Structure of mouthparts and feeding habits of
Potamanthus luteus (LINNÉ)
(Ephemeroptera: Potamanthidae)

By C. ELPERS and I. TOMKA
University of Fribourg, Switzerland

With 10 figures in the text

Abstract

Feeding behaviour and morphology of the mouthparts of larvae of *Potamanthus luteus* (Potamanthidae) have been investigated. The results indicate that larvae of *P. luteus* mainly gather food by raking movements of prothoracic legs and labial and maxillary palps. Nevertheless the larvae have the capability of filter-feeding movements, although filter-feeding behaviour was less frequently observed. According to the results, the larvae of *P. luteus* have to be classified into the "collector-gatherer" functional feeding group with filter feeding capability. The feeding behaviour reveals a close relationship of *P. luteus* to *Ephemerella needhami* (Ephemerellidae), rather than to *Antopothamus verticis*, another Potamanthidae.

Introduction

Macroinvertebrates are classified into functional feeding groups (FFG) by several authors (e. g. MERRITT et al. 1984, CUMMINS & KLUG 1979, McSHAFFREY & McCAFFERTY 1988). Classification of mayfly larvae into functional feeding groups has been done mainly on the basis of investigations observing feeding habits of larvae without the possibility of film or video documentation (e. g. BROWN 1961; FROEHLICH 1964; SOLDAN 1979; STRENGER 1979, 1975, 1970, 1953; WALLACE & O'HOP 1979; WISELY 1962). Videomacroscopical techniques give the opportunity for a more detailed analysis of the behaviour and feeding movements of the larvae of macroinvertebrates (McSHAFFREY & McCAFFERTY 1991). Observations of feeding behaviour on the basis of videomacroscopy have been done on larvae of several mayfly species (ELPERS & TOMKA 1992; McCAFFERTY & BAE 1992; CRAIG 1990; SOLUK & CRAIG 1990, 1988; McSHAFFREY & McCAFFERTY 1990, 1988, 1986; BRAIMAH 1987a, b). The combination of videomacroscopy of the feeding behaviour, scanning electron microscopy (SEM) of the mouthparts and the analysis of the

ingested food thus presents the information necessary for a correct FFG classification.

The family Potamanthidae is a member of the family group Ephemeroidea (EDMUNDS & TRAVER 1954), the members of which are burrowing or sprawling mayflies (McCAFFERTY 1975) and feed as filter feeders or sediment feeders in more or less well established burrows (e. g. BIDWELL 1979; GOBAS et al. 1989; HARTLAND-ROWE 1953; LADLE & RADKE 1990; NOLTE 1987; OTTO & SVENSSON 1981; SATTLER 1967). CUMMINS et al. (1984) and MUNN & KING (1987) placed the potamanthid larvae into the FFG "detritivore collectors/gatherers". McCAFFERTY & BAE (1992) made the first detailed study on the feeding behaviour of a potamanthid larva using videomacroscopy, the eastern North American *Anthopotamus verticis*. The results of their investigations indicate that larvae of *A. verticis* have to be classified into the FFG "filter feeders". Until now limited information was available on the feeding behaviour of larvae of *Potamanthus luteus* (Potamanthidae), thus making the classification into one of the FFGs very difficult and speculative. Our study of *Potamanthus luteus*, a species of the Old World genus *Potamanthus* (Potamanthidae), gives the possibility to compare the feeding habits of species of two genera of the same family, distributed on different continents.

Methods

The larvae of *Potamanthus luteus* were sampled from March to July 1992 in the river Rhine near Stein am Rhein, Switzerland. At the collection site the river is about 100 meters wide. The larvae were found at different distances from the river bank, depending on the larval stage. Small larvae, found in March to May, were collected among small "islands" consisting of stones (>15 cm diameter) on a sandy substrate. This substrate was covered with broken shells of *Dreissena polymorpha*. Nearly all of the stones where covered with green algae (cf. *Cladophora* sp.). The water depth at these sites was 50–70 cm and the water had a current velocity of about 1.5 m/s; current speed was estimated by the method of drifting bodys (SCHWOERBEL 1986). The older larval stages, found in June and July, were mostly collected beneath stones (6–16 cm in diameter) near the river banks at a water depth of 10–40 cm and a current velocity of 0.5–0.7 m/s. The stones at this site built a layer on the sandy substrate; particulate organic material (POM) was found among the stones. Detailed information on particle size distribution of substrate, and colonization of benthic invertebrate fauna at the collection site is given by REY et al. (1992).

Several larvae were preserved in ethanol (80%) for examination of the structure of mouthparts and in formol (4%) for gut content analysis by light and scanning electron microscopy. About 100 larvae were collected alive for detailed analysis of feeding behaviour and mouthpart movements.

Living larvae were held in an artificial channel (ELPERS & TOMKA 1992). Water was circulated by a pump at a temperature of 17° ± 1 °C. The last meter of the channel was filled with substrate from the collection site, including some algae covered stones and fine material; light was provided by computer controlled fluorescent lamps for 12 h; dusk and dawn were simulated for 30 minutes each.

The observational methods used for investigations of the feeding habits of *Oligoneuriella rhenana* (ELPERS & TOMKA 1992) were applied in this study: a Panasonic NV-180

videorecorder, a SONY high resolution AVD-C7 videocamera in combination with (I) extension tubes and videolenses or (II) a microscope. Feeding of the larvae was observed using two techniques: (a) examination of the feeding behaviour through the glass bottom of the artificial channel by camera and extension tubes; (b) detailed observation of the mouthpart movements under microscope while the larvae were situated in a flow cell (ELPERS & TOMKA 1992; modified for *P. luteus*). In both cases (a + b) suspended particles were introduced into the water pumped through the observational chambers, simultaneously algal threads and different sized particulate organic material (POM) were presented.

Feeding behaviour of 25 larvae were observed; about 40 feeding sessions of 13 larvae were analyzed in detail (slow motion, single frame), each of these sessions consisted of multiple feeding cycles, ranging from about 10 cycles to more than 80 cycles.

For scanning electron microscopy the mouthparts or the whole head were sonicated for 30 seconds; some were left without sonification to keep food particles in original position. The mouthparts were critical point dried and platinum coated. The prepared parts were then examined in a Hitachi S-700 SEM.

Designation of the mouthparts follows the proposals given by ARENS (1990, 1989) and BROWN (1961). In the anatomical descriptions the terms posterior and anterior are used in the relation to the posterior and anterior poles of the longitudinal axis of either the animals or the mouthparts.

Results

Morphology of the mouthparts

Figure 1 shows the fronto-ventral (a) and lateral (b) view of the head and the mouthparts of the prognatheous larva of *Potamanthus luteus* in the resting position. The preoral cavity is shielded ventrally by the labium and dorsally by the head capsule and parts of the mandibles.
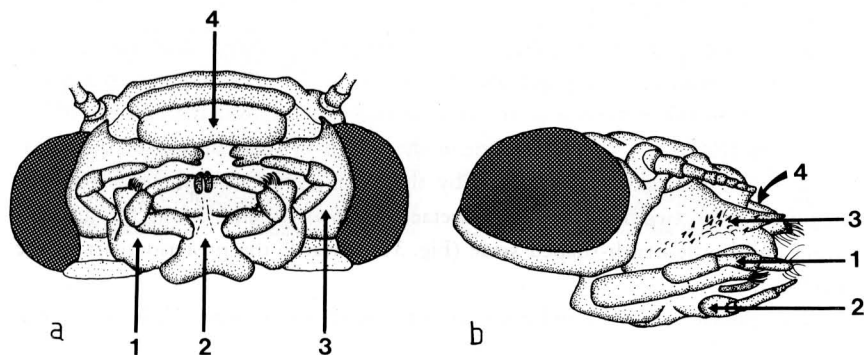

Fig. 1. Larval head of *Potamanthus luteus*. a: fronto-ventral view, b: lateral view [maxilla (1), labium (2), mandible (3), labrum (4)].

Prothoracic leg

The dorsal side of the prothoracic leg is covered with short setae; a curved row of longer setae is present near the hind margin of the femur. Some long setae are sparsely distributed at the dorsal side of tibia and tarsus (Fig. 2a). The ventral side of the prothoracic leg bears short, stout setae (Fig. 2b). Ventral and dorsal side of the femur, tibia and tarsus are covered by dense small hairlike but cuticular structures which may serve to enlarge the surface and ensure that food particles can be fixed more easily between the prothoracic legs (Figs. 2e, f). The outer margin of the femur and the inner margins of the femur, tibia and tarsus each bear longer setae (Figs. 2a, b), those of the tarsus are interspersed with short, stout setae (Fig. 2d). Longer setae are distributed more densely along the inner margin of the tibia (Fig. 2c). The longer setae at the inner margin of the prothoracic leg, mainly those of the prothoracic tibia are the main food gathering tools when the larva feeds on small particles raked towards the mouth by movements of the prothoracic legs and during filter feeding, where they serve as filtering tools (Figs. 2a,b,c). The short, stout setae at the inner margin of the tarsus (Fig. 2d) may function as kind of hooks to fix coarse particles between the two protoracic legs during feeding (see "Feeding movements: coarse particles").

Labium

The labial palps consist of three segments of nearly equal length. The first segment is broadened and slightly longer than the second and third ones (Fig. 3a). Short setae are sparsely distributed on the surfaces of the first and second segments, mainly found along the outer edges whereas the terminal segment bears long setae at its distal end (Figs. 3a, b). These setae catch particles which are loosened during the activity of the galealacinia or the mandibles (see: Feeding movements) and transport them to the paraglossae.

The paraglossae are laterally broadened and much larger than the glossae; the dorsal surfaces of the paraglossae are covered with setae bearing two rows of microtrichae to the setal shaft (3d), and pointing to the longitudinal axis of the mouthparts (Fig. 3b). Particles caught in the bunch of setae on top of the galealacinia (Fig. 4) are taken over in part by these setae. The ventral surfaces of the paraglossae bear two kinds of setae: setae as shown in Fig. 3d at the anterior margin and bottle-brush-shaped setae (Fig. 3c) towards the posterior part of the paraglossa.

The glossae are small and covered with short, stout setae. Their transversal axis is perpendicular to the transversal axis of the paraglossae.

The praementum is flexible in its connection to the postmentum and can be retracted; a ventrad tilting of the labium is possible as well.
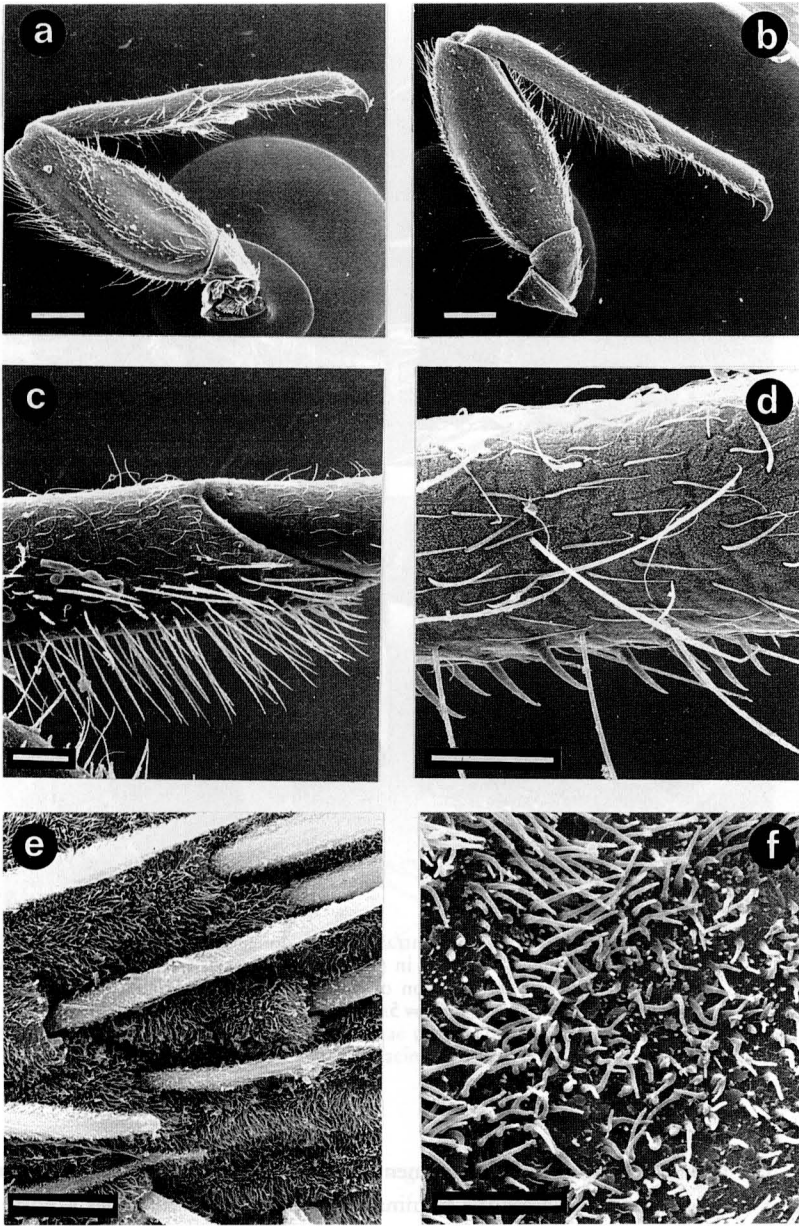
Fig. 2. Prothoracic leg of *Potamanthus luteus*. a: dorsal view; b: ventral view; c: setae at the inner margin of the tibia; d: short, stout setae at the inner margin of the tarsus; e: hairlike cuticular structure on the surface of the tibia; f: detail of the structure shown in (e) (scale: a, b = 500 μm; c = 50 μm; d = 250 μm; e = 25 μm; f = 5 μm).
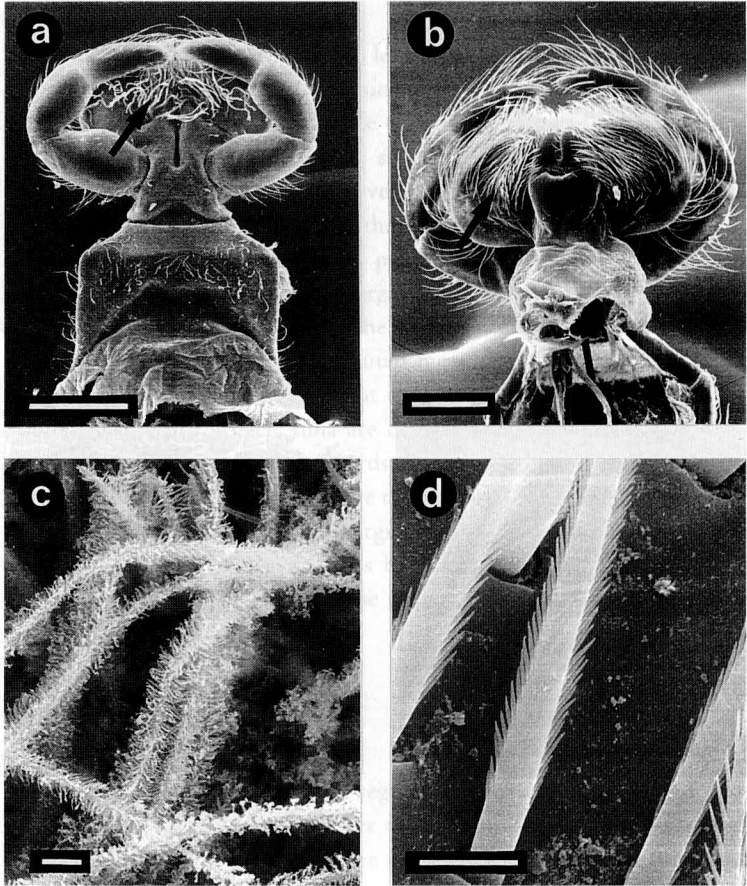
Fig. 3. Labium of *Potamanthus luteus*. a: ventral view; b: dorsal view; c: setae on the ventral side; d: setae on the dorsal side. The arrow in (a) indicates the position of the setae shown in (c), the arrow in (b) indicates the position of setae shown in (d) (scale: a, b = 250 μm; c, d = 5 μm).

Maxillae

The maxillary palps are three-segmented. The first and second segments are nearly equal in length, whereas the terminal segment is up to 1.5 times as long as the first segment (Fig. 4a). The ventral surfaces of the second and third segments bear some short setae; additionally some long, microtrichae covered setae are distributed on the ventral surface of the third segment (Fig. 4a). A few setae are situated along the outer edge of the segments. Besides some long setae on the second segment, the dorsal surface of the first and second segment of the palps is nearly setaeless; the dorsal surface and the tip of the third segment bear long micro-
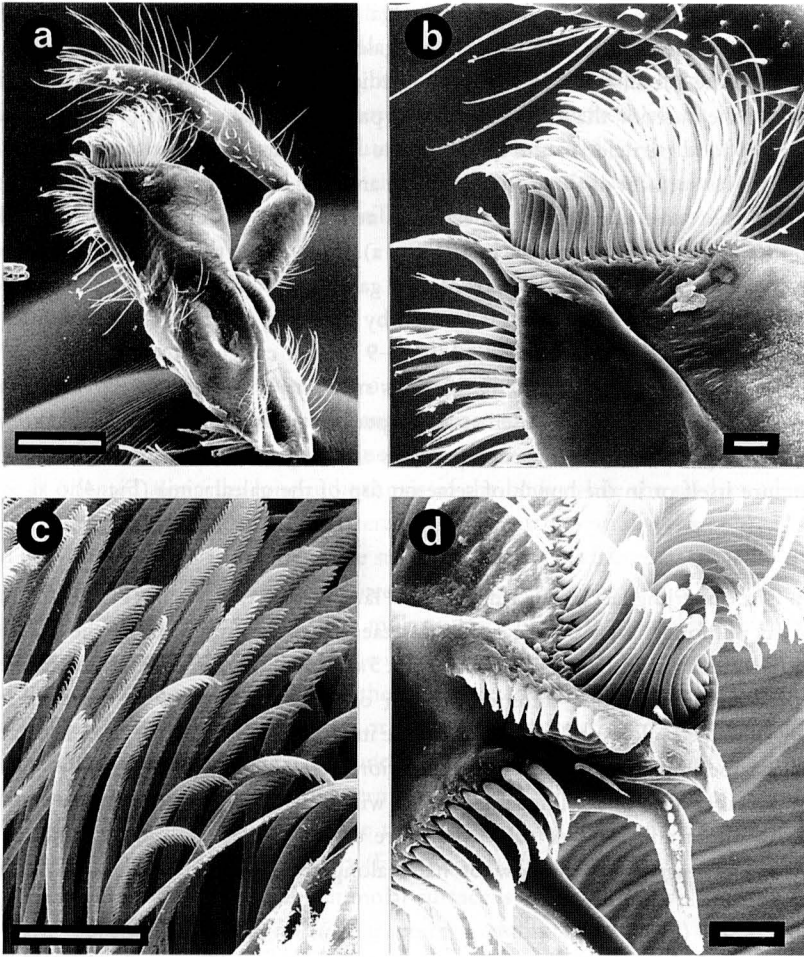
Fig. 4. Left maxilla of *Potamanthus luteus*. a: ventral overview; b: top of the ventral side of the galealacinia; c: setae of the bunch of setae on top of the galealacinia; d: ventro-median view of the rake at the top of the galealacinia (scale: a = 250 μm; b, c, d = 25 μm).

trichae covered setae. Setae of the third segment of the maxillary palp (Fig. 4 a) take over food particles caught in the setae of the prothoracic legs during the raking movement of the prothoracic legs or the filter feeding movements of the larvae.

The galealacinia of *P. luteus* is a highly structured part of the maxilla (Figs. 4 b, d). Although fused, the galea and lacinia are to be differentiated by a groove. The top of the galea is covered with a dense tuft of inward bent, microtrichae covered setae (Fig. 4 c); they decrease in length towards the median edge of the galea (Figs. 4 b, d). These setae act as filtering setae or net in which particles

are caught that had been loosened from algal threads or coarse particles by action of the excavator-like structure of the galealacinia (Figs. 4b, d). Microtrichae covered setae are distributed along the median edge of the lacinia and are more dense at the anterior than at the posterior part of the galealacinia (Fig. 4a). They transport food particles to the lingua of the hypopharynx and push them further to the molar surfaces of the mandibles. The anterior part of the galealacinia is tilted towards the outer edge of the galealacinia at a degree of 30−35°, relative to the longitudinal axis of the galealacinia (Fig. 4a). Two long, thick spinous processes are situated along the tilted part of the galealacinia (Figs. 4b, d). The medio-anterior edge of the galealacinia is formed by three big cuticular teeth which form an excavator-like structure, followed by 8−9 smaller cuticular teeth on the ventral surface of the galealacinia (Figs. 4b, d). This structure is the most effective scraping tool with which the larvae loosen attached periphytes and POM from algal threads and coarse particles. The loosened particles are caught either in the excavator-like structure itself or in the bunch of setae on top of the galealacinia (Fig. 4).

Hypopharynx

The superlinguae are broadened and larger than the lingua (Fig. 5a). Long inward pointing, microtrichae covered setae are to be found along the anterior and inner margin of the superlinguae (Fig. 5a). Some fine, long setae are sparsely distributed on the dorso-anterior portion of the superlinguae. A more or less triangle-shaped pilose pad extends along the inner medial part on the dorsal surfaces of the superlinguae (Fig. 5b). The posterior edge terminates in a row of hairs. The dorsal surface of the lingua is covered with a dense hairy pad which is divided into an upper and a lower part by a more or less horizontal groove. The hairy pad of the lingua and the row of hairs along the posterior margin of the left
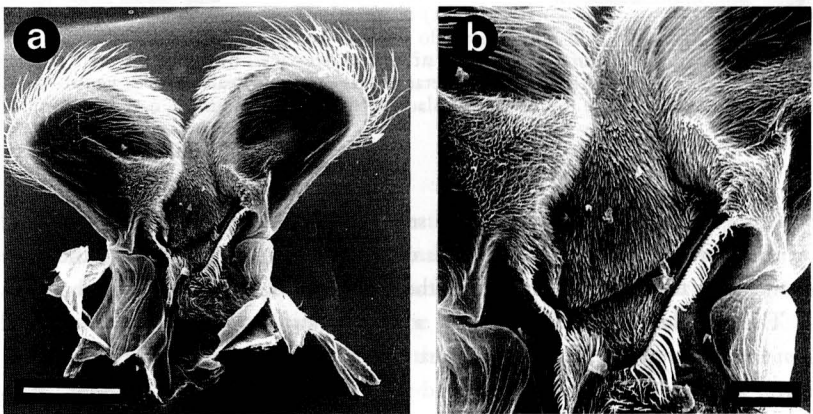

Fig. 5. Hypopharynx of *Potamanthus luteus,* dorsal view (scale: a = 250 μm, b = 50 μm).

superlingua terminate in a proximal, sharply pointed hairy brush (Fig. 5 b). During the inward movement of the maxilla the setae along the inner margin of the galealacinia push material that is caught in the setae of the superlinguae onto the pilose pad of the lingua and further towards the molar surfaces of the mandibles. When the maxilla swings laterally outwards the pilose pad of the lingua retains material caught in the setae at the inner margin of the galealacinia while the setae of the superlinguae retain particles still caught in the bunch of setae on top of the galealacinia.

Mandibles

The body of the mandibles can roughly be divided into two parts; the lateral edge which includes the articulation and the base of the mandibular tusk and the median edge which includes the canines, prosteca and molar surface. The lateral edge is oriented along the longitudinal axis of the body while the median edge is more or less perpendicular to the lateral edge, directed ventrally (Fig. 6 a). Right and left mandibles are asymetric in the structure of their median parts (Figs. 6 c, 6 d).

The most obvious difference between left and right mandible is given by the orientation of the molar surface. The molar surface of the left mandible resembles a flat, oval dish which is situated at the inner edge of the distal mandibular portion and follows the longitudinal axis of the mandible (Fig. 6 d). The molar surface is studded with ridges which run more or less transverse relative to the longitudinal axis of the mandible (Fig. 6 d). The molar surface of the right mandible is more oval shaped than the left one and terminates in a flexible broom-like structure. The surface is oriented parallel to the transverse axis of the mandible, the ridges decrease in size towards the pharynx (Figs. 6 c, 7 a).

Each ridge of the left and right molar surface is divided into two "subridges": a "hard" subridge, showing no fine structure (possibly worn down) and a "soft" subridge, consisting of a brush-like cuticular structure (Figs. 6 c, 6 d, 7 a, c, d). The soft, brush-like subridges of the right molar surface always form the outer-lateral part of each ridge (Fig. 7 a) whereas the soft, brush-like subridge of the left molar surface builds the lower part of each ridge (Fig. 6 d). The hard subridge probably serves as a structure to crush food particles like periphyton and algal filaments whereas the soft subridge serves simultaneously as a structure to strain off water and to "roughen" the surface of the mola so that particles are not squeezed out of the mandibles while they are pressed together.

The outer and inner canines of the left mandible (Fig. 6 d) each consist of three teeth. The inner canine bears along its lateral teeth a row of setae. The prosteca articulates at the base of the inner canine, consisting of two teeth; the base of the prosteca is covered with short setae, and a bunch of long setae is situated at the distal part of the prosteca (Fig. 6 d). The outer canine of the right mandible (Fig. 6 c) is equivalent to the canine of the left mandible whereas the inner canine
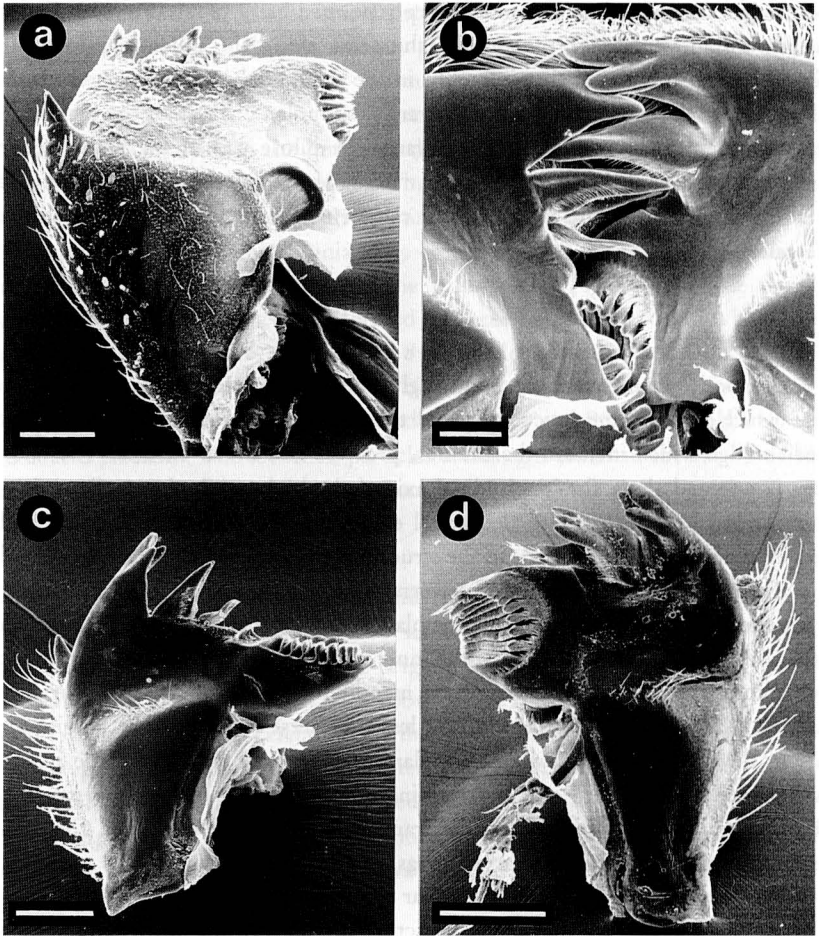
Fig. 6. Mandibles of *Potamanthus luteus*. a: left mandible, dorsal view; b: ventral view of left and right mandible in a resting position, inner and outer canines fit perfectly together; c: right mandible, ventral side; d: left mandible, ventral side (scale: a, b = 100 μm; c, d = 250 μm).

of the right mandible terminates in only two teeth (Fig. 7a). The prosteca on the right mandible is smaller than that on the left one and terminates in one sharp and one rounded tooth. The prosteca of the left and right mandible probably transport food particles further to the molar surfaces. When the mandibles close, the prosteca of the left mandible moves along the inner surface of the inner canine collecting food particles found there and simultaneously wipes across the setae of the ventral surface of the labrum. The prosteca of the right mandible may act in a similar way and transport food particles along the dorsal surface of the lingua or the super-
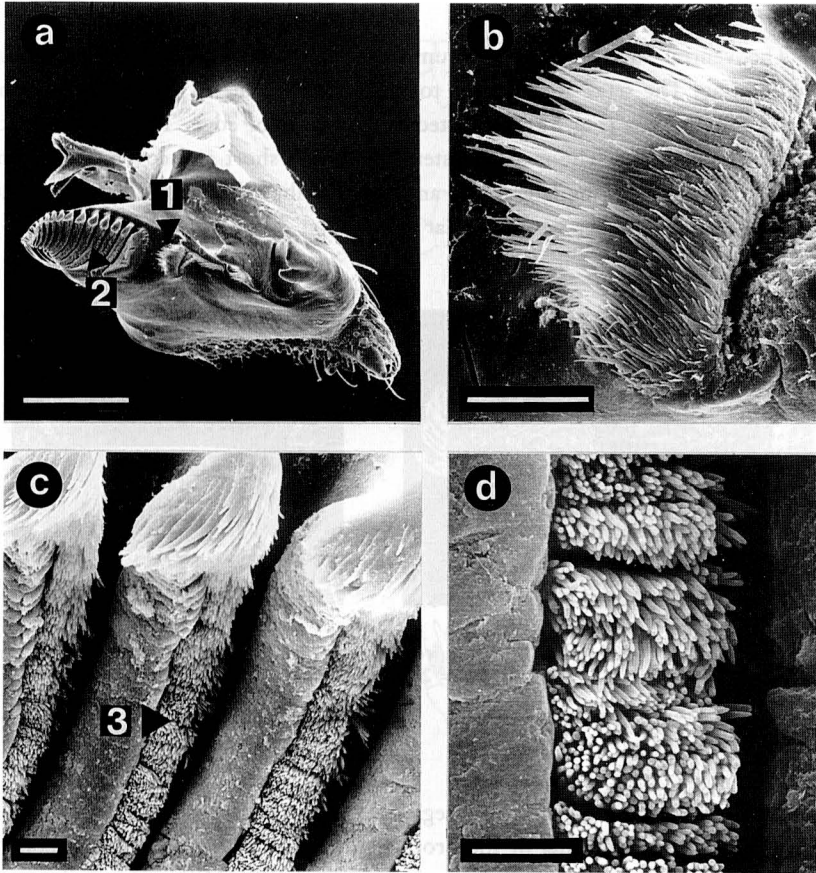
Fig. 7. Right mandible of *Potamanthus luteus*. a: top view of the molar surface, prosteca and canines; b (= enlargement of position 1 shown in Fig. 7a): cuticular barrier structure between molar surface and prostheca; c (= enlargement of position 2 shown in Fig. 7a): ridges of the molar surface; d (= enlargement of position 3 shown in Fig. 7c): cuticular broom-like subridge (scale: a = 250 µm; b = 25 µm; c, d = 5 µm).

linguae, although the right prosteca is smaller than the left one. A brush-like structure arises halfway between the prosteca and the molar surface of the right mandible (Figs. 7a, b). The brush is tilted towards the molar surface, consisting of fine, hairlike but cuticular structures (Fig. 7b).

The teeth of the outer canine of the left mandible fit perfectly into recesses of the outer edge of the outer right mandibular canines (Fig. 6b). They serve as food gathering structures as described in the feeding movements and as guiding structures to ensure an effective and safe closing of the mandibular surfaces.

Labrum

The ventral surface of the labrum bears two fields of long, microtrichae covered setae. The setae are oriented towards the median. A pilose pad pointing towards the pharynx (Fig. 8 a) is situated at the posterior edge. The dorsal surface is covered with setae. The medio-posterior ones are short and covered with fine microtrichae, whereas the lateral and anterior distributed setae are long and bear two rows of microtrichae perpendicular to the setal shaft (Fig. 8 b).
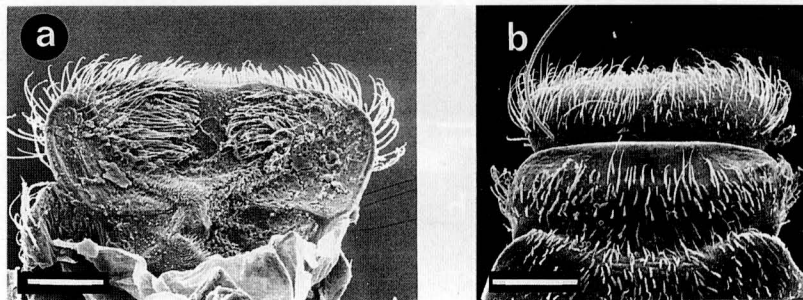

Fig. 8. Labrum of *Potamanthus luteus*. a: ventral view; b: dorsal view (scale: a = 100 μm; b = 250 μm).

Feeding movements

Two general food gathering strategies have been observed:
– mainly raking movements of the prothoracic legs and the labial and maxillary palps in order to gather particulate organic material (POM) from the substrate.
– additionally filtering of suspended particles by in- and outward movements of the prothoracic legs, exposing them to the current.

Raking process

The most dominant feeding activity observed was harvesting food particles by raking movements of the prothoracic legs and the labial and maxillary palps. The prothoracic legs are stretched out laterally, the femora then move anterior while the tibiae bent inward. Material which is in reach of the prothoracic legs is raked towards the mouthparts. In addition the maxillary palps transport food towards the mouthparts, the palps functioning like a pair of forceps while the labial palps move alternately in- and outward in order to obtain and transport food towards the preoral cavity. Nevertheless the raking movement of the prothoracic legs is the most effective food gathering process. Food processing is mainly performed by a periodic circular movement of the maxillae, consisting of the phases shown in Fig. 9 A–D. This periodic maxillary cycle takes about 0.8 seconds time.
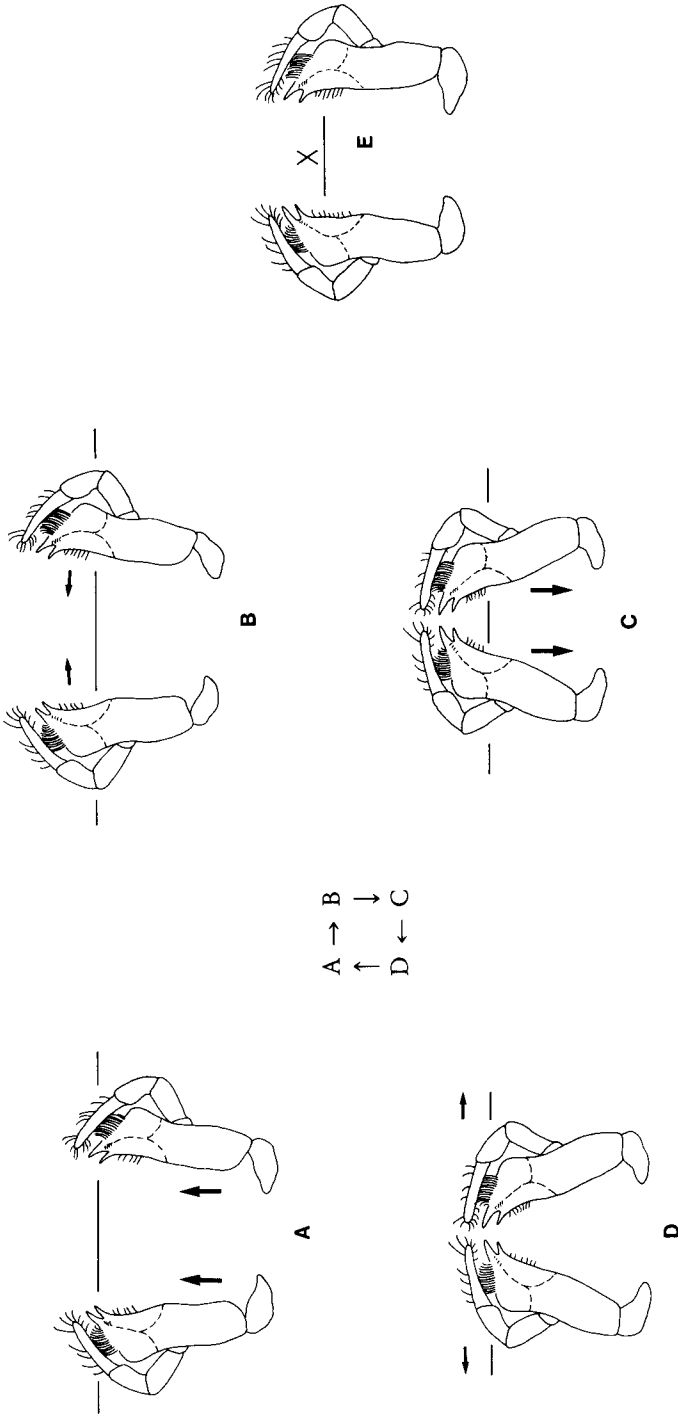
Fig. 9. Periodic circular maxillary movement of *Potamanthus luteus*. A: maxillae in posterior, opened position; B: maxillae in posterior, opened position; C: maxillae in anterior closed position, thus squeezing particles between the galealaciniae; D: maxillae in posterior closed position, squeezed particles between the galealaciniae are transported towards the preoral cavity; E: resting position of the maxillae (arrows indicate the direction of the following movement, the line (X) indicates a marked position within the preoral cavity to show the anterior-posterior movement of the maxillae). The cycle takes about 0.8 seconds time.

According to the type of processed food, the periodic circular movement of the maxillae is supported by the other mouthparts.

I: Coarse particles

The size of a coarse particle is defined as bigger than half of the width of the larval head capsule and the particle is of hard consistency. The particle is fixed between the prothoracic femora and tibiae and is brought into reach of the mouthparts, supported by the maxillary palps. The mandibles are in an opened position, allowing the prothoracic legs and the maxillary palps to bring food particles into the gap between the outer canines of the mandibles. Subsequently the mandibles move inwards and the outer canines bite into the food particle, disintegrating the coarse particles to support ingestion. A facultative bending of the head dorsally may support disintegration. Simultaneously the labial palps are in a continuous, circular in- and outward movement in order to gather smaller particles loosened by the mandibular activity. The maxillary palps function as a guiding structure for the particle fixed between the mandibles and prothoracic legs. After a process of three or four continuous biting attempts, the larva lifts its head so that the galealacinia of the maxillae can reach the particle. They also try to collect loosened particles by the above described movement of the maxillae (Fig. 9 A–D). In addition the rakes of the galealacinia scratch over the surface of the particle, dislodging possible epiphytes or material which is associated with the coarse particle. The loosened particles are either caught in the rake or in the bunch of setae on top of the galealacinia (Fig. 4).

II: Algal threads

An algal thread is oriented parallel to the longitudinal axis of the larval body between the outer canines of the opened mandibles by the labial and maxillary palps. Simultaneously with the periodic circular maxillary movement there is a coordinated movement of the mandibles to process algal threads:

The mandibles close, thus biting into the thread. The galealaciniae of the maxillae are in a posterior, laterally opened position. The maxillae shift forward; after reaching their most anterior position they close, thus pressing the thread between the galealaciniae. In a next step, the mandibles open laterally while the maxillae in their closed position move backwards and the algal thread is forced into the preoral cavity. When the maxillae reach their final posterior position, the mandibles close again, biting into the algal thread while the maxillae open and move forward. The cycle immediately starts again.

During these movements the rakes on the galealacinia may dislodge material (e. g. epiphytes, algal parts) which is then caught in the bunch of setae situated at the top of the galealacinia. As a result of the backward movement of the maxillae, the material caught in the bunch of setae on top of the galealaciniae is transported

to the hairy pads of the hypopharynx; in addition the molar surfaces of the mandibles crush the algal thread, dislodging more material. The pressure of the biting mandibles in most cases crushes the thread at the biting points, and sometimes causes the thread to bend. In a few cases the outer canines of the mandibles cut off pieces of the algal thread.

The larvae do not always swallow harvested food particles. Often, a piece of algal thread is removed from the preoral cavity. In this case, the direction of the periodic circular maxillary movement (Fig. 9A−D) is inverted (D−A). This inverted movement proceeds until the particle is completely removed from the preoral cavity. The particle will then be handed over to the current by two or three quick movements of the labial palps.

In this basic sheme all types of non-swallowed particles (e. g. mineral particles, sometimes algal etc.) are transported out of the preoral cavity.

III: Fine or soft particles

The size of the particles range from single diatoms and fine POM up to agglomerations of POM of half of the width of the larval head capsule. Particles or agglomerations at the upper limit of the size range are treated in the described way only if they are of soft consistency, otherwise the particles are treated as described in I: Coarse particles.

Loose laying particles are raked towards the mouthparts by movements of the prothoracic legs or the palps. The particles are finally brought into reach of the mouthparts where they are forced into the preoral cavity by alternately movements of the labial palps. Once the particles are in reach of the galealaciniae the maxillae move according to the periodic circular maxillary movement (Fig. 9A−D). The mandibles are involved only in the final processing and further transport to the pharynx. There is no mandibular biting process of food by means of action of the mandibular canines. This is in contrast to the processing of algal threads (I) or coarse particles (II).

Filtering process

Filtering is the less frequent method of the described food gathering techniques in spite of the fact that there was sufficient suspended material in the current. Not more than 10% of the feeding activities of *P. luteus* is done by filter feeding. Moreover filter feeding habits had not been observed in the artificial stream.

In the filtering process, the larva fixes itself to the substrate by the meso- and metathoric legs, oriented with the head against the current. The prothoracic legs are exposed to the current in the plane of the body.
− The femora of the prothoracic legs are held at an angle of 90°, relative to the longitudinal axis of the body; the tibiae pointing forward are held at an angle of 90° relative to the longitudinal axis of the femora (Fig. 10A). The setae at the inner
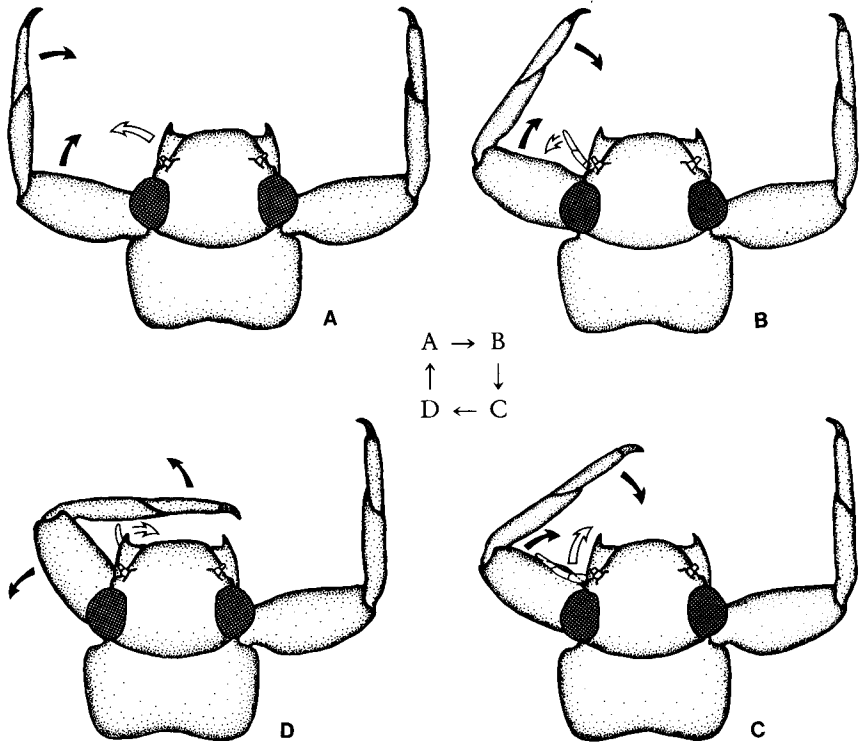
Fig. 10. Filtering process of *Potamanthus luteus*, dorsal view (arrows indicate the direction of the following movement). A: starting position, legs exposed to the current; B: inward movement of the prothoracic leg while the maxillary palp moves laterally outwards; C: the prothoracic leg still moves further inwards while the maxillary palp has reached its final lateral outstretched position; D: the prothoracic leg has reached its final inward position while the maxillary palp moves inwards (the movement of the maxillary palps are supported by the maxillary-circulation movement). The cycle takes about 0.6 to 1.0 seconds time.

margins of femora and tibiae are the main filtering tools in which drifting particles are caught, supported by labial and maxillary palps. The described exposed position of the prothoracic legs can be regarded as the starting point of the filtering cycle.
– The next phase is the adduction of the prothoracic leg (Fig. 10 B). The femur moves forward while the tibia moves inward. Meanwhile the maxillary palp shifts outwards; the outward stretching of the maxillary palp and the periodic circular maxillary movement is performed simultaneously, resulting in a greater radius of action of the maxillary palp (nevertheless outward shift of maxillary palps before inward movement of the prothoracic legs was observed as well).
– Finally the maxillary palp lies on the dorsal surface of the femur (Fig. 10 C). While femur and tibia are still on their way towards the anterior margin of the head, the maxillary palp begins its inward movement. The femur rests at a position

of about 45° relative to the longitudinal axis of the body while the tibia moves further inwards to a position of approximately 70° relative to the longitudinal axis of the femur.

– This results in a position of the tibia nearly perpendicular to the longitudinal axis of the body, in front of the head (Fig. 10 D). Particles, which are caught in the setae of the inner margin of the femur are combed out by setae on the distal segment of the maxillary palp. When the maxillary palps reaches more or less the junction between tibia and tarsus, the tibia begins with its outward movement, followed by the posterior movement of the femur. Finally the starting position (Fig. 10 A) is reached and the cycle starts immediately again.

The larvae can filter with only one leg or with both legs. In all cases the maxillae move simultaneously, regardless whether one or two legs perform filtering. The larvae may filter in a continuous in and outward movement of the legs or with a short exposing period of the prothoracic legs of 1–3 seconds. Each filtering cycle (Fig. 10 A–D) lasts between 0.6 and 1.0 seconds.

Transport of food to the pharynx

Once food particles are situated in the setae on top of the galealacinia and in the setae of the labial and maxillary palps they have to be transported to the molar surfaces. The particles caught in the setae of the palps are taken over from the setae of the paraglossae and glossae. During the periodic circular maxillary movement (Fig. 9) these particles are transported to the dorsal surface of the lingua by the setae at the median edge of the galealacinia. Simultaneously particles in the bunch of setae on top of the galealacinia are retained as well by the setae on the dorsal surface of the paraglossae as by the setae at the median edge of the superlinguae while particles in the setae of the superlinguae and in the pilose pad on the dorsal surface of the lingua are transported towards the molar surfaces by the spinous process and the setae at the median edge of the galealacinia. In addition the new incoming food particles probably push food particles already situated at the dorsal surface of the lingua into reach of the mandibular surfaces where the food is squeezed and excess water is restrained before the food is pushed to the pharynx.

In the above described process the working position of the maxillae is above the labium and the lingua but below the superlingua; no direct contact between galealaciniae and mandibles is possible. Occasionaly a second type of movement was observed whereby the maxillae and mandibles could act in close contact and with which particles could be transported to the pharynx. Larvae of *P. luteus* can move their labium and hypopharynx ventrad while the maxillae stay in their normal position. As a result the maxillae are now situated dorsal of the superlinguae of the hypopharynx and could transport food towards the molar surfaces.

First own examinations of the food of *P. luteus* reveal a diet consisting of about 60% POM and 40% mineral particles. Detailed studies on the diet of the larvae of *P. luteus* will be treated in a separate publication.

Cleaning movements of the head

The prothoracic legs are exposed to the current as during the filtering process (Fig. 10A). In the first phase, the femur is tilted forward to a degree of 100° relative to the longitudinal axis of the body (LAB), the tibia bends inward to a degree of 45° relative to the longitudinal axis of the femur. Additionaly the prothoracic leg is slightly lifted out of the plane of the body, the head turns arround its longitudinal axis towards the lifted leg. The tibia then moves further inwards; as a result, the tibia lies dorsally on the head, behind the antennae. When the leg moves forward the setae on the tibia clean the antennae and the surface of the head capsule; subsequently the head turns back to its starting position. Finally, the tibia lies perpendicular to LAB in front of the mouthparts while the femur moves further forward, creating an angle of about 30° relative to LAB. The setae of the tibia are now combed out by the maxillary palp (see filtration process, Fig. 10). The duration of a single cleaning cycle takes 0.9−1.2 seconds and will usually be repeated 2−4 times. The same cleaning procedure was observed during all described feeding strategies. The cleaning of the head is therefore not part of the filtering movement; in addition it is executed not frequently enough to be an efficient part of the filtering strategy.

Discussion

The larvae of *Potamanthus luteus* have been observed under artificial conditions, especially when enclosed in the flow cell. Nevertheless feeding habits were the same when compared to observations made in the artificial stream which presented more natural conditions. Similar observations on the stereotypic nature of feeding movements despite artificial conditions were made on *Oligoneuriella rhenana* (ELPERS & TOMKA 1992), *Ephemerella needhami* (MCSHAFFREY & MC CAFFERTY 1990), *Stenacron interpunctatum* (MCSHAFFREY & MCCAFFERTY 1988), and *Rhithrogena pellicuda* (MCSHAFFREY & MCCAFFERTY 1986). Moreover feeding behaviour of *Ephemerella ignita* was the same when observed in the laboratory and in the field using an endoscope (ELPERS & TOMKA, unpublished). The micro-habitat of *E. ignita* reveals optimal conditions for observations in the field since the larvae feed on the upper surface of the substrate. This observational technique could not be used for observations on the feeding behaviour of larvae of *P. luteus* since they live on the underside of stones.

The larvae of *P. luteus* were provided with natural food conditions found at the collection site at the river Rhine (suspended particles, different sized POM,

algal threads). These different food resources were presented simultaneously, thus giving the larvae a choice to feed on prefered material. The main food gathering process of *P. luteus* is the raking movement of the prothoracic legs as well as movements of the maxillary and labial palps in combination with the periodic circular maxillary movement (Fig. 9). This type of food gathering movements is found as well in feeding habits of *E. needhami* (McSHAFFREY & McCAFFERTY 1990). The feeding cycle of *E. needhami* contains the "maxillary brushing cycle" and the "mandibular biting cycle". During the "maxillary brushing cycle" larvae of *E. needhami* remove POM and epiphytes from *Cladophora* threads. This movement is similar to the periodic circular maxillary movement of *P. luteus*. *P. luteus* as well as *E. needhami* mainly use the galealaciniae of the maxillae to obtain food. In addition to this the maxillae of *P. luteus* performe a forward-backward directed movement (Fig. 9). In the "mandibular biting cycle" of *E. needhami* (McSHAFFREY & McCAFFERTY 1990) and the way *P. luteus* processes algal threads (feeding movements, II: Algal threads) both larvae use their mandibular canines in a similar way to process algal threads. In addition larvae of *P. luteus* use the canines of their mandibles to disintegrate coarse particles.

BROWN's (1961) observations on feeding habits of *Cloeon dipterum* and *Baetis rhodani* revealed a variation of feeding movements, according to the kind of food ingested (fine detritus, aggregated detritus, rotted higher plant tissue, and filamentous algae). This agrees with observations made on *P. luteus* which feed on the same type of food. Feeding behaviour of *B. rhodani, C. dipterum* (BROWN 1961), *E. needhami* (McSHAFFREY & McCAFFERTY 1990) and *P. luteus* is very similar.

In addition to the feeding movements, the structure of mouthparts of *P. luteus* resembles those of *E. needhami*. The shape of the mandible, the molar surfaces, inner and outer canines, and the laterally enlarged paraglossae of the labium of the larvae of both species are very similar. The most striking correspondence is to be found when the galealaciniae of *E. needhami* (McSHAFFREY & McCAFFERTY 1990, Fig. 5) and *P. luteus* (Fig. 4) are compared. The cuticular rake at the top of the inner margin of the galealaciniae, the bunch of filtering setae on the crown of the galealaciniae, and the fine structure of the setae themselves are nearly identical. It is, however, remarkable that the structure of the mouthparts and the feeding habits of the prognatheous larvae of *P. luteus* are similar to those of the hypognatheous larvae of *E. needhami*. No close phylogenetic relationship of *P. luteus* to *E. needhami* is given (TOMKA & ELPERS 1991; McCAFFERTY 1991). The similarity in the mouthpart structure of *P. luteus* and *E. needhami* thus has to be regarded as a result of convergent development on ground of similar feeding behaviour. Food resources of both larvae comprise first of all POM, but also food associated with algal threads and algal threads themselves. McSHAFFREY & McCAFFERTY (1991) found about 50% POM and up to 30% algal threads in the diet of *E. needhami*.

Although larvae of *P. luteus* have been observed feeding on algal threads there is no close association given between algae and larvae as is reported for *E. needhami* and algal threads of *Cladophora* sp. by McSHAFFREY & McCAFFERTY (1991). Larvae of *P. luteus* have never been observed sprawling on algal threads distributed on the upper surface of the substrate. Nevertheless BARTHOLOMAE & MEIER (1977) found a strong correlation between stones which were overgrown by filamentous algae and larvae of *Anthopotamus myops* in the Huron river [*Potamanthus myops* (WALSH) described by BARTHOLOMAE & MEIER 1977 is a synonym for *Anthopotamus myops* (WALSH) described by BAE & McCAFFERTY (1991)]. This is true for early larval stages of *P. luteus* in the River Rhine as well. During the day, larvae of *A. myops* prefer the underside of stones while they feed on detritus found on the upper surface of the rocks during night (MEIER & BARTHOLOMAE 1980). Whether there is a similar pattern for larvae of *P. luteus* remains unknown since no observations have been made during night. Larvae of *P. luteus* process and transport algal threads into the preoral cavity, although the threads are often rejected to the current instead of being ingested. Probably the larvae do not feed on the algae themselves but on the epiphytes found along the algal threads.

Passive filtering behaviour of *P. luteus* (Fig. 10) is similar to that of *Anthopotamus verticis* (Potamanthidae) (McCAFFERTY & BAE 1992) and of *O. rhenana* (ELPERS & TOMKA 1992). *A. verticis* does not remove particles caught in the setal fields of the prothoracic legs by direct movement of the labial and maxillary palps but seems to resuspend particles by moving the setal fields of prothoracic legs across the head and the mandibular tusks; the resuspended particles are then filtered out of the water by setal fields on the mouthparts (McCAFFERTY & BAE 1992). This leg movement across the dorsal surface of the head has been observed for *P. luteus* and *O. rhenana* (ELPERS & TOMKA 1992) as well, here being a movement cleaning the dorsal head surface and the antennae, rather than being a movement for resuspending already filtered particles. These movements are less frequently performed, thus they can not be an effective filter feeding mechanism. Filtering behaviour was seldomly observed in larvae of *P. luteus* and has to be seen only as an additional method of food gathering strategy. Moreover the filtering setae found along the prothoracic legs of *P. luteus* (Fig. 2) are only weakly evolved compared to those of *O. rhenana* and *A. verticis*.

McCAFFERTY & BAE (1992) classify *A. verticis* as "active/passive deposit filterer" (sensu McSHAFFREY & McCAFFERTY 1988) whereas *P. luteus* (this study) has to be classified mainly into the "collector-gatherer/brusher" FFG with occasional filter-feeding capability (sensu McSHAFFREY & McCAFFERTY 1988).

Besides differences in the feeding behaviour, as stated above, there are differences in the mouthpart structure as well. Long mandibular tusks are present in *A. verticis* (McCAFFERTY & BAE 1992; Fig. 1) whereas those of *P. luteus* are only poorly developed (Figs. 1, 6a). Setal fields on prothoracic legs and maxillary and labial palps are much more developed and adapted to filter-feeding in *A. verticis*

(McCAFFERTY & BAE 1992; Figs. 1, 2) than in *P. luteus* (Figs. 2 a, b, 3 a, 4 a). The second segment of labial and maxillary palps of *A. verticis* is max. 0.4 times as long as the third segment (BAE & McCAFFERTY 1991). The articulation between second and third segment of labial and maxillary palps is more or less inflexible. The structure of the palps of *A. verticis* in terms of mobility resemble the structure of the labial palps of *O. rhenana*, a pure filter-feeder (ELPERS & TOMKA 1992), rather than those of *P. luteus*.

Each segment of the labial and maxillary palps of *P. luteus* is nearly equal in length; articulation is well developed between each of the three segments (Figs. 3 a, 4 a). Larvae of *P. luteus* use their palps for positioning of food particles and raking movements, necessitating a greater mobility of palps when feeding on a variety of food resources, as compared to feeding on suspended particles of uniform size only, like the filter-feeding larvae of *A. verticis* (McCAFFERTY & BAE 1992) and *O. rhenana* (ELPERS & TOMKA 1992).

The transport of harvested food particles to the pharynx is done in more or less the same way in all ephemeropteran larvae: particles are brought to the hypopharynx by the maxillae, then pushed towards the molar surfaces by maxillary movements as described by ARENS (1989). He stated that the cibarium of mayfly larvae is divided into two compartments by the laterally elongated superlinguae of the hypopharynx. The normal working position of the galealaciniae of the maxillae is above of the lingua but below of the superlinguae. Maxillae and mandibles therefore can not come into contact because they work in different compartments (ARENS 1989). Observations presented here indicate that larvae of *P. luteus* can move their labium (hypopharynx included) ventrad, thus giving maxillae and mandibles the opportunity to work in a common compartment. Nevertheless no direct observations of the results of this movement were possible. Probably food particles could now be pushed into the pharynx or towards the mandibular surfaces by direct maxillary movement as well as a cleaning of mandibles and setal fields on the dorsal surface of the lingua and superlinguae by direct contact of setae of the maxillae would be possible.

Special care is to be taken when feeding behaviour is postulated only on the basis of the mouthpart structure or of the ingested food. McCAFFERTY & BAE (1992) and BAE & McCAFFERTY (1991) postulate filter feeding habits for the genus *Potamanthus* by comparing the structure of their mouthparts with the structure of mouthparts found among the larvae of the family Potamanthidae and the observed feeding habits of *A. verticis*. Their morphological analysis of the Potamanthidae indicate that the genus *Rhoenanthus* mainly belongs to the "collector-gatherer" FFG with filter feeding capability. The genera *Anthopotamus* and *Potamanthus* were considered as specialized for filter feeding and have the most highly developed filtering apparatus found among the Ephemeroidea (BAE & McCAFFERTY 1991).

Our observations of the feeding habits of the larvae of *Potamanthus luteus* show that their feeding behaviour is more related to feeding behaviour reported for *Rhoenanthus* spp. by BAE & McCAFFERTY (1991) and *E. needhami* (McSHAFFREY & McCAFFERTY 1990) than to those of *Anthopotamus verticis* (McCAFFERTY & BAE 1992). The results of this study clearly indicate that the larvae of *P. luteus* belong to the functional feeding group "collector-gatherer" (sensu MERRITT et al. 1984) with occasional filter feeding capability.

Summary

Larvae of *Potamanthus luteus* (Potamanthidae) have been observed using video-macroscopy and scanning electron microscopy. The morphology of mouthparts (Figs. 1–8) of the prognatheous larvae of *P. luteus* is very similar to the structure of mouthparts of the hypognatheous larvae of *Ephemerella needhami* (Ephemerellidae). Both larvae feed in a similar way. Larvae of *P. luteus* rake food particles towards the mouthparts by movements of the prothoracic legs and the labial and maxillary palps (see: Raking movements). The main food processing tools are the maxillae, especially the galealaciniae (Figs. 4, 9). According to the type of food, other mouthparts are involved in a characteristic way (I: Coarse particles; II: Algal threads; III: Fine or soft particles). Filter feeding behaviour (Fig. 10) was observed as well, but occurred less frequently when all types of food were presented. The larvae of *P. luteus* are classified into the "collector-gatherer" functional feeding group with occasional filter feeding capability.

Acknowledgements

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Address of the authors:

Christian Elpers and Ivan Tomka, Institute of Zoology, Entomol. Dept., University of Fribourg, Pérolles, CH-1700 Fribourg, Switzerland.