 and, near the pyloric valve anastomoses for a longer or shorter extent with the ventral branch of the postero-lateral nerve (v.-pl.n.) (see above). The configuration is variable, but generally the v.-pl.n. runs backward from the p.d.n. to join the py.n. above the ampulla and forms a triangle whose three sides consist of v.-pl.n., p.d.n., and py.n.

The pyloric nerve (py.n.) runs over the surface of the pyloric muscles, giving off small side branches to them. Near the posterior edge of muscle p.1, the v.-pl.n. joins the py.n. and a ventrally directed ampullary nerve (ap.n.) runs down along the forward margin of the ampulla to ramify among the muscles on its surface. Shortly behind the origin of the ampullary nerve, the py.n. gives rise to the medially directed internal pyloric branch (i.p.n.) which dives beneath muscle p.8. The py.n. then continues, sending branches to the posterior pyloric muscles and to the hepatopancreatic duct. The extent to which the pyloric nerve anastomoses with nerves from the midgut and the possibility of exchange of fibres between the foregut and midgut has not been investigated in *Callinectes*.

Discussion

Comments on the stomach muscles

Table 1 summarizes our interpretation of the gastric musculature in the three species examined. Columns 1 and 4 identify the muscle and muscle bundle according to our numerical scheme, and the numerical scheme of Cochran (1935) respectively. Columns 2 and 3 give the origin and insertion of all bundles. The final three columns indicate the presence or absence of a particular muscle bundle in each of the three species, *Callinectes sapidus*, *Homarus americanus*, and *Panulirus argus*.

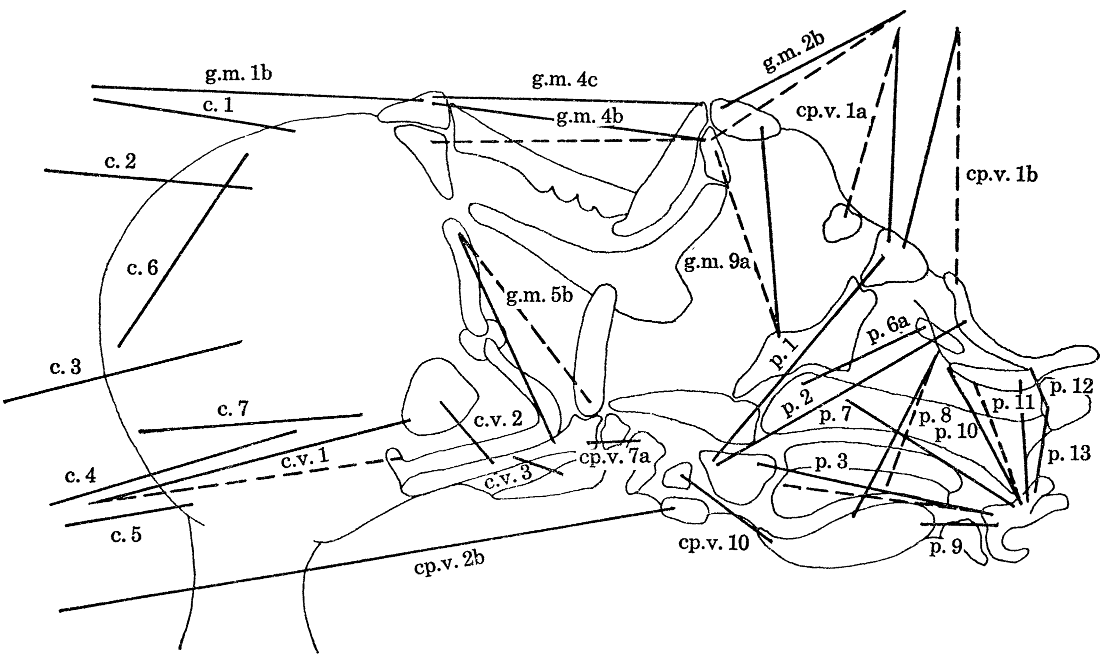

Figure 17. A diagram illustrating the muscle bundles common to all three species. Bundles are illustrated by lines connecting the idealized ossicles of figure 1. The broken lines indicate minor variations in the attachments of bundles in different species.

Of the total of 44 muscles and 63 muscle bundles identified, most were found in *Callinectes* where there are 41 muscles and 51 muscle bundles. *Homarus* has 37 muscles and 49 muscle bundles, while *Panulirus* has 38 muscles (including three questionable pyloric muscles) but only 44 muscle bundles. The superficial observation that *Panulirus* has the least complex musculature would therefore seem to be supported by numerical counts. It is interesting to note that all of the variation in muscle number, and most of the variation in muscle bundle number, occurs among the intrinsic musculature and more particularly among the musculature of the gastric mill and cardio-pyloric valve. This point is illustrated by figures 17 and 18 where muscle bundles common to all three species are compared with those present in only one or two.

Comments on the stomatogastric nervous system

The main axis of the stomatogastric system in the three species discussed is essentially the same, and includes the stomatogastric nerve, the stomatogastric ganglion, the dorsal and lateral ventricular nerves, the anastomosis with the posterior stomach nerve, the pyloric nerve (including the internal branch), and the pyloric dilator nerve. The general course of the postero-lateral nerve and its various components from the hepatopancreatic duct to the commissural ganglia along the ventro-lateral aspect of the stomach is also similar in the three species. Differences occur in the detailed patterns of branching in the pyloric region and in the nature of the lateral nerves leaving the stomatogastric nerve, the stomatogastric ganglion or the dorsal

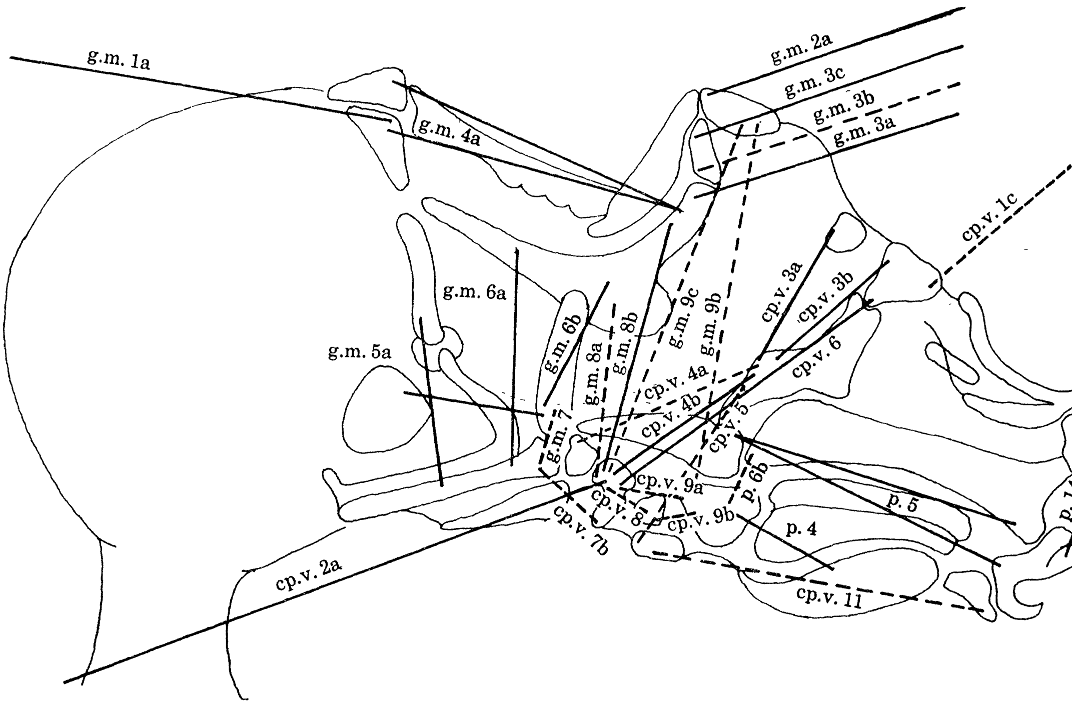

FIGURE 18. A diagram illustrating the muscle bundles common to only two or only one (broken line) species. The idealized ossicles are used as in figure 17.

ventricular nerve. The most critical difference for the neurophysiologist is not the geometrical pattern nor necessarily the intraspecific variability in nerve location that is commonly found, but rather the fact that fibre combinations within nerves may differ significantly (see above, discussion of the median ventricular nerve in *Homarus* and *Panulirus*) in the different species. Some of these differences are documented in the comments on individual species in the preceding sections. We do not yet have sufficient information from methylene blue preparations and physiological measurements, however, to trace the course of a majority of the stomatogastric neuron axons from cell body to muscle in *Homarus* or *Callinectes*. Until this is available a comparison of the finer detail of the stomatogastric system among the three groups is impractical, and one cannot assume that nerves having the same name or the same geometrical location will necessarily contain the same fibres from species to species. The diagrams of figures 19–21 are designed as road maps leading through the rather complex neural network of

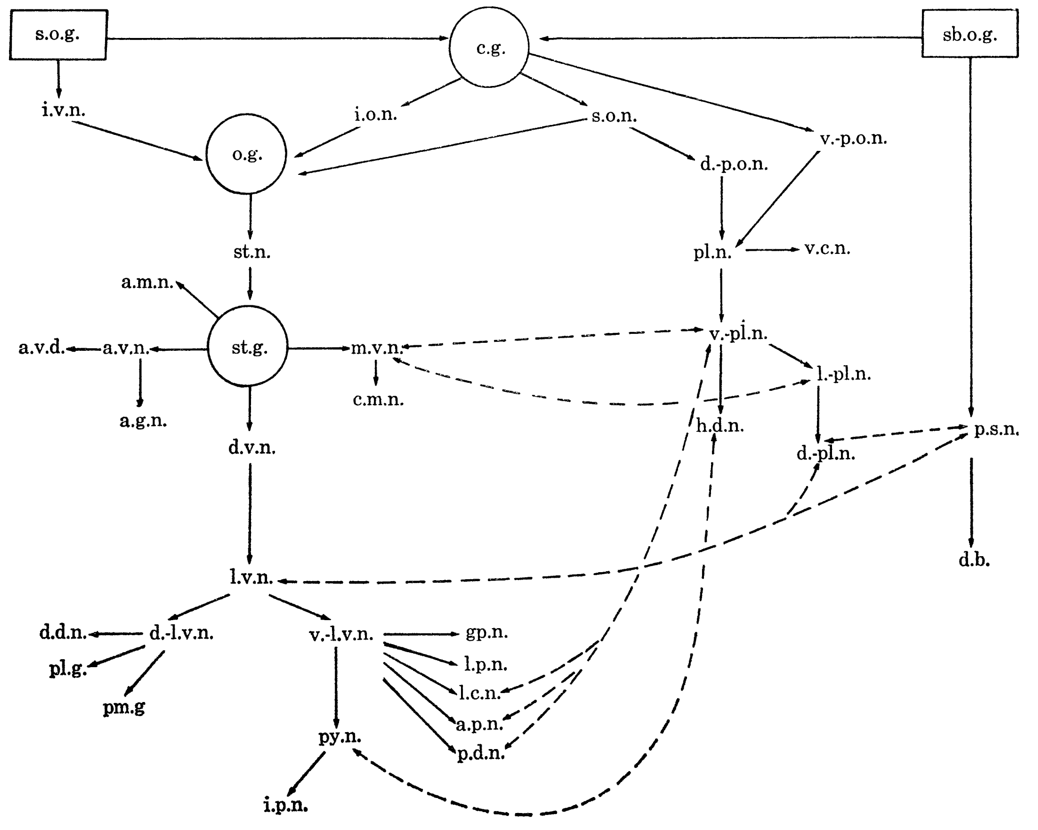

Figure 19. A diagram illustrating the layout of the stomatogastric nervous system of *Panulirus*. The supra- (s.o.g.) and sub- (sb.o.g.) oesophogeal ganglia are shown in rectangular boxes. The commissural (c.g.) oesophogeal (o.g.) and stomatogastric (st.g.) ganglia are shown circled. Stomatogastric nerves are illustrated by full lines with arrowheads shown by convention pointing away from the c.n.s., and anastomoses are shown by broken lines with double arrowheads.

Table 2. The stomatogastric ganglion motor neurons of *Panulirus argus*†

name	initial	locus of cell body	nerve	muscle(s) innervated	muscle(s) innervated (?)
anterior median	A.M.	st.g.	a.m.n.	c.6, c.7	—
anterior dilator	A.D.	?	a.v.n.	c.1	c.2
cardiac dilator$_1$	C.D.$_1$	?	pl.n.	c.3	—
cardiac dilator$_2$	C.D.$_2$	?	d.-p.o.n.	c.4	c.v.1
gastric mill$_{1-4}$	G.M.$_{1-4}$	st.g.	a.v.n., d.v.n.	g.m.1, g.m.2	(c.1, c.2)
lateral gastric$_{1-2}$	L.G.$_{1-2}$	st.g.	d.v.n.	g.m.3	g.m.2
cardio-pyloric	CP.	st.g.	cp.n.	g.m.4	—
lateral cardiac	L.C.	st.g.	d.v.n.	g.m.5, g.m.6	g.m.7
gastro-pyloric	GP.	st.g.	d.v.n.	g.m.9, cp.v.3	—
ventricular dilator	V.D.	st.g.	m.v.n.	c.v.1	—
inferior cardiac	I.C.	st.g.	m.v.n.	c.v.2	c.v.3
pyloric dilator$_{1-2}$	P.D.$_{1-2}$	st.g.	d.v.n.	cp.v.1, cp.v.2	—
lateral pyloric	L.P.	st.g.	d.v.n.	cp.v.4, cp.v.5, p.1	cp.v.7
pyloric$_{1-2}$	PY.$_{1-2}$	st.g.	d.v.n.	p2, p.8	p.3, p.5, p.6, p.7, p.9
pyloric$_{3-4}$	PY.$_{3-4}$	st.g.	d.v.n.	—	p.3, p.5, p.6, p.7, p.9
pyloric$_{5-6}$	PY.$_{5-6}$	st.g.	d.v.n.	p.2, p.8, p.10, p.11, p.13	p.12, p.14
pyloric$_{7-8}$	PY.$_{7-8}$	st.g.	d.v.n.	p.10, p.11, p.13	p.12, p.14

† Mulloney & Selverston (1974) have used a slightly different terminology in their work on the stomatogastric ganglion of *Panulirus interruptus*. They call our CP. neuron the dorsal gastric (D.G.) neuron. Similarly our GP. neuron is called the median gastric (M.G.), our L.C. neuron is called the lateral gastric (L.G.), and our L.G. neurons are called the lateral posterior gastric (L.P.G.) neurons.

The first and second columns give the name and initial proposed for each element according to the muscle that it innervates. The third column gives the locus of the cell body and the fourth column gives the nerve (or nerves) by which the axon leaves the stomatogastric ganglion (with the exception of the three neurons for which the locus of the cell body is not known when the main nerve trunk containing the axon is given). The fifth column gives the muscles definitely innervated and the sixth column gives the muscles probably innervated.

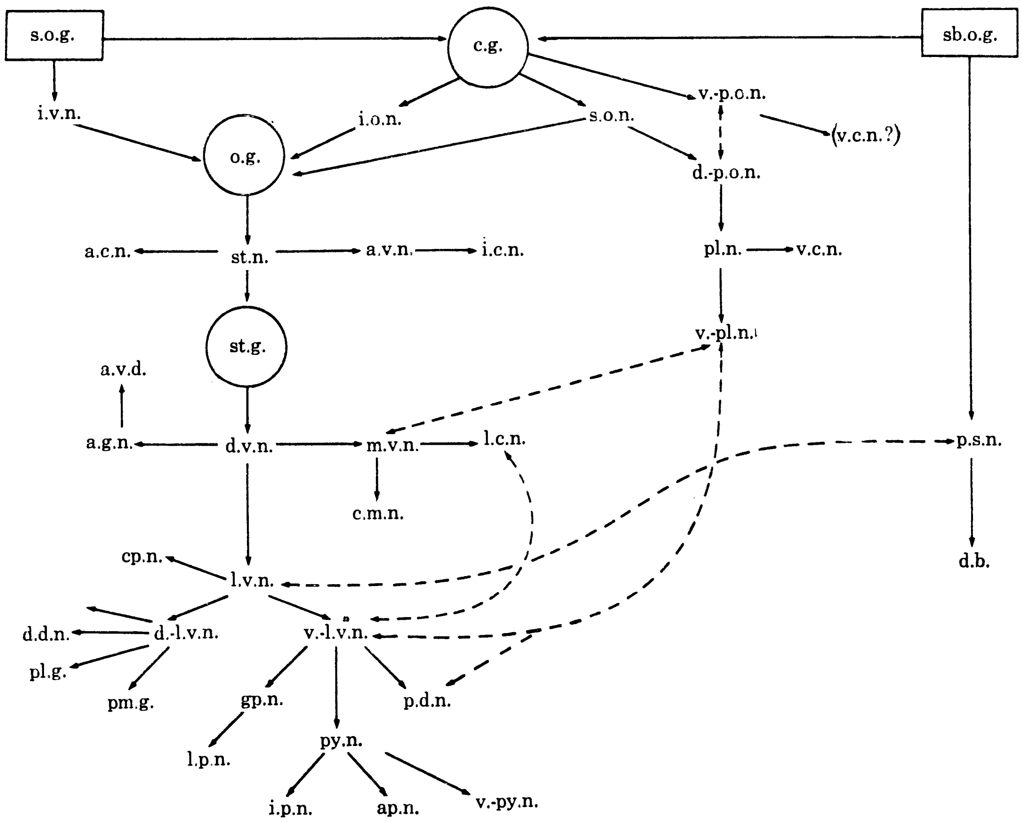

FIGURE 20. A diagram illustrating the stomatogastric nervous system of *Homarus* by the same system as in figure 19.

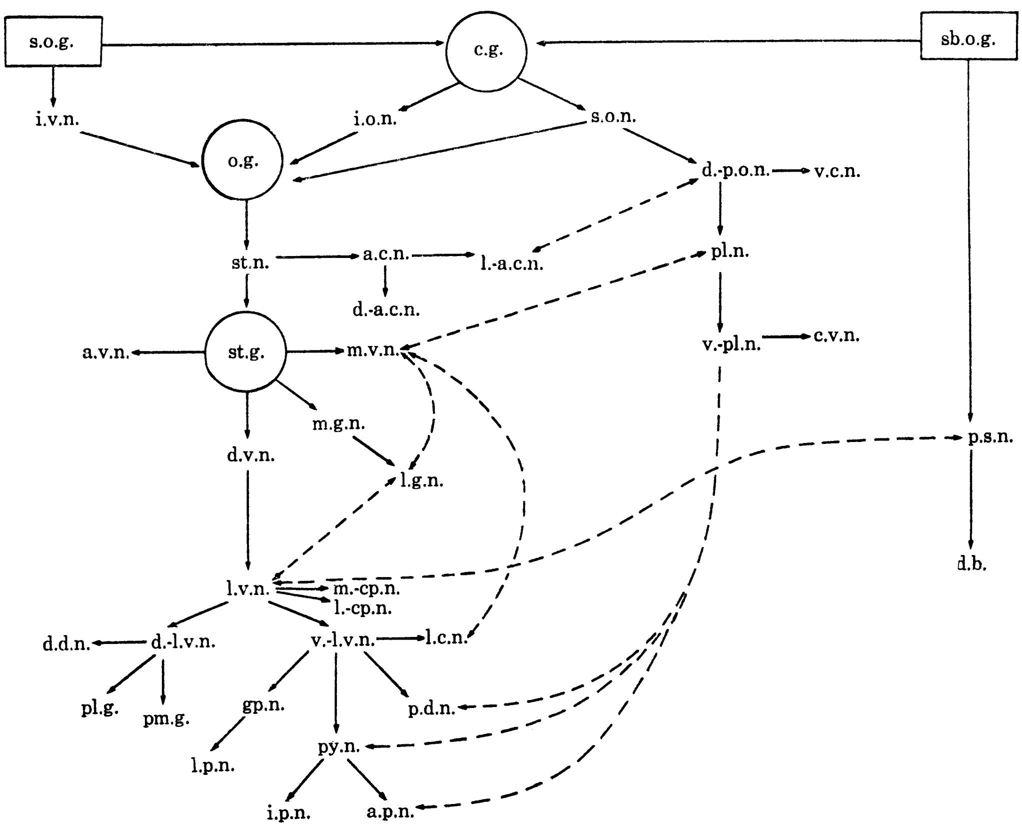

FIGURE 21. A diagram illustrating the stomatogastric nervous system of *Callinectes* by the same system as in figure 19.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the stomatogastric system for each of the three species. Names of each nerve or nerve branch are given together with solid arrows indicating their connexions with proximal (toward the c.n.s.) and distal nerves, ganglia, or branches, and anastomoses are indicated by dashed, double-headed arrows.

Table 2 summarizes the present state of our knowledge of the innervation of specific muscles by specific motor neurons in *Panulirus argus*. Despite the incomplete nature of our present data on the other two species it seems possible to conclude (given the homologies established by Mocquard) that our classification schemes will provide a basis for the consistent identification of the stomatogastric ganglion motor neurons throughout the reptantian Decapoda Crustacea. Strong support for this conclusion has been provided by the detailed physiological investigations of the stomatogastric systems in *Panulirus interruptus* (Mulloney & Selverston 1974) and *Callinectes sapidus* (Govind & Atwood 1974) in which the schemes presented here have been used successfully for the identification of large numbers of the stomatogastric motor neurons.

This work was supported by USPHS grants nos NS06017 and NS09474 to Professor Maynard. Contribution no. 572 was from the Bermuda Biological Station, St George's West, Bermuda.

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BIOLOGICAL SCIENCES
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PHILOSOPHICAL TRANSACTIONS OF

Key to abbreviations used on figures

ossicles
see pages 165–6

muscles
see table 1, pages 212–13

stomatogastric neurons (*Panulirus*)
see table 2, page 216

stomatogastric nerves and ganglia

a.c.n.	anterior cardiac nerve
a.g.n.	anterior gastric nerve
a.m.n.	anterior median nerve
ap.n.	ampullary nerve
a.v.d.	anterior ventricular dilator nerve
a.v.n.	anterior ventricular nerve
c.g.	commissural ganglion
c.m.n.	cardiac branch of the median ventricular nerve
cp.n.	cardio-pyloric nerve
c.v.n.	cardiac valve nerve
d.-a.c.n.	dorsal branch of the anterior cardiac nerve
d.-l.v.n.	dorsal branch of the lateral ventricular nerve
d.-pl.n.	dorsal branch of the postero-lateral nerve
d.b.	dorsal branch of the posterior stomach nerve
d.d.n.	dorsal dilator nerve
d.-p.o.n.	dorsal posterior oesophageal nerve
d.v.n.	dorsal ventricular nerve
gp.n.	gastro-pyloric nerve
gv.a.	gastro-ventricular anastomoses
h.d.n.	hepatopancreas duct nerve
i.c.n.	inferior cardiac nerve
i.o.n.	inferior oesophageal nerve
i.v.n.	inferior ventricular nerve
i.p.n.	internal pyloric nerve
l.-a.c.n.	lateral branch of the anterior cardiac nerve
l.-pl.n.	lateral branch of the postero-lateral nerve
l.c.n.	lateral cardiac nerve
l.-cp.n.	lateral cardio-pyloric nerve
l.g.n.	lateral gastric nerve
l.p.n.	lateral pyloric nerve
l.v.n.	lateral ventricular nerve
m.-cp.n.	median cardio-pyloric nerve
m.g.n.	median gastric nerve
m.v.n.	median ventricular nerve
o.g.	oesophageal ganglion
p.d.n.	pyloric dilator nerve
pm.g.	postero-median gastric nerve
pl.g.	postero-lateral gastric nerve
pl.n.	postero-lateral nerve
p.s.n.	posterior stomach nerve
py.n.	pyloric nerve
s.o.g.	supra-oesophageal ganglion
sb.o.g.	sub-oesophageal ganglion
s.o.n.	superior oesophageal nerve
st.g.	stomatogastric ganglion
st.n.	stomatogastric nerve
v.-l.v.n.	ventral branch of the lateral ventricular nerve
v.-pl.n.	ventral branch of the postero-lateral nerve
v.-py.n.	ventral branch of the pyloric nerve
v.c.n.	ventral cardiac branch of the postero-lateral nerve
v.-p.o.n.	ventral posterior oesophageal nerve