Crustaceana 26 (2), 1974. E. J. Brill, Leiden

A COMPARATIVE STUDY OF THE DIGESTIVE TRACTS OF *CAPRELLA EQUILIBRA* SAY AND *CYAMUS BOOPIS* LÜTKEN (AMPHIPODA, CAPRELLIDEA)

BY

DONALD E. KEITH
Department of Biology, Texas Christian University, Fort Worth, Texas, U.S.A.

INTRODUCTION

The morphology of the crustacean digestive tract has been widely studied but detailed studies of the gut of amphipods are lacking, particularly the Caprellidea and Hyperiidea.

Martin (1964) reviewed earlier work on amphipod digestive tracts and gave a functional and morphological description of the stomach of *Marinogammarus obtusatus* (Dahl). Agrawal (1964) published a very short article dealing with the stomach of *Caprella linearis* (L.), but it lacked details with respect to internal structure; and the relationship of the digestive diverticula to the stomach was not shown. A comprehensive paper by Agrawal (1965) listed a number of amphipods, their feeding habits, and general digestive tract morphology in an attempt to determine if any correlation existed between habitats, feeding habits, feeding appendages, and alimentary canals of amphipods. He concluded that the character of the feeding appendages and the form of the gut was related to the type of food taken. Brief descriptions of the digestive systems of *Hyperia galba* (Montagu) and *Cyamus ovalis* Roussel de Vauzème were given by Agrawal (1967a, 1967b).

The most recent and most detailed analysis of the functional morphology of the gammarid stomach is given by Kanneworff & Nicolaisen (1969). They examined the stomach of 12 gammarids and found that their stomach structure was remarkably uniform. Minor differences were attributed to variations in the relative size of the elements involved.

For this study nine gammarid, four caprellid and three cyamid species were examined. The gammaridean digestive tract morphology agreed with Martin (1964) and Kanneworff & Nicolaisen (1969). Emphasis in this study was placed on the comparative morphology of the digestive tracts of the two families of Caprellidea, the Cyamidae and the Caprellidae. *Caprella equilibra* and *Cyamus boopis* are used as "typical" representatives of each family with respect to stomach anatomy.

METHODS

The structure of the stomach and digestive glands was determined by microscopic examinations of living specimens when they were available, by removing and clearing the digestive tracts, by staining and clearing whole specimens, and from transverse and longitudinal sections. Digestive tract dissections were made from specimens fixed in formalin, alcohol, Bouin's and Zinker's solutions. Those fixed in Bouin's seemed easier to dissect.

In caprellids, the stomach and digestive glands were most easily removed by carefully picking away the exoskeleton in the head region. A cut was made through the specimen behind the third pereonite and the mid-gut and digestive glands pulled through the body cavity by lightly grasping them just behind the stomach. This process did not work with the cyamids because of their massive shape. The exoskeleton was very carefully picked away and the digestive tract lifted out.

Specimens which were to be sectioned and stained with Mallory's triple stain were fixed in Zinker's fixative. Heidenhain's iron haematoxylin with eosin counterstain and Paragon multiple stain were also tried, but the most satisfactory results were obtained with Mallory.

RESULTS AND DISCUSSION

Table I lists the species of amphipods examined for this study.

TABLE I

Amphipod species examined

Gammaridea
- *Ampelisca compressa* Holmes, 1903
- *Corophium acherusicum* Costa, 1857
- *Gammarus annulatus* Smith, 1873
- *Gammarus minus* Say, 1818
- *Haploops laevis* Hoek, 1882
- *Jassa falcata* (Montagu, 1808)
- *Podocerus brasiliensis* (Dana, 1853)
- *Talitrus saltator* (Montagu, 1808)
- *Unciola irrorata* Say, 1818

Caprellidea
- Caprellidae
  - *Caprella californica* Stimpson, 1857
  - *Caprella equilibra* Say, 1818
  - *Paracaprella tenuis* Mayer, 1903
  - *Titrella pilimana* Mayer, 1890
- Cyamidae
  - *Cyamus boopis* Lütken, 1870
  - *Cyamus ovalis* Roussel de Vauzème, 1834
  - *Cyamus scammoni* Dall, 1872

Martin's (1964) terminology was judged to be the most descriptive and is followed with a few exceptions in this study.

The digestive tract of *Caprella equilibra* Say

The digestive tract morphology of *Caprella equilibra* and other species of caprellids studied was similar to that of the Gammaridea. A narrow muscular esophagus leads from the mouth to the cardiac chamber of the stomach (fig. 1). The esophagus is lined with a cuticle and supports posteriorly directed setae. It may be contracted by a series of circular muscles. Dilator muscles are attached to the dorsal and ventral walls of the esophagus.

The stomach is divided into two well defined chambers: an anterior cardiac and a posterior pyloric chamber. At the entrance of the cardiac chamber are two large spinose papillae which arise from the dorsolateral walls and extend downward and posteriorly into the stomach (pl. 1 fig. A). These large folds carry rows of spines which presumably act to push the food through the stomach during its contractions. Above the papillae a dorsal channel is formed by two dorsolateral folds. This channel apparently allows for the anterior recirculation of partially digested food from the pyloric chamber as described in gammarids by Kanneworff

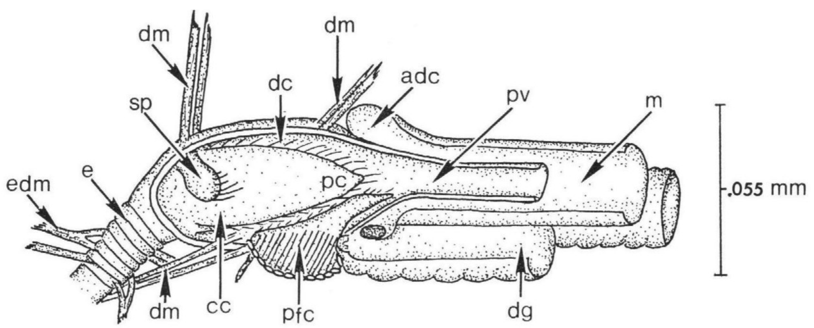


Fig. 1. Lateral view of the fore-gut and mid-gut of *Caprella equilibra* Say. adc, anterior dorsal caecum; cc, cardiac chamber; dc, dorsal channel; dg, digestive gland; dm, dilator muscle; e, esophagus; edm, esophageal dilator muscles; m, mid-gut; pc, pyloric chamber; pfc, pyloric filtering chamber; pv, pyloric valve; sp, spinose papilla.

& Nicolaisen (1969). A channel is formed in the floor of the cardiac chamber by two ventrolateral folds. Anteriorly this channel is divided into two parts by a ventral ridge, but this ridge shortens posteriorly as the ventrolateral folds increase in length. A comb-like row of setae arise from both the dorsolateral and ventrolateral folds preventing particulate material from entering the ventral channel. Two pairs of dilator muscles extend from the roof of the cardiac chamber and one pair from the floor (fig. 1).

The beginning of the pyloric chamber is marked by a very large ridge bearing long setae arising from the floor (pl. 1 fig. B). The setae serve to filter the food, diverting large particulate material toward the mid-gut and allowing juices and fine material to enter the inner filtering channels which open into the digestive glands. Only one set of inner filter channels was clearly observed in *C. equilibra* whereas two pairs were seen in the gammarids studied. Contractions of the digestive glands pumped a light green fluid back and forth facilitating final digestion and absorption.

A large ventrolateral fold divides the pyloric chamber into a dorsal food chamber and a ventral filtering chamber. These folds merge posteriorly with the dorsolateral folds and their setae form a ringlike valve (pl. 1 fig. C). This "setal ring" is also found in gammarids and is said to act as a one-way valve allowing food to pass from the pyloric food chamber into the pyloric valve (Martin, 1964). The pyloric valve in caprellids is a tubular structure formed by the sublateral folds and the posterior extension of the floor of the dorsal caecum (pl. 1 fig. D).

The posterior margin of the ventral pyloric ridge extends upwards and posteriorly as in gammarids. The posterior extension of this structure was termed the ventral valve by Martin (1964) and the central valve by Kanneworff & Nicolaisen (1969). Unlike in gammarids, a pair of sublateral folds (pl. 1 fig. C) arise ventral to the lateral pyloric folds just anterior to the opening of the digestive glands. The lateral and sublateral folds and the ventral valve appear to act together as a barrier preventing undigested material from entering the digestive glands at their entrance into the posterior end of the stomach at its junction with the mid-gut. In gammarids, a tongue-like structure arises from the mid-ventral floor of the pyloric chamber beneath the ventral valve. This structure was not observed in the caprellid cross sections. The setae in the cardiac and pyloric chambers are oriented posteriorly and serve to keep the food moving in a posterior direction during stomach contractions.

Two sets of muscles serve to constrict the pyloric chamber: an inner longitudinal and an outer transverse layer. A pair of dilator muscles are connected to the dorsal posterior wall and ventral anterior wall of the pyloric chamber.

The ventral pyloric chamber divides posteriorly to form two long caeca termed digestive glands. These diverticula extend posteriorly ending in the middle of the fifth pereonite. The anterior margins of these glands project forward a very short distance as anterior ventral caeca. The mid-gut divides dorsally and projects a short distance as paired anterior dorsal caeca. In gammarids, this anterior dorsal extention of the mid-gut is not divided and is considerably longer.

The cardiac and pyloric food chambers are lined with a chitinous lining which is carried upwards by the lateral pyloric folds. This lining continues into the mid-gut as the peritrophic membrane protecting it from the undigested food particles. The filtering chamber and digestive glands are unlined.

The mid-gut terminates posteriorly in a short muscular rectum. The anus bears two papillae which separate as fecal pellets are extruded.

The digestive tract of *Cyamus boopis* Lütken

Because of the nature of the cyamid morphology and the limited number of specimens, studies of the digestive tracts of cyamids were not as detailed as were those of caprellids.

A long narrow esophagus connects the mouth with the cardiac chamber of the stomach. The esophagus is lined with a cuticle and bears a dorsal, a ventral and two lateral folds.

The stomach of *C. boopis* is not clearly divided into cardiac and pyloric chambers as in caprellids and gammarids. Externally the divisions are not evident, but they may be distinguished by differences in internal structures.

The dorsal wall of the cardiac chamber is very thick and folded down into the lumen. The ventral wall is also thick and bears two channels formed by the ventro-lateral folds (pl. 2 fig. A). In the pyloric chamber a broad ventral ridge arises from the floor forming a tongue-like process which projects dorsally and is topped with short setae (pl. 2 fig. B). This structure is quite different from the ventral pyloric ridge of caprellids and gammarids as it is not as long and does not bear inner filtering canals. The pyloric chamber is not divided into a dorsal food chamber and ventral filtering chamber as in the caprellids and gammarids.

Posterior to the base of the tongue, the floor of the stomach gives rise to two large ventral folds (pl. 2 fig. C). These folds increase in length posteriorly encircling the stomach lumen (pl. 2 fig. D). Large food particles were observed in sagittal sections to be held dorsally by folds posterior to the tongue. From their appearance the particles were believed to be pieces of skin from the whale. The tongue may function to press juices from the food.

There are no dorsal or ventral anteriorly directed caeca as in caprellids and gammarids; but there is one pair of ventral caeca, or digestive glands, posteriorly directed as in caprellids. They differ, however, in that they join the digestive tract much more posteriorly than in caprellids and gammarids and they were highly convoluted. Agrawal (1967a) reported that the digestive glands divide into two pairs in *Cyamus ovalis*, but it is assumed that he was looking at the convolutions in cross section which make it appear as though the digestive glands divide. Large particles are prevented from entering the digestive tract by large chitin-lined folds which appear to be continuous with the peritrophic membrane of the mid-gut.

The drastic modifications in the cyamid digestive tract from that of other amphipods is assumed to be correlated with its parasitic existence on the skin of whales. *C. boopis* was obtained from the humpback whale *Megaptera novaeangliae* (Borowski).

Specimens of *Cyamus scammoni* from the gray whale *Eschrichtius gibbosus* (Erxleben) and *C. ovalis* from the North Pacific right whale, *Balaena glacialis* (Borowski), were also studied and found to be similar to *C. boopis*.

CONCLUSIONS

The digestive tracts of caprellids are similar to those of gammarids except for the following differences:

1. Absence of posterior dorsal digestive glands.
2. A reduced anterior dorsal caecum which is paired rather than single.
3. Presence of a slight anterior protuberance of the digestive glands.
4. Absence of a subventral pyloric ridge.
5. Presence of sublateral folds in the posterior pyloric chamber.

The parasitic existence of cyamids has apparently resulted in a number of modifications from the digestive tracts of gammarid and caprellid amphipods. The cyamid stomach is not clearly divisible into cardiac and pyloric chambers. There are no spinous papillae in the anterior cardiac portion of the stomach. The number of folds in the cardiac and pyloric chambers are reduced. The pyloric ridge appears to have lost its filtering function since no inner filtering channels are evident. Two large ventrolateral folds arise from the floor of the pyloric chamber and extend posteriorly into the mid-gut, diverting large food particles dorsally. The paired digestive glands enter the mid-gut more posteriorly than in caprellids and gammarids, and are highly convoluted.

ACKNOWLEDGMENTS

Appreciation is expressed to the Texas Christian University Research Foundation for financial support and to the Allan Hancock Foundation, University of Southern California for research facilities for a portion of this study. The author would also like to express his appreciation to Dr. Thomas E. Bowman, United States National Museum of Natural History and Mr. Yuk-Maan Leung, University of Southern California for their cooperation in supplying certain amphipods.

RÉSUMÉ

L'appareil digestif de *Caprella equilibra* et de *Cyamus boopis* a été étudié et comparé à celui d'un gammaride. L'appareil digestif de *C. equilibra* ressemble à celui d'un gammaride sauf sur les points suivants: absence de la glande postérieure, caecum dorsal antérieur réduit qui est double au lieu d'être simple, présence d'une petite protubérance antérieure des glandes digestives, absence d'une arête pylorique subventrale et des plis pyloriques postérieurs.

Le parasitisme des cyamides a amené des modifications nombreuses de l'anatomie de l'appareil digestif qu'on ne trouve pas chez les gammarides et les caprellides. L'estomac du cyamide n'est plus divisé nettement en région pylorique et en région cardiaque. Les épines et les plis sont bien différents et l'arête pylorique a, semble-t-il, perdu sa fonction de filtration. Les glandes digestives, par deux, forment des circonvolutions et elles entrent dans l'intestin moyen plus postérieurement que celles des gammarides et des caprellides.

REFERENCES

AGRAWAL, V. P., 1964. Functional morphology of the stomach of Caprella linearis (L.). Curr. Sci., **33**: 618-619.

——, 1965. The digestive system of some British amphipods, 3. The alimentary canal. Proc. nation. Acad. Sci. India, (B, biol. Sci.) **34**: 429-458.

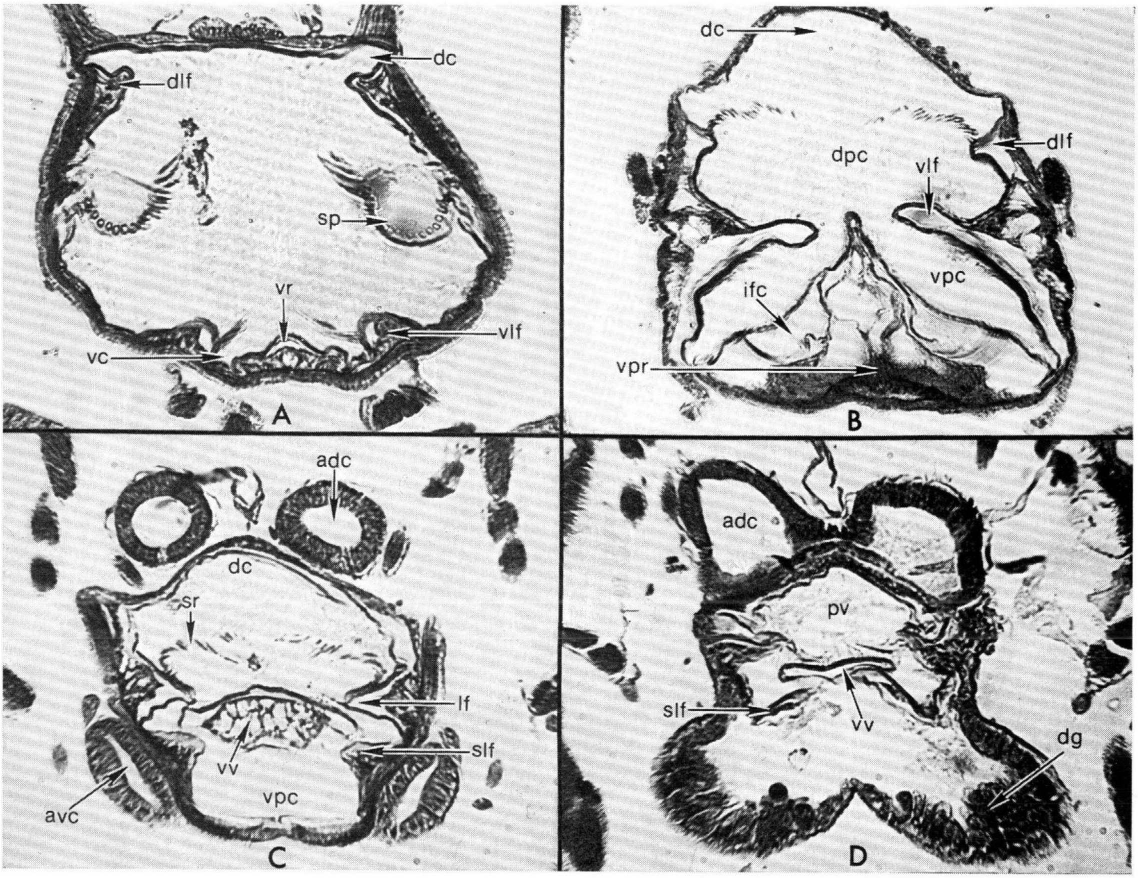
——, 1967a. The feeding appendages and the alimentary canal of Cyamus ovalis (L.). Proc. Symposium on Crustacea, Ernakulam, 549-552.

——, 1967b. The feeding habit and digestive system of Hyperia galba. Proc. Symposium on Crustacea, Ernakulam: 545-548.

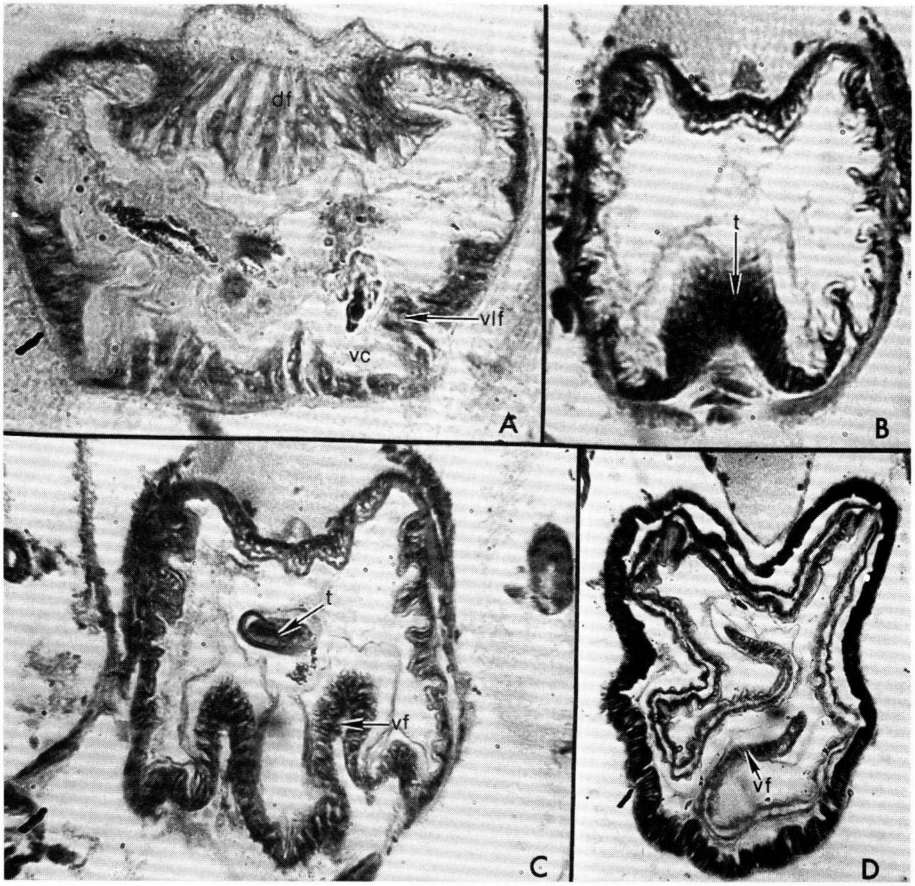
KANNEWORFF, E. & W. NICOLAISEN, 1969. The stomach (fore-gut) of the amphipod, Bathyporeia sarsi Watkin. Ophelia, **6**: 211-229.

MARTIN, A. L., 1964. The alimentary canal of Marinogammarus obtusatus (Crustacea, Amphipoda). Proc. zool. Soc. London, **143** (4): 525-544.

Received for publication 4 February 1972.



The stomach of *Caprella equilibra* Say. A, cross section through the anterior cardiac chamber, × 2070; B, cross section through the middle pyloric region, × 1800; C, cross section through the posterior pyloric chamber, × 1400; D, cross section through stomach at junction of digestive glands, × 1540. adc, anterior dorsal caecum; avc, anterior ventral caecum; dc, dorsal channel; dg, digestive gland; dlf, dorsolateral fold; dpc, dorsal pyloric chamber; ifc, inner filtering channel; lf, lateral fold; pv, pyloric valve (beginning); slf, sublateral fold; sp, spinose papilla; sr, setal ring; vc, ventral channel; vlf, ventrolateral fold; vpc, ventral pyloric chamber; vpr, ventral pyloric ridge; vr, ventral ridge; vv, ventral valve.



The stomach of *Cyamus boopis* Lütken. A, cross section through anterior cardiac chamber, × 4000; B, cross section through anterior pyloric region, × 2250; C, cross section through middle pyloric region, × 2025. D, cross section through posterior pyloric region anterior to digestive glands, × 1350. df, dorsal fold; t, tongue; vc, ventral channel; vf, ventral fold; vlf, ventrolateral fold.