

## COMPARATIVE FUNCTIONAL MORPHOLOGY OF FEEDING IN THREE SPECIES OF CAPRELLIDS (CRUSTACEA, AMPHIPODA) FROM THE NORTHWESTERN FLORIDA GULF COAST

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**Abstract:** The functional morphology of feeding has been investigated in three species of caprellid amphipods. Feeding preferences are correlated with the increased setation and stoutness of the head appendages, the denser the setae the greater the trend toward filter-feeding. It was found that *Caprella penantis* Leach fed primarily by filter-feeding and scraping; *Paracaprella tenuis* Mayer relied on filter-feeding, scraping, scavenging, and predation; and *Luconacia incerta* Mayer depended almost entirely on predatory habits. The observed feeding patterns were verified by stomach content analysis.

### INTRODUCTION

Caprellid amphipods are small marine or brackish water peracarids which occur from the littoral to depths of 4790 m (Laubitz & Mills, 1972), usually clinging to bryozoans, hydroids, sponges, algae, or other organisms (McCain, 1968). They are characterized by a reduced abdomen, a cephalon fused with the first and second thoracic segments, and a reduction or loss of the third and fourth pereopods.

Historically, caprellid literature has emphasized systematics (*e.g.*, Mayer, 1882; McCain, 1968; Laubitz, 1970). The study of the living animals, until recently, has either been published in obscure journals (see Harrison, 1939) or must be gleaned from taxonomic articles which briefly report casual observations. Recent investigators, however, have examined growth (Harrison, 1940), and material on ecology has begun to appear, primarily describing feeding and substratum preferences (Costa, 1960a, b; Saunders, 1965; Keith, 1969, 1971).

A variety of feeding mechanisms have been reported. Lockington (1875), Mayer (1882) and MacKay (1945) stated that caprellids parasitize or eat hydroids, while Green (1963) concluded that the hydroids were utilized solely as a substratum. MacGinitie & MacGinitie (1968) included algae and bryozoans in the "substrate utilization" category of Green. McDougal (1943) reported that caprellids invade hydroid colonies for food and shelter and concluded that while the substratum was eaten to some extent, the major food sources were the diatoms and sessile protozoans occurring in profusion on the hydroid stems which were obtained by scraping; and this was confirmed by Costa (1960b) and by Keith (1969).

Patton (1968) suggested filter-feeding of suspended detritus by the antennae as another method of food acquisition. This was earlier suggested by Saunders (1965) on the basis of her analysis of stomach contents and was verified by Keith (1969).

Harrison (1939) has given the most complete account of the active capture of copepods and other small organisms: the prey is captured by the caprellid with a rapid down-thrust of both antennae and a ventro-medial movement of the second gnathopods. More detailed observations were made by Costa (1960b), and MacGinitie & MacGinitie (1968). Saunders (1965) and Keith (1969) made stomach content analyses on west coast caprellids and both reported primarily detritus, diatoms, and crustacean fragments. Unfortunately, those examinations refer to species different from those whose feeding mechanisms have been studied.

Seven species of caprellids have been reported from the Gulf of Mexico (Steinberg & Dougherty, 1957), but from the area studied here only five species have been reported (Swift, unpubl.). Of these sympatric species, all are relatively euryhaline and also exhibit a tolerance to slow temperature fluctuations. Classically, sympatry has been thought to denote utilization of different micro-habitats, and the possible utilization of different food sources, correlated with the respective appendage morphology has, therefore, been examined.

#### METHODS AND MATERIALS

*Caprella penantis* Leach (Fig. 1), *Paracaprella tenuis* Mayer, (Figs 2, 3) and *Luconacia incerta* Mayer (Fig. 4) were collected from St. Marks Lighthouse, Wakulla County, Florida, westward to Panama City, Bay County, Florida. All suitable substrata were collected and placed in containers with the ambient water, the samples being retained whether caprellids were visibly present or not. Caprellids on which feeding observations were to be made were taken to the laboratory and placed in aerated aquaria with different substrata in separate aquaria. Parts of a substratum, with caprellid inhabitants, were selected at random; the caprellids were identified and the feeding mechanisms observed with the aid of a dissecting microscope.

Animals to be used for analysis of the stomach contents were killed with ethanol upon collection; in the laboratory they were sorted to species, substratum, and collection site. Analyses were made by the method of Saunders (1965) with the addition of fast green to facilitate gross identification of material.

Microscope slides of whole mounts and dissected mouthparts were prepared by first staining the caprellid in fast green and then dissecting away the mouthparts from the cephalon.

Drawings of whole mounts and antennae were made with the aid of a camera lucida mounted on a Wild dissecting microscope. The remainder of the feeding appendages were drawn by tracing the images cast by a microscope slide projector. Additional details were observed with the aid of a compound microscope.

Predaceous food pathways were verified by staining copepods with toluidine blue and then feeding the copepods to the caprellids, which were then dissected and mounted, unstained by any other method. Those parts of the appendages which were stained were considered to have been used in food transport towards the mouth.

differ only slightly in form. The major differences in structure are: 1) the presence or absence of a palp on the mandible; 2) the shape of the endites of the maxillipeds; 3) the relative length of the first and second antennae; and 4) the associated setae of the second antenna. Furthermore, the morphology of the appendages changes only little with growth, being confined to the formation of an indentation in the palmar surface of the propodus of the second gnathopod, to the flagellum of the first antenna, which increases one section with each molt at its proximal end and to the increase in body spination (Harrison, 1940). These changes, except for body spination, are illustrated in Figs 2 and 3.

The first antenna of *Caprella penantis* (Fig. 5) consists of a proximal peduncle of three robust, elongated segments and a distal flagellum composed of a variable number of articles (11 in the largest male observed). The length of each of the flagellar segments is about twice its diameter, and all of the antennal setae are acutely inclined distally.

*Paracaprella tenuis* exhibits a similarly shaped antennule (Fig. 6) (flagellum with nine articles in the largest male observed), except that the setae are longer. The first antenna of *Luconacia incerta* (Fig. 7) is half the diameter of the other two species. The length of each article of the flagellum (11 the maximum observed in the largest male) is about three and a half times its diameter, so that at the same growth stage the first antenna of *Luconacia* is approximately one and a half times the length of those of the other two species.

The second antenna of *Caprella* (Fig. 8), approximately three quarters the length of the first antenna, is characterized by two short proximal segments, three elongated segments, and a short, terminal segment. The third, fourth, and fifth segments have flattened ventral surfaces from which numerous plumose setae (termed swimming setae by Mayer, 1882; Wenzel, 1932) extend. The setae are similar on all three segments, being short proximally and progressively longer distally. The terminal segment is extremely setose, with a pair of specialized spines which form pincers provided with intermeshing serrations.

The second antenna of *Paracaprella* (Fig. 9) is similar to that of *Caprella* in the number of antennal segments. The length is only about one half that of the first antenna and the diameters of the segments decrease progressively from the proximal portion of the appendage to the distal end. The randomly placed setae, usually single, project ventrally from the third to fifth segments; they are one third the length of similarly placed setae in *Caprella*. The third segment also has a distal ring of setae which surrounds the proximal portion of the fourth segment. The sixth segment bears five short apical setae.

As with the first antenna, the second antenna of *Luconacia* (Fig. 10) is half the diameter of the second antenna of the preceding two species. The length is almost two thirds that of the first antenna. The single or paired setae, irregularly dispersed on the ventral portion of segments three and four, are much less dense than in the other two species. On segment five there is only one pair of ventrally located setae.

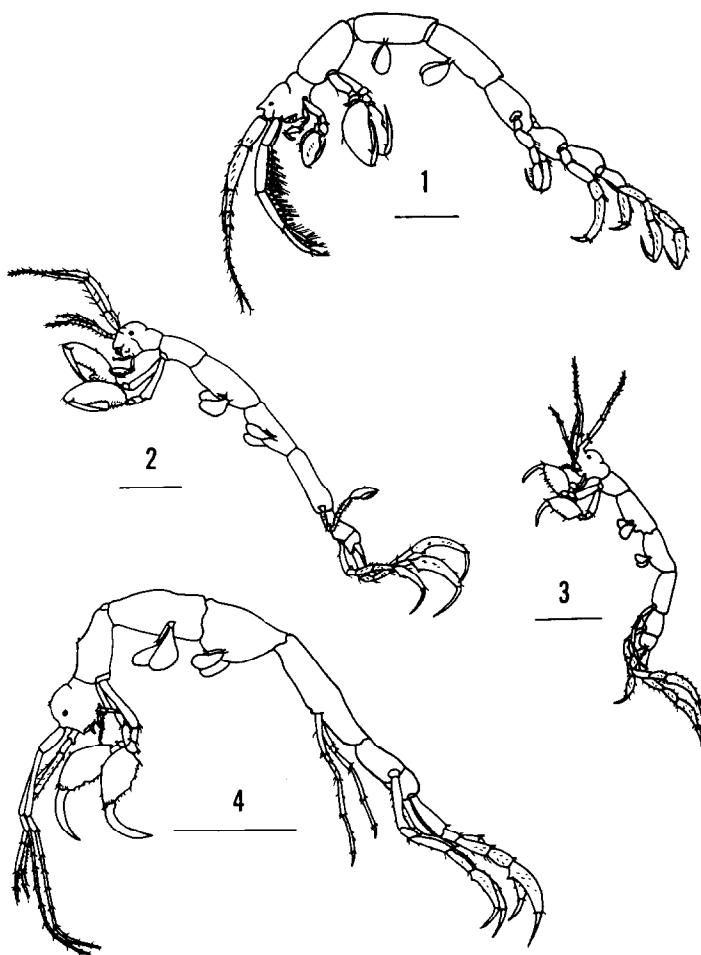


Fig. 1. *Caprella penantis*, adult.

Fig. 2. *Paracaprella tenuis*, adult.

Fig. 3. *Paracaprella tenuis*, juvenile. Note that the only morphological differences from the adult are the lack of an indentation on the palmar surface of the propodus of gnathopod 2 and a smaller number of articles in the flagellum of antenna 1.

Fig. 4. *Luconacia incerta*, adult.

Scale bar: 1 mm

Filter-feeding was similarly verified, using stained starch particles a small amount being placed in the antennal area with a fine pipette.

#### OBSERVATIONS

It is evident from the present observations and those of Calman (1909), McCain (1968), and Laubitz (1970) that the feeding appendages of the Suborder Caprellidea

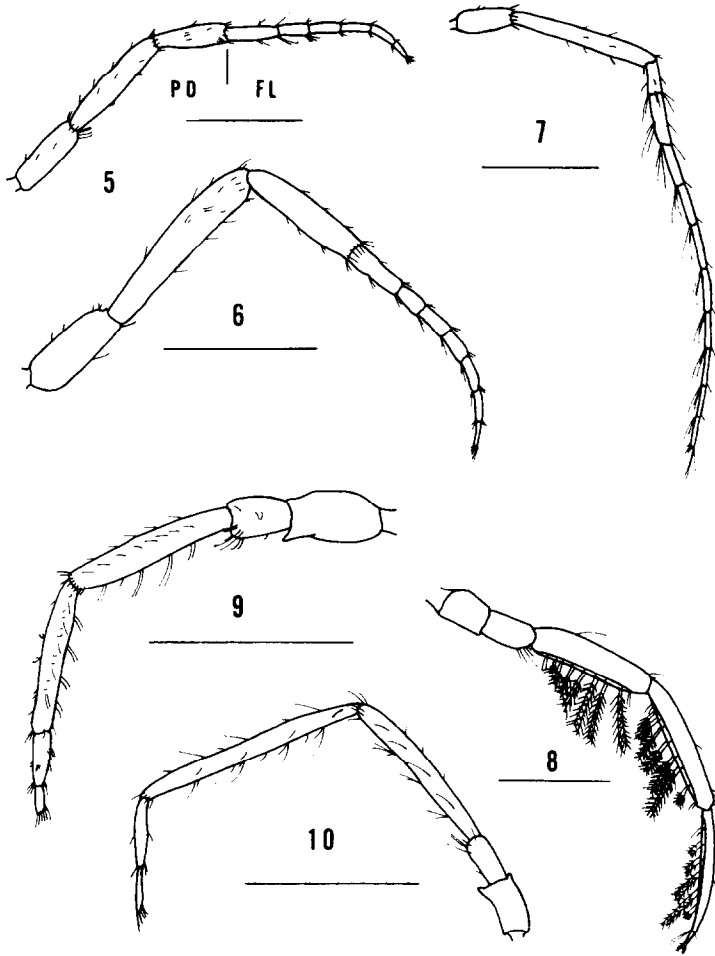


Fig. 5. *Caprella penantis*, antenna 1. Note that it is relatively stout and densely setose. PD, peduncle; FL, flagellum.

Fig. 6. *Paracaprella tenuis*, antenna 1. Note the relative stoutness and the smaller number of setae.

Fig. 7. *Luconacia incerta*, antenna 1. Note relative thinness and a lack of setae.

Fig. 8. *Caprella penantis*, antenna 2. Note relative stoutness and the long plumose setae extending from the flattened, ventral surfaces of articles three to five.

Fig. 9. *Paracaprella tenuis*, antenna 2. Note relative stoutness and the presence of numerous, unspecialized setae.

Fig. 10. *Luconacia incerta*, antenna 2. Note relative thinness and the presence of fewer, but relatively longer, simple setae.

Scale bar: 500  $\mu\text{m}$

The setae on the ventral portion of the antenna are two to three times longer than those on the antenna of the other two species.

The mandible is of major taxonomic importance. It is without a palp in *Caprella* (Fig. 11). Both mandibles have an incisor process and a lacinia mobilis (both five-toothed), and a serrate row of setae, three on the left and two on the right mandible.

A single plumose seta, reported to be located near the molar process by McCain (1968) was never found.

The mandible of *Paracaprella tenuis* (Fig. 12) bears either a rudimentary palp or none at all. When present, it is either one or three segments in length, usually with a single apical seta (the individual illustrated in Fig. 12 had a pair of setae). The incisor is five-toothed on the left mandible and finely serrate on the right; the remainder of both mandibles is as found in *Caprella*.

*Luconacia* (Fig. 13) has a pronounced mandibular palp consisting of three segments. The terminal segment displays a  $1 \times 1$  setal arrangement (one large, (1–10) smaller, and one large). The remainder of the mandible is similar to that of *Paracaprella*.

The first maxilla (Figs 14–16) is five-segmented and is similar on all three species. The fourth and fifth segments comprise a palp, and an endite extends from the base of segment three. The apical spines on the palp of *Caprella* (Fig. 14) are simple, with slight serrations on the bases of the medial spines. The ventral surface of the palp has a double row of simple setae and two ventro-lateral setae, with the latter three times the length of the former. Seven apical spines are present on the endite (E3); they are simple, except for serrations on the distal half of the lateral spines. The medial spines are without serrations.

*Paracaprella* (Fig. 15) has four apical and a single dorso-medial spine on the palp. The endite is without setation, but has either five or six spines. *Luconacia* (Fig. 16) has one lateral and six apical spines (McCain, 1968, reported only three, but his illustration, p. 36, features five). The endite has only four apical setae.

The second maxilla of the three species also shows little variation. It is three-segmented with endites on the second and third segments, forming the inner (E2) and outer (E3) lobes, respectively. The inner lobe is densely setose in *Caprella* (Fig. 17), bears four setae in *Paracaprella* (Fig. 18), and has four to five apical setae in *Luconacia* (Fig. 19). The outer lobe is again densely setose in *Caprella*. In *Paracaprella* there are six apical setae (McCain, 1968, lists four setae), and the number varies from five to six apical setae in *Luconacia*. Only simple setae are present on the second maxilla.

The maxillipeds are a fused pair of appendages. Like the mandibles, they are useful in classification of Gulf Coast caprellids to the generic level. The major variations are: 1) the serrations or setation on the grasping margin of the dactylus; 2) the shape of the inner lobe; and 3) the presence and number of setae on each segment, especially on the endites and the sixth segment.

The maxilliped of *Caprella* (Fig. 20) is characterized by a serrate tip on the pointed distal segment. Segments comprising the palp, excluding the dactylus, are densely setose on the medial margins, with the proximal portion of segment seven encircled by setae extending from the distal end of the sixth segment. Endite three, the outer lobe, is egg-shaped and densely setose, with a row of two to five spines on the medial margins. Endite two, the inner lobe, is almost as large as the outer lobe; the apical portion is setose and angularly flattened descending toward the median plane. The bases of both endites are densely setose, and all setae on the maxilliped are simple.

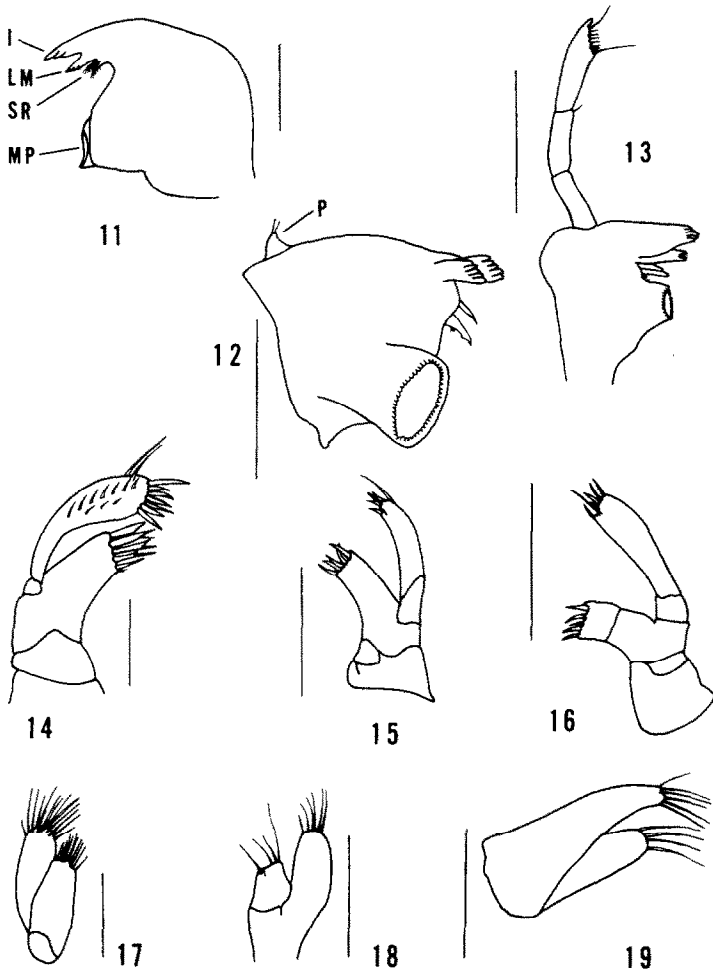


Fig. 11. *Caprella penantis*, right mandible. Note the lack of a palp. I, incisor; LM, laciniam obilis; SR, setal row; MP, molar process.

Fig. 12. *Paracaprella tenuis*, right mandible. Note the reduced palp. P, palp.

Fig. 13. *Luconacia incerta*, right mandible. Note the well developed palp.

Fig. 14. *Caprella penantis*, maxilla 1. Note the setae on the lateral margins of the palp and the numerous spines on the apical end of both the palp and endite three.

Fig. 15. *Paracaprella tenuis*, maxilla 1.

Fig. 16. *Luconacia incerta*, maxilla 1.

Fig. 17. *Caprella penantis*, maxilla 2. Note the density of the setae.

Fig. 18. *Paracaprella tenuis*, maxilla 2. Note the presence of few, short setae.

Fig. 19. *Luconacia incerta*, maxilla 2. Note the sparse, long setae.

Scale bar: 100  $\mu$ m

The dactylus of *Paracaprella* (Fig. 21) is without serrations and bears two to five small setae near the tip (Fig. 22). The palp is covered with setae, as in *Caprella*, but the setae are less numerous. Endite three is flattened apically and without spines, but

displays one or two apical setae and is densely setose on the medial margin. The inner lobe is smaller than the outer lobe and is rounded apically with four to six setae.

The entire grasping margin of the seventh segment of *Luconacia* (Fig. 23) is finely serrate; the palp is sparsely setose, setae being most dense on the medial margins. Endite three bears a single apical seta, and two to five setae on the medial margin. Endite two is smaller than endite three; it displays a pair of simple setae, one on either side of the medial pair of plumose setae arising from the slightly convex, laterally sloping apical end. The tip of the dactylus is tripartate (Fig. 24).

The first gnathopod is a seven-segmented appendage. The second segment, the coxa, is elongated, and the next three segments shorter. The final two segments, the propodus and the dactylus, stand away from the body and allow the appendage to flex in any direction.

In *Caprella* (Fig. 25) a lateral row of five to nine setae is present on the propodus, whose distal end has a ring of setae around the dactylus: the palmar surface is toothed, with short, heavy setae or small spines, and a bifurcate grasping spine on the proximal region. The palmar portion of the dactylus is serrate, with secondary rows of setae and spines on the palmar surfaces.

The propodus of *Paracaprella* (Fig. 26) is more slender than that of *Caprella*. It displays a bifurcate grasping spine, as in *Caprella*, but its proximal portion is stouter than the distal portion. Setation is more sparse than on *Caprella*, except at the distal end of the propodus, from which a row of setae extend. The palmar surface of the propodus is finely spinose and short, stout setae are irregularly spaced on the surface. The dactylus is serrate distally, and finely spinose proximally. At the tip of the dactylus, the serrations are greatly increased in size (Fig. 27).

Among the three species, the propodus is most slender in *Luconacia* (Fig. 28), where it has a simple grasping spine. The palmar surface is toothed and pairs of setae oppose spines present on the dactylus. Four spines are spaced along the palmar surface of the dactylus, and the tip is trifurcate (Fig. 29). The palmar surface of the dactylus is finely serrate for the distal third of its length.

The second gnathopod of *Caprella* (Fig. 30) is stout with variable setation. The palmar surface of the propodus has two distal 'poison teeth', the remainder being without teeth or serrations; however, pairs of setae are spaced immediately lateral to the palmar surface. Except for several serrations on the medial margin, the dactylus is simple with a simple point.

*Paracaprella* has a relatively larger second gnathopod (Fig. 31) than *Caprella*. The palmar surface of the propodus is characterized by an indentation which appears after the seventh molt (number of molts determined by the number of articles on the flagellum of the antennule), and a large 'poison tooth' with a small projection at the proximal end. The space between the 'poison tooth' and the indentation is finely toothed and densely setose; the remainder of the palmar surface has sparse setation. The dactylus is simple without palmar armament.



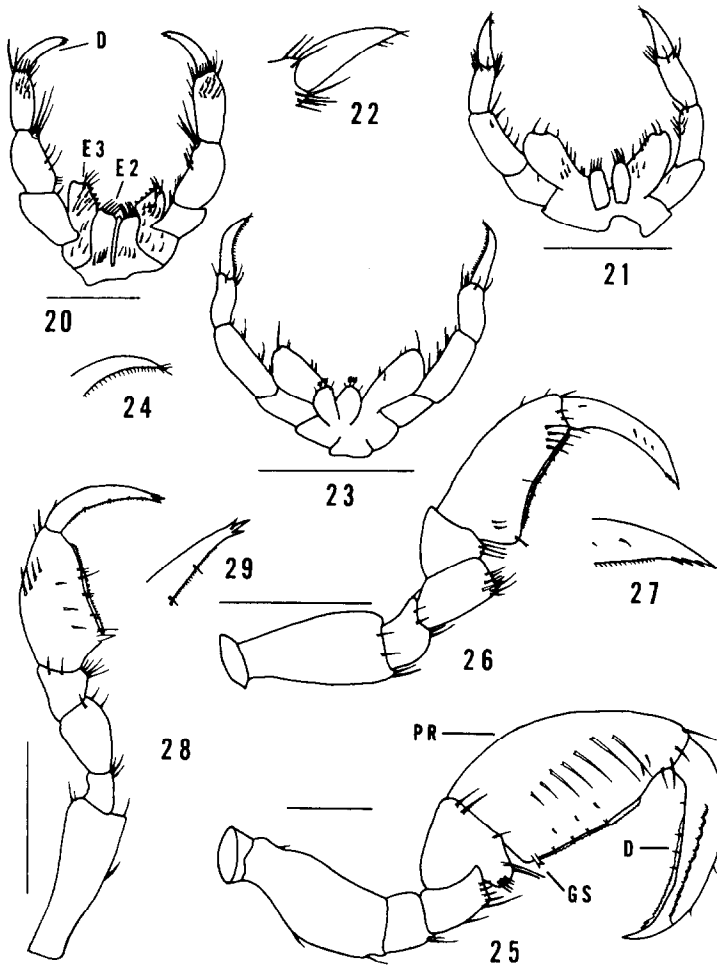


Fig. 20. *Caprella penantis*, maxillipeds. Note the dense setae on the palp and that both endites are with spines and setae. D, dactylus; E2, endite two; E3, endite three.

Fig. 21. *Paracaprella tenuis*, maxillipeds. Note the relative reduction in the number of setae and the lack of spines.

Fig. 22. *Paracaprella tenuis*, enlargement of one dactyli of the maxillipeds. Note setae placement.

Fig. 23. *Luconacia incerta*, maxillipeds. Note the sparseness of the setae and the lack of spines.

Fig. 24. *Luconacia incerta*, enlargement of one dactyli of the maxillipeds. Note setae placement.

Fig. 25. *Caprella penantis*, gnathopod 1. Note the relative stoutness, the serrate tip of the dactylus, and the serrations and spines on the lateral side of the dactylus. D, dactylus; GS, grasping spine;

PR, propodus.

Fig. 26. *Paracaprella tenuis*, gnathopod 1. Note the relative thinness.

Fig. 27. *Paracaprella tenuis*, enlargement of the dactylus of gnathopod 1. Note the serrations at the tip.

Fig. 28. *Luconacia incerta*, gnathopod 1. Note the relative thinness.

Fig. 29. *Luconacia incerta*, enlargement of the dactylus of gnathopod 1. Note the trifurcate tip.

Scale bar: 250  $\mu$ m

The second gnathopod of *Luconacia* (Fig. 32), like that of *Paracaprella* is less stout than the second gnathopod of *Caprella*. The palmar surface of the propodus is superficially similar to that of *Paracaprella*, but the 'poison tooth' is simple; spines are present between the 'poison tooth' and the indentation, and the palmar indentation is present from the sixth molt. The dactylus bears setation on the proximal half of the palmar surface, and the remainder is variably scalloped.

#### FEEDING MECHANISMS

There are four methods of food acquisition: predation, scavenging, scraping, and filter-feeding. Predation is dependent on an abundance of potential prey, usually copepods or similarly sized organisms (2 mm). An upright stance is assumed (Figs 33, 34) with the first and second antennae projected anteriorly and the second gnathopods extended laterally. When the prey swims or is carried by the current between the second gnathopods and the first antenna, a ventral movement of the antennae and a medial movement of the second gnathopods traps the animal and forces it against the pointed dactyli of the maxillipeds. As the prey is captured, it is held by the second gnathopods. From the relative rapidity of death of the captured animal (*e.g.*, cessation of struggling) and the presence of gland type cells at the base of the large palmar tooth, Costa (1960) and others have referred to the spine as the 'poison tooth'. The prey is held by the first gnathopods, primarily by the dactylus, the palmar surface of the propodus and the grasping spine (the grasping spine differs from the 'poison tooth' in that the gland-type cells are absent from its base) and then directed into the oral area by the second gnathopods which push it with the inner lateral part of the propodi. The prey appears to be torn apart by the mandibles and the maxillipeds, the former finely masticating the material before ingestion. Fragments of the prey are held in the oral area by the combined action of the maxillae.

*Caprella* is relatively inactive in its predatory habits. While in an upright stance, a slow dorso-ventral rocking of the body of about thirty degrees may occur (the rocking being inversely proportional to the velocity of the water current) the articulation between the sixth and seventh segments acting as a fulcrum. The antennae and the second gnathopods are immobile relative to the body, but in relation to the habitat they are moving through the water. *Caprella* will occasionally sweep small animals from its body, rather than capture them for food. *Paracaprella* is more active than *Caprella*, but only to the extent that it will bend its body toward the prey instead of remaining passive. It was never observed to fail to attack a suitably-sized organism within its reach. *Luconacia* is much more active than either of the other two species and will actively chase its quarry along the substratum; the second gnathopods grasp the substratum as the caudal portion of the body is moved and the pereopods anchor the amphipod as the cephalic portion of the body is advanced forward. It will not, however, leave the substratum to catch prey.

When a caprellid picked an object or dead animal from the bottom and either

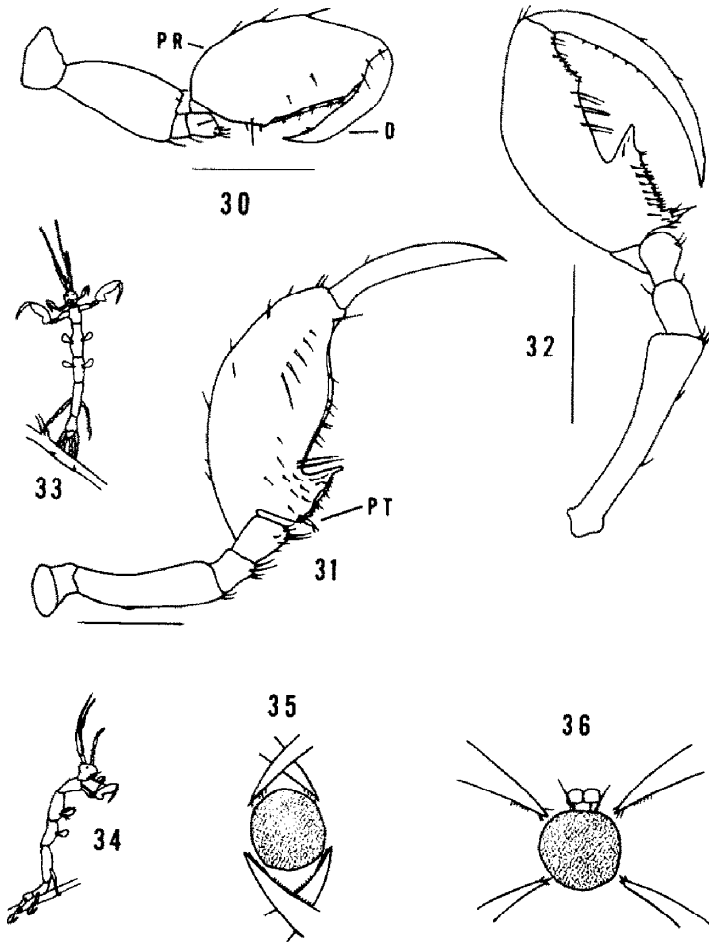


Fig. 30. *Caprella penantis*, gnathopod 2. Note the relative stoutness. D, dactylus; PR, propodus.  
 Fig. 31. *Paracaprella tenuis*, gnathopod 2. Note the setation and the palmar indentation on the propodus.  
 Fig. 32. *Luconacia incerta*, gnathopod 2. Note the palmar indentation on the propodus and the setation and spination.  
 Scale bar: 500  $\mu$ m  
 Fig. 33. *Luconacia incerta*, 11 mm, exemplifying the upright stance, frontal view. Note the anteriorly projected antennae and the laterally extended second gnathopods.  
 Fig. 34. Upright stance, lateral view.  
 Fig. 35. *Paracaprella tenuis*, antennal cleansing.  
 Fig. 36. *Luconacia incerta*, antennal cleansing.

scraped the sessile organisms from it, or ingested it whole, the mode of feeding was classified as scavenging. This form of feeding was not noted in *Caprella*. Both *Paracaprella* and *Luconacia* feed in the same way. An object is picked from the bottom with the second and then grasped by the first gnathopods. The external parts of the

object are then thoroughly scraped for encrusting organisms by the palp and endite of the first maxilla and by the lacinia mobilis and incisor process of the mandibles. After scraping the material several times, the maxillae fold over the mandibles and appear to force the material into the molar region. If the scavenged material is a small organism, and not long dead, the entire organism may be ingested.

The scraping of diatoms and sessile protozoans from the substratum is a third mode of feeding. Occasionally, on substrata such as *Leptogorgia* or algae, the caprellid may bite into the stem while capturing nutritional material, and ingest some of the substratum. When this occurs, the oral area of the caprellid may take on any characteristic colour of the substratum and, if it continues, the entire body of the amphipod may take on this coloration. *Caprella penantis* is a species scraping extensively. The second gnathopods are used to hold the oral area of the amphipod against the substratum by grasping it. A restraining container is formed by the bases and endites of the maxillipeds, the lateral edges of which are formed by the second maxillae and the top by the oral area. The setae of these appendages are in contact with the substratum, and the material is retained as it is loosened. While the animal is in close contact with the substratum, the first maxilla and the lacinia mobilis on the mandibles probably scrape or bite encrusting organisms from it. The molar processes of the mandibles crush diatoms and protozoans. The caprellid usually maintains a stationary position for thirty to forty-five seconds, and the number of encrusting organisms remaining after scraping is slight.

In contrast, *Paracaprella* retains oral contact with the substratum for less than two seconds each time. The manner of scraping is similar to that of *Caprella* but the second gnathopods remain extended laterally and do not hold the amphipod in contact with the substratum. There is no rhythm to the scraping pattern, which may be more appropriately termed 'pecking'. Since the caprellid is not in extended contact with the substratum, the number of encrusting organisms remaining after scraping is relatively large. *Luconacia* scrapes much as does *Paracaprella*, but exhibits the trait less frequently.

Filter-feeding involves the acquisition of suspended material from the water by the antennae, especially the second. A secretion is involved in the process and since the secretion stains purple with toluidine blue, it is presumed to be a mucus. While filtering, the caprellid assumes an upright stance (Figs 33, 34) and either remains motionless, if currents circulate the water, or rocks up to thirty degrees, as *Caprella* does in predation. To cleanse the antennae, *Caprella* brings them ventrally one at a time into the grasp of the second gnathopod. A simple extension of the antennae anteriorly pulls it through the grasp, and the material is transferred to the setae on the palmar surface of the propodus and to the serrations on the palmar surface of the dactylus. The second gnathopod is cleansed by the first gnathopod, primarily by the setal row on the lateral sides of the dactylus (Fig. 25). The first gnathopod is cleansed by the setal ring around the terminal segment of the maxillipeds (Fig. 20), and the material then moved to the tip of the dactylus of the maxilliped by alternately brushing

the palps from the base to the tip. After being formed into a mucous ball the material is passed into the mandibular region by the maxillae. If it can be masticated it is ingested, otherwise it is rejected. The mucus is removed from the mandibles and pulled from the oral region by the dactylus of the maxillipeds. While the rejected material is still on the maxillipeds, alternate brushing of the palps is again used to form a mucous ball on the tip of the dactylus. Rejection is then by an outward sweeping of the maxillipeds. If the material is entrapped by the setal ring around the dactylus, this movement may be repeated until the mucous material is shaken off.

*Paracaprella* follows a similar pattern, except that the material is removed from the antennae solely with the first gnathopods and the maxillipeds. The terminal segments of the appendage pairs are crossed, and a box is formed with the dactylus of the maxillipeds nearer the oral area (Fig. 35). The maxillipeds remove the material from the first gnathopods and the procedure follows that of *Caprella*.

*Luconacia* uses a method more similar to that employed by *Paracaprella* than to that of *Caprella*, and differing from *Paracaprella* in the way the dactylus is utilized in antennal cleansing and in the use of the mandibular palp. The points of the two pairs of dactyli are uncrossed and form the corners of a box. The mandibular palps form the side of the box nearest the oral area (Fig. 36). The setae on the terminal articles of the mandibular palps cleanse the ventral side of the antennae. The cleansing appears to be less effective than that employed by the other two species and it may be repeated up to five times. The palp is cleansed by the setal ring around the dactylus of the maxillipeds.

While the feeding mechanisms employed by the different genera are functionally similar, the extent of utilization of the mechanisms is variable. *Caprella penantis* feeds primarily by scraping and filter-feeding. Analyses of the stomach contents of some 150 animals from varied places and substrata show a predominance of detritus (80 %) and diatoms (15 %+) with a few crustacean fragments. *Paracaprella tenuis* lacks feeding preferences and appears to utilize the most abundant food material in its micro-habitat. Detritus was the major constituent of stomachs (80 %), followed by diatoms (10 %) and crustacean fragments. Predation is the principle feeding activity of *Luconacia incerta*, but scavenging is frequent. Rarely, and only in the absence of suitable prey, *Luconacia* relies on filter-feeding or scraping to obtain food. Stomach

TABLE I

Feeding preferences of the respective species of caprellids in the presence of abundant food material of all experimental categories: ++ method in > 40 % of feeding observations; + method in 15-40 % of the feeding observations; - method in < 15 % of the feeding observations; 0 not noted as used.

	<i>Caprella</i>	<i>Paracaprella</i>	<i>Luconacia</i>
Filter-feeding	++	+	-
Scraping	++	+	-
Predation	-	+	++
Scavenging	0	+	++

contents were found to contain detritus (80 %) and crustacean fragments (10 %+) with a few diatoms.

Feeding methods and preferences, as determined by observations of caprellids with abundant food sources of all types, are depicted in Table I.

#### DISCUSSION

Feeding preferences of caprellids are directly correlated with the morphological variations of the head appendages. The first antenna functions primarily in the capture of motile prey. The relative length of the antenna is a reflection of the emphasis on predatory habits; since the antenna also functions as a sensory receptor, the lack of feeding modifications, except for length, may be expected. Setae on the second antenna reflect more filter-feeding. Caprellids with 'swimming setae' on the appendages gather food primarily by filtration. Those species without such setae may also filter-feed, but simple setae are not so efficient, and supplementary means of obtaining food are required.

The relation of the mandibles to feeding habits is less clear; the variability of the mandibles relates to the palp in the species being considered. The palp is not necessarily a feeding structure and its gradual loss may represent a trend within the Suborder away from a predatory type of existence to a filtering one, so that the presence of a mandibular palp would be indicative of a form morphologically more similar to the ancestral stock and not a necessity for a predatory existence. A study of *Tritella*, a west coast genus with a mandibular palp but also with swimming setae (Laubitz, 1970), and *Hemiaegina*, a circumtropical, monotypic genus without either a mandibular palp or swimming setae (McCain, 1968), would aid in understanding this relationship.

The first maxilla exhibits only slight variations among the species, the only significant morphological difference being the setae on the palp. These setae probably compliment the second maxilla in holding small particles in the mandibular region. The setae on the second maxilla are important mainly in the restraining chamber formed while scraping, although they also function in filter-feeding. Species which lack numerous setae do relatively little scraping.

Numerous setae and spines on the endites and the palp of the maxilliped again reflect an emphasis on filter-feeding and scraping. Filter-feeding is closely allied to the setae on the palp. Dense setae near the terminal segment are utilized in the formation of the mucous balls with entrapped detritus which are passed to the mandibles. Scraping habits are correlated with the density of setae on the endites; the setae forming an integral part of the restraining container.

The first gnathopods are also difficult to relate to feeding preferences. There is a relative trend toward stoutness and increased setation on the lateral surfaces of the dactylus from *Luconacia* to *Caprella*, but to relate these variations to one type of feeding is not warranted. A correlation may, however, be drawn from the grasping

spine. The more predatory species tend to have a simple grasping spine on the palmar surface, while those which rely on scraping tend to have a bi- or trifurcate spine.

The relative size of the second gnathopods is correlated with the degree of emphasis on predation. As with the first antenna, increased length enables the caprellid to capture prey over a greater area. The reduction in length and increased stoutness of the second gnathopod is related to the emphasis on scraping and the grasping of the substratum.

Of the species studied, *Luconacia incerta* relies almost exclusively on predatory habits to obtain food. This is correlated with the greater relative length of the first antenna and the second gnathopods, the primary raptorial appendages, and a general sparsity of setae on the other feeding appendages. Long antennae and long second gnathopods imply a greater area of successful prey capture, while the slenderness of these appendages would reduce the resistance to rapid movement. Dense setae would tend to increase resistance, slow the capture movement, and thus make prey difficult to capture. *Luconacia* is almost without setae on the endites of the maxillipeds and thus lacks a scraping type of feeding mechanism. The setation of the palp, however, is not radically different from that of the other two species, and this may indicate that *Luconacia* relies on filter-feeding more than was apparent from my observations, or that filter-feeding is merely a modification of antennal cleansing. If the latter is the case, as I suspect, the presence of such setae is not surprising. *Caprella penantis* depends primarily on filter-feeding and scraping. The elongated, plumose swimming setae on the second antenna function as the primary filtering structures aided by a mucus secretion. Most of the suspended detritus is entrapped as the antennae are swept through the water by the dorso-ventral rocking of the body. Since a water current is required to ensure contact with floating detritus, the rocking motion is probably not primarily concerned with predation, but prey is opportunistically captured while *Caprella* is filter-feeding. When scraping, *Caprella* remains in oral contact with the substratum for extended periods of time, and the quantity of material dislodged is probably more than can be held by the mandibles alone. The restraining container aids in the retention of the loosened organisms in the oral region. The dense setae on the apical ends of the maxilla are in contact with the substratum, and those on the base of the palp and on the endites of the maxillipeds create barriers posteriorly. The feeding appendages of *Paracaprella* are intermediate between the short, stout, densely setose appendages of *Caprella*, and the slender, elongated, sparsely setose appendages of *Luconacia*. *Paracaprella* may be considered generalized with regard to its feeding appendages, so that it is therefore not surprising that *Paracaprella* has no feeding preferences.

In the face of the morphological differences and corresponding feeding preferences the close similarities in stomach contents may be surprising. The well-developed molar processes on the mandibles often masticate hard materials such as diatom shells and crustacean exoskeletons beyond recognition and soft parts were never found

intact: this would tend to increase the percentage of material classified as detritus found in the stomachs. The feeding preferences are more accurately evaluated by studying the second most common constituent of the stomach (diatoms in *Caprella* and *Paracaprella*, and crustacean fragments in *Luconacia*).

#### ACKNOWLEDGEMENTS

I would like to thank Dr C. R. Stasek, whose comments and criticisms aided and added to this paper, and without whose help this paper would not have been possible.

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