MOUTHPARTS AND FEEDING BEHAVIOUR OF TAHITIAN LARVAL SIMULIIDAE (DIPTERA: NEMATOCERA)

D.A. CRAIG
Department of Entomology
University of Alberta
Edmonton, Canada
T6G 2E3

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Larvae of Simulium tahitiense *Edwards and* S. oviceps *Edwards were observed feeding in the laboratory. Larvae of* S. tahitiense *filter feed in typical fashion, as can larvae of* S. oviceps *with their reduced cephalic fans. However, the latter does not twist the body longitudinally more than 90°.* S. oviceps *larvae can keep their fans abducted and rays open while browsing the substrate. A detailed scanning electron microscope study of larval mandibular structure of both species shows that raking bristles on larval* S. tahitiense *mandibles are important in removing food from the closed, adducted, cephalic fans. Such bristles are absent from larval* S. oviceps *mandibles. Homologies are proposed between mandibular structures of simuliid larvae and those of other larval nematocerans.* S. tahitiense *larvae have a double socket on the dorsomedian mandibular articulation which allows two planes of motion. This structure is reduced in larval* S. oviceps. *Mandibular and hypostomial teeth in* S. oviceps *larvae are highly coadapted and probably used for cutting the salivary silk thread. These teeth in larval* S. tahitiense *are not as closely coadapted. Hairs of the maxillary, labiohypopharyngeal and anterior palatal brushes are generally directed toward the cibarium. Food introduced into this system of brushes probably is directed into the cibarium. The brushes appear to be self-cleaning.*

Nous avons étudié le comportement nourricier des larves de Simulium tahitiense *Edwards et de* S. oviceps *Edwards. Les larves de* S. tahitiense *se nourrissent d'une facon typique à l'aide de filtres, il en est de même des larves de* S. oviceps *malgré un éventail plus petit. Ce dernier cependant ne peut pas se retourner longitudinalement plus de 90°. Les larves de* S. oviceps *garder leurs éventails levés et les rayons de l'éventail ouverts pendant qu'elles broutent la surface. Une analyse détaillée des structures mandibulaires des larves des deux espèces à l'aide du microscope électronique à balayage démontre que les soies racleuses des mandibules larvaires de* S. tahitiense *sont importantes pour enlever la nourriture des éventails cephalique retombés et fermés. De telles soies sont absentes des mandibules larvaires de* S. oviceps. *Nous proposons les homologies entre les structures mandibulaires de larves de simuliides et celles d'autres nematocères larvaires. Les larves de* S. tahitiense *ont deux orbites sur l'articulation dorso-mediale des mandibules; ces orbites permettent le mouvement sur deux plans. Cette structure est réduite chez les larves de* S. oviceps. *Les dents des mandibules et de l'hypostome chez les larves de* S. oviceps *sont très hautement coadaptés et sont probablement utilisés à couper le fil de soie des glandes salivaires. Ces meme dents chez* S. tahitiense *ne sont pas aussi étroitement associés. Les soies des brosses du maxillaire, du labiohypopharynx et du palais anterieur sont généralement dirigées vers le cibarium. Aussi la nourriture introduite dans ce système de brosses probablement s'achemine dans le cibarium. Ces brosses semblent être autonettoyantes.*

INTRODUCTION

The small complex of closely related Tahitian Simuliidae species is unique. Nowhere else do simuliid larvae of one taxon, bearing typical cephalic fans, share the same habitat with larvae of a closely related taxon (Craig 1975) bearing reduced cephalic fans.

Head and mouthpart structure of larval *Simulium tahitiense* Edwards and of the probable larva of *S. cheesmanae* Edwards are typical (Craig 1975). However, heads of larval *S. oviceps* bear reduced cephalic fans and labropalatum, and modified mandibular and hypostomial teeth (Edwards 1935, Dumbleton 1962, Davies 1965 and Craig 1974, 1975).

While more widely spread on Tahiti, *S. tahitiense* larvae occur with *S. oviceps* larvae in larger rivers. Why should larvae of *S. oviceps*, presumably exposed to the same evolutionary pressures as larvae of *S. tahitiense* and *S. cheesmanae*, develop reduced fans and the concomitant reduced labrum? After studying the position of larval *S. oviceps* cephalic fans and size of their retractor muscles, I (Craig 1974) suggested that their fans did not function. Further study though, with more material (Craig 1975), showed that the labropalatum is keel-shaped and that the tips of the fan rays could probably extend into the cibarium as do those of typical simuliid larvae (Fortner 1937, Chance 1970). I suggested then that a study of feeding behaviour of *S. oviceps* larvae might show why the larval head of this species became atypical.

Such a complex of closely related species consisting of the typical, fully fanned *S. tahitiense*, and *S. cheesmanae* larvae and the atypical *S. oviceps* larvae, with reduced fans, also provides a unique situation for studying which of the structures on the complex mandibles, on the more simple maxillae and on the labiohypopharyngeal region are used with the cephalic fans in filter feeding.

Observations on live *S. oviceps* larvae in Tahiti showed that their mandibles had an apparently exaggerated movement when compared to mandibular movement of *S. tahitiense* larvae. This observation led to investigation of mandibular articulations of both *S. oviceps* and *S. tahitiense* larvae. This, in turn, led to consideration of coadaptation of mandibular and hypostomial teeth.

Observations made here provide further information about how larval simuliids transfer filtered food from the adoral surface of the cephalic fan to the cibarium. Because much mouthpart movement of simuliid larvae is too fast to follow by eye, most explanations of mouthpart function by others have been deduced from structure and coadaptation of parts (Fortner 1937, Chance 1970). Such is done here, aided by dissections.

Specimens figured here with SEM micrographs have been selected to show the assumed true relationships of the mouthparts. My belief that the figures do this and do not show fixation artifacts, is based on observations of live *S. tahitiense* and *S. oviceps* larvae and on high speed macrocinephotography of larval *S. vittatum* feeding (Craig, unpublished work).

MATERIALS AND METHODS

Both *Simulium oviceps* and *S. tahitiense* larvae were collected from the Punaruu River, Tahiti and returned to the Louis Malardé Institute of Medical Research, Field Station at Maraa, for study. Larvae were transported in a thermos flask containing ice water agitated with a portable aquarium air bubbler.

In the laboratory, larvae were transferred to a large cylindrical glass jar (diameter approximately 30 cm, depth approximately 15 cm). Water in this jar was circulated rapidly with a variable-speed laboratory stirrer and propellor. This system was successful and larvae of both species fed, moved and pupated on the glass walls of the jar.

Observations were made through a Wild M5 stereomicroscope laid on its side. Photomicrographs were made with a 35 mm camera attached to the microscope with illumination provided by an electronic flash. Although this photomicroscopy provided a permanent record of observations, the various events in larval feeding behaviour occurred so rapidly that they were over before the camera shutter could be released. However, these photomicrographs provided the basis for Fig. 42-44 which show general stance of *S. oviceps* larvae during feeding.

Preserved larvae for scanning electron microscopy were hydrated and washed for approximately 15 sec. with detergent in a sonicating bath. This treatment cleaned well, but occasionally produced damage (Fig. 23, 26). Larvae were then dehydrated through a graded series of ethanol into 100% amyl acetate and dissected if required. Specimens were then critical-point

dried, mounted on specimen stubs, sputter-coated with gold and examined at 10-20 kv with an S4, Stereoscan, scanning electron microscope.

To observe the relationship of mandibular apical teeth and hypostomial teeth at full mandibular adduction, larval heads of both species were dissected to remove all mouthparts except mandibles and hypostomium. The heads were cleared in boiling lactic acid (Anthon and Lyneborg 1968) and then examined while mounted in glycerine. The mandibles could easily be manipulated to full adduction to make contact with the hypostomium. Meeting of the teeth was observed from the foramen magnum (Fig. 37, 38). Diagrams were made with the use of a Wild M20 compound microscope equipped with a drawing tube.

Larval simuliid mandibles are complex, and bear many teeth, hairs and brushes. The only detailed descriptions of them are provided by Baranov (1935), Rubtzov (1959) and Chance (1970). However, mandibular apical teeth are important taxonomically and many terms for these structures have been coined. Table 1 collates some of these systems of names and indicates homologues of simuliid mandibular structures to those of other larval nematocerans (Anthon 1943, Knight 1971). The basis for homologizing some mandibular structures of simuliids and culicids (marked by asterisk in Table 1) is strengthened by similar innervation to mandibular structures of both these taxa (Yin 1970, Craig, pers. obs.).

The terms used here for mandibular structures have been chosen because they indicate function and appearance, or because they have been used previously for homologous structures. For example, the term "comb teeth" (*sensu* Smart and Clifford 1965) is not used because the structures so named are not known to comb and are not the single array of teeth as should be a comb.

The maxillae are relatively simple, with fewer hairs and brushes. Where applicable, the terms of Chance (1970) are used. Terms for the cephalic fans and labropalatum are those used by me elsewhere (Craig 1974).

The terms "adoral" and "aboral" refer respectively to mouthpart surfaces that are directed toward and away from the mouth. Similarly, "adduct" and "abduct" refer respectively to mouthpart movements toward and away from the mouth. "Open" and "closed" describe positions of the cephalic fan rays.

OBSERVATIONS

Structure

Cephalic Fans. – Although cephalic fans (cf) of larvae of both species are illustrated here (Fig. 1, 2, 21, 22) they are not further described. Detailed studies of cephalic fans of *S. oviceps* larvae are given by Dumbleton (1962), Davies (1965) and myself (Craig 1975). Cephalic fans of *S. tahitiense* larvae have not been described in as much detail as those of *S. oviceps* larvae, however, my personal observations show that the fans have structure which is considered typical for larval Simuliidae (Craig 1974, Davies 1974).

Mandibles. – Edwards (1935), Grenier and Rageau (1960), and Dumbleton (1962) briefly described larval mandibles of both simuliids, but because of structural complexity and their importance in feeding, redescriptions are given here.

S. tahitiense. – Distally, the *covering brush* (cb) extends over part of the *distal adoral brush* (dab) (Fig. 6) and occasionally over the *outer teeth* (ot) (Fig. 8). The covering brush has a *sulcus* (su) delimiting it from the rest of the mandible. Only a single row of hairs is associated with the sulcus, the longer, robust, more medial hairs of the covering brush (cb) attaching directly to the mandible (Fig. 7).

There are four sharp, curved, robust outer teeth (ot), of which the second is hidden on the

Table 1. Some Homologies and Terms for Structures of Mandibles of Larval Simuliids

Term used here	Anthon (1943)[1]	Knight (1971)[2]	Puri (1925)	Baranov (1935)[3]	Rubtzov (1959)	Dumbleton (1962)	Stone (1964)	Smart and Clifford (1965)	Crosskey (1969)	Chance (1970)	Crosby (1974)
Preapical sensilla (ps) *	------	Mandibular spurs *	Sensory hairs	Double bristles	Innere, aussere sinnesborsten	------	------	------	------	Sensory hair pair	------
Covering brush (cb)	Fegebor sten	Mandibular comb	Brush	Apical comb	Deckborsten	External hair brush (?)	------	------	------	Covering brush	------
Apical brush (ab)		Pectinate brush (?)	------	Roof brush	Kleiner oberer Kamm	------	------	------	------	Apical bristles	------
Outer teeth (ot) *			Black teeth	2nd & 3rd teeth	Aussere Zähne		Outer teeth	Outer teeth	------	------	
Apical tooth (at) *	Distalglied des mandibels	Cutting * organ		Main (1st) tooth	Spitzenzähne	Apical teeth	Apical tooth	Apical tooth	Apical teeth	Apical tooth	Apical teeth
Preapical teeth (pat) *			Small teeth	Mandibular comb	Zähne vor d. Spitze		Subapical teeth	Preapical teeth	Comb teeth	------	Comb teeth
Spinous teeth (st)	Zahreihen auf dem Distalglied		Bristle-like teeth		Innenzähne	Bristle-like teeth	Inner teeth	Comb teeth	Spinous comb	Inner teeth	Inner teeth
Mandibular serrations (ms) *	hakenförmiger . . .	Membranous * process	Tooth-like processes	Minor tooth-toothlets	Randzähne	Internal sub-apical teeth	Mandibular serrations	Serration teeth	Mandibular serrations	Marginal teeth	Mandibular serrations
Distal adoral brush (dab)	------	Mandibular brush	Fan setae	Apical brush	Aussere Kamm	------	------	------	------	First external brush	------
Raking bristles (rb)	------		------	------	------	------	------	------	------	------	------
Adoral median lobe (ml)	rudimentäre Trennungsfurche . . .		------	------	------	------	------	------	------	Middle lobe	------
Proximal adoral brush (pab)	------		------	------	------	------	------	------	------	Second external brush	------
Prosthecal brush	Prostheca	Mandibular hairs (mdh)	Fringe setae	------	------	------	------	------	------	------	------
Distal prosthecal brush (dpb)		MdH_2	------	Basal brush	Mittlerer Kamm	Sub apical internal hairs	------	------	------	Middle brush	------
Medial prosthecal brush (mpb)		------	------	------	Kleine Basalborste	------	------	------	------	Small basal brush	------
Proximal prosthecal brush (ppb)		MdH_1	------	Sharp bristle tuft	Grosse Basalborste	Basal internal hairs	------	------	------	Large basal brush	------
Spinose area	------	Spinose area	------	------	------	------	------	------	------	------	------

1. Rhyphidae, Trichoceridae, Psychodidae, Ptychopteridae
2. Culicidae
3. Translated from Croatian

* Homologous innervation with simuliid mandibles (Yin 1970 and Craig, pers. ob.)

adoral surface by the curved first outer tooth (Fig. 7). The *apical tooth* (at) is slightly fluted and protrudes from the general line of the other teeth. There are three *preapical teeth* (pat) (Fig. 8) the most distal of which is similar to the apical tooth (at). The other two, proximal teeth are more like the following arrays of *spinous teeth* (st) (Fig. 7). The spinous teeth are often figured in taxonomic works as a single array of teeth, but clear in Fig. 6, 8, 12 are at least three rows of teeth. Immediately posterior to the spinous teeth are *mandibular serrations* (ms) (Fig. 7); one large one and a very small one that does not show well on any of the figures (Grenier and Rageau 1960, reported the presence of three such serrations). Dorsad of the preapical and spinous teeth is the flattened *apical brush* (ab) (Fig. 6, 8). The most anterior row of stout hairs of this brush are short and curved and are raised off the mandible (Fig. 6, 12). The major mandibular brushes are borne on the adoral surface. The *distal adoral brush* (dab) is between the covering brush and the *adoral median lobe* (ml) with the portion nearest the lobe modified to form the long, *proximal adoral brush* (pab) (Fig. 9, 10). Most of the distal adoral brush (dab) is composed of softly pectinate hairs (Fig. 7), but a very important part of the brush is a single row of smoothly tapering and curved *raking bristles* (rb) between the pectinate hairs and the mandible proper (Fig. 6, 7). The raking bristles extend beyond the leading edge of the mandible (Fig. 6, 9), and are the structures usually figured as typical for the distal adoral brush.

The *prostheca* bears three complex brushes. The *distal prosthecal brush* (dpb) has six or seven fan-shaped hairs that together have a fan-like arrangement (Fig. 6, 8). Proximal and partly covered by that brush is the *median prosthecal brush* (mpb) (Fig. 9) which is a single row of stout, tasseled bristles. This row abruptly lengthens into the seven or eight bristles of the *proximal prosthecal brush* (ppb) (Fig. 9). There is a small spinose area (sa) just dorsal of the *dorsomedial articulation* (dma) (Fig. 9).

A few trichoid sensilla are scattered along the dorsal edge of the mandible. A pair of prominent, trichoid, *preapical sensilla* (ps) are located just proximal to the covering brush (Fig. 6, 8, 10).

Simulium oviceps. – In contrast to those of larval *Simulium tahitiense*, larval mandibles of this species are strikingly sclerotized and robust as shown by the *dorsal ridge* (dr) in Fig. 26. Another major difference is that the covering brush and the distal adoral brush are poorly developed.

There are three outer teeth (ot), the most dorsal of which is small and well caudad of the other two (Fig. 28). Although not clearly evident in the figures, the apical tooth (at) protrudes markedly from the other teeth (Fig. 25), and is cone-shaped apically. This apex fits closely into the gap between the *hypostomial teeth* (hypt) (Fig. 35, 36). Of the three preapical teeth, the anterior two are similar to the other apical teeth, the last is more like the following single array of spinous teeth (st) (Fig. 27, 28). There are two mandibular serrations (ms) (Fig. 27, 28).

The apical brush (ab) has only two rows of closely appressed bristles, plus a few irregularly arranged (Fig. 25). The covering brush (cb) does not have a delimiting sulcus (Fig. 24) and cannot be clearly distinguished from the greatly reduced distal adoral brush (Fig. 28). All the raking bristles of the distal adoral brush (dab) are absent and only a double row of softly pectinate hairs remain (Fig. 28). The proximal adoral brush (pab) consists of a few long tasseled hairs, directed medially by the adoral median lobe (ml) (Fig. 28). The distal prosthecal brush (dpb) is less well developed, but the other two prosthecal brushes are normal (Fig. 27, 28).

Mandibular Articulation

Simulium tahitiense. – The *ventrolateral articulation* (va) of a mandible is a simple ball and socket, albeit broad, with the ball formed from the anteroventral edge of the *antennal*

buttress (abt) (Fig. 37). The *dorsomedial articulation* (dma) is more complex, and is positioned at the end of an anteromedially-directed strut (as) of the antennal buttress (abt). Instead of a simple ball there are two lobes fitting a similarly-shaped socket (Fig. 9, 37). This bilobed ball and socket probably provides the mandible with two planes of movement. When the mandible is adducted medially the more medial lobe of the articulation would give axis of rotation "a". When the mandible is abducted past a certain point (unknown), the medial lobe would cease to articulate and the lateral lobe would assume this function, thereby giving axis of rotation "b" (Fig. 37). The mandibular movements of *S. tahitiense* larvae were too fast to observe any such change in plane of movement, but as discussed later, such changes in plane of movement have been observed for mandibles of larval *S. vittatum* (Craig, unpublished data).

S. oviceps. – In larvae of this species, mandibular articulation is quite different from that of the more typical *S. tahitiense* larvae. Instead of the articulations being essentially dorsoventral, they are mediolateral (Fig. 38). The *lateral articulation* (la) (originally the ventrolateral) is still a simple ball and socket (Fig. 27, 38). The *median articulation* (ma) (originally the dorsomedial) has now only a simple ball, but still retains the double grooved socket (Fig. 28, 38). Such articulation appears to allow only one axis of rotation, "a" (Fig. 38), with perhaps some small plane changes being allowed. Mandibular movements of larval *S. oviceps* were much slower than those of larval *S. tahitiense* and observations confirm an essentially single, almost vertical, plane of movement parallel to the sides of the labropalatum (lp), with some other movements at maximum adduction. The antennal buttress and supports for the mandibular articulations are heavily pigmented, sclerotized and massive (Fig. 38).

Maxillae

S. tahitiense. – Larval maxillae are typical and consist of a *maxillary lobe* (mxl) and of a one segmented *palpus* (mxp) (Fig. 3, 5). The lobe has three brushes, an adoral bare sculptured area, two sets of prominent sensilla, and lacinial bristles (not shown here). Fig. 13, 15 and 20 illustrate the following, the *dorsal brush* (db) of short hairs generally directed medially, the *apical brush* (ab) of long closely-packed hair curved towards the cibarium and the *aboral apical brush* (aab) covering the outer surface of the maxillary lobe. Between the apical brush and the aboral apical brush is a prominent papilla from which arise a thick *basiconic sensillum* (bs) and a thinner *trichoid sensillum* (ts) (Fig. 13, 15, 16). The basiconic sensillum is probably chemoreceptive as methylene blue staining of this sensillum in larval *Cnephia dacotensis* (Dyar and Shannon) shows a dendrite extended to the sensillum tip. A dendrite extends only to the base of the trichoid sensillum (Craig, unpublished data). A more proximal papilla having similar sensilla is also borne by the maxillary lobe immediately above the sculptured area, but does not show well on any of the figures of *S. tahitiense* larval maxillae (cf, Fig. 29 of *S. oviceps* maxilla). Proximally, on the adoral surface, is a bare *sculptured area* (sca) (Fig. 15).

The palpus (mxp, Fig. 5) is one-articled, tubular, with a membranous apex supporting at least nine sensilla (Fig. 17). Three robust, socketed, *cone-shaped sensilla* (cs) have fluted tips, and single *tubular sensillum* (tus) also has some apical complexity. The fluted, *ovoid sensilla* (os) shows a probable ecdysal scar proximally. Two small *sensilla* (s) having apical finger-like projections, protrude from deep sockets on either side of the palpus apex. Laterad of these are two small, *nipple-like sensilla* (ns).

The prominent *palpifer* (ppg) supporting the palpus proximally, is coadapted to the *aboral mandibular infection* (ami) (Fig. 5, 8) when the mandible is fully adducted (Fig. 3, 4).

Simulium oviceps. – Fig. 29 illustrates that the maxillae are very similar to those of larval *S. tahitiense*, but the brushes tend to be shorter, the adoral sculptured area smaller and the *lacinial bristles* (lcb) more prominent. The two pairs of sensilla on the adoral surface can clearly

be seen (bs, ts). The palpus and its sensilla are very similar to those of larval *S. tahitiense*. Relative to size of other mouthparts, a maxilla appears large as it has not been reduced as have the cephalic fans, labropalatum and mandibles (Fig. 22, 42).

Labiohypopharyngeal Complex

Simulium tahitiense. – The *hypopharynx* (hypx) is a smooth sheet of shallowly-depressed cuticle (Fig. 18). On its anteromedial border is a raised ridge bearing approximately 15 *dichotomous bristles* (ds). These bristles overhang a lower row of smaller, dichotomous bristles that run the full width of the hypopharynx (Fig. 18). These bristles cover the opening of the salivary duct and partly cover the *labial palpi* (lap). The palpi (Fig. 19) bear five obvious sensilla, four *cone-shaped* (cs), and another, *globular* (gs), with a pore at its apex. The remainder of the palp is highly sculptured and massively sclerotised (Fig. 19). The palpi are separated medially by thin *ligular plates* (lig) (Fig. 18, 19). The two *labial brushes* (lb) consist of dense, flattened, tasseled hairs. The *hypostomial teeth* (hypt) (Fig. 18, 10) have been described and figured by Edwards (1935). At full adduction, the apical mandibular teeth show coadaptation to the hypostomial teeth (Fig. 39).

Simulium oviceps. – As for larvae of *S. tahitiense*, the hypopharynx (hypx) of *S. oviceps* is a smooth sheet of shallowly-depressed cuticle (Fig. 30, 32). The anteromedian ridge has fewer dichotomous hairs (ds) and these are arranged into three groups (Fig. 32). The labial palpi (lap) are smaller and not so heavily sculptured, but have the five sensilla present in larval *S. tahitiense* (Fig. 33). The position of the salivary duct opening can be seen in Fig. 34 and some suggestion is given there that the dichotomous hairs of the hypopharynx determine the shape of the *salivary silk strand* (sas).

Labial brushes (lb) are not prominent, but are also composed of flat, tasseled hairs (Fig. 32, 36).

The hypostomial teeth in larval *S. oviceps* are striking in the amount of wear shown (Fig. 35, 36). Also striking is the close coadaptation between the apical tooth of the mandible and the space between the hypostomial teeth (Fig. 35). This is better shown in Fig. 36 where an apical tooth has been superimposed.

Feeding Behaviour

Stance. – Larvae of *Simulium tahitiense* show a feeding stance similar to that of other typical simuliid larvae as variously described by Fortner (1937), Chance (1970), Crosskey (1973), and Kurtak (1973). A larva attaches to the substrate with their posteroventral circlet of hooks and twists its body, longitudinally often through 180°, so that its ventral surface and the adoral surface of the open cephalic fans face the current.

The abdomen of *Simulium oviceps* larva expands abruptly at the fifth segment and is slightly flattened ventrally (Fig. 42). Anteriorly, it is subcylindrical and the thorax slightly flattened laterally. Larvae attach themselves in typical fashion by the circlet of hooks to the substrate and a wide, flattened portion of the abdomen is closely applied to the substrate (Fig. 42). The larval body normally subtends an angle of about 20° to the substrate during most activities. However, it is often so close to the substrate that large particles in the water become lodged between the anterior abdomen and the substrate. The body angle occasionally reaches, but never exceeds 45° during filter feeding. During browsing and browsing-filtering, the proleg is attached to the substrate (Fig. 42) and probably assists in holding the powerful mandibles against the substrate.

Like that of larval *S. tahitiense*, the fan of *S. oviceps* is adducted rapidly, too fast for the eye to follow, but the abducting fan moves much more slowly and the rays flick open one at a time beginning with the more medial rays.

During filter feeding, the body is not twisted longitudinally more than 90° either way (Fig. 44). Filter feeding was also observed with the body not twisted longitudinally at all and with the fans directed at the substrate as in Fig. 43. At times, the larvae had fans open while browsing on the substrate (Fig. 43).

Large particles of material in the water passing close to, or striking the larva, caused an avoidance reaction. A larva then assumed a V-shaped position (extreme position of Fig. 43), or more rarely thrashed about and changed position. If the fans caught a large piece of material, it was normally passed to the mandibles, manipulated and either forced into the cibarium or released.

Mouthpart Movements

As cephalic fan adduction in larval *Simulium tahitiense* is too fast to observe, the sequence of events proposed here for movement of mouthparts is deduced from the little that could be observed with live larvae, and from scanning electron microscopy of preserved material. The event sequence has been substantiated by high speed macrocinephotography of feeding larval *S. vittatum* (Craig, unpublished work).

During normal filter feeding, both fans are open and directed toward the current (Fig. 1,2). This usually requires that the larva twist its body longitudinally 180° either way to present its ventral surface to the current. (Normally the fan is further extended than shown in the figures, but critical-point-drying causes a small amount of shrinkage). The fans are adducted alternately (Fig. 3) and only when severely disturbed or during locomotion are both fans adducted at once. This involves a greater forward movement of the fan stem (fs) with the fans being pushed deeper into the cibarium (Fig. 4).

As the fan rays begin to close, both mandibles abduct to their fullest extent, probably rotating about axis of rotation "b" (Fig. 37). This enables one mandible to extend onto the adoral surface of the closing cephalic fan rays. The ray tips of the closed and adducted fan partly enter the cibarium as the adducting mandible sweeps over the aboral surface of the rays (Fig. 5). The mandible appears to be capable of sweeping only the distal two thirds of the closed fan since it reaches only to its aboral concave portion (Fig. 5). Neither does the mandible appear able to sweep the full width of the fan (Fig. 5, 6), nor do the apical (at) or spinous teeth (st) make contact with the fan rays (Fig. 6). The structures that appear more important are hairs of the covering brush (cb) and its more adoral robust hairs. Of particular importance are raking bristles (rb) of the distal adoral brush. These can clearly be seen interdigitating with the fan rays in Fig. 6. However, there are not enough raking bristles to interdigitate with all the fan rays. The softly pectinate hairs of the distal adoral brush (dab) merely sweep over the aboral surface of the closed fan rays as do hairs of the distal prosthecal brush (Fig. 6, 7); they do not interdigitate with the fan rays. Study of Fig. 6, 10, and 11 suggest that the ventrolateral rays of the closed fan are guided by the adoral median lobe (ml) of the mandible. This is shown by the squeezing together of the rays, best seen in Fig. 6 just under the distal prothecal brush (dpb). Figure 11 shows the proximal adoral brush (pab), directed by the adoral median lobe (ml), protruding under the closed and adducted fan. That the proximal adoral brush does in fact wipe the adoral surface of the closed fan has been confirmed by study of other larvae. The dotted outline (cf) on Fig. 10 shows the relationship of the closed, adducted cephalic fan rays to the adoral mandibular brushes.

During normal filter feeding, the tips of the closed fan rays which enter the cibarium are probably directed dorsally by the almost vertical hypopharynx (hypx) (Fig. 14, 18). But, even when fully retracted as in Fig. 4, not more than half the length of the fan rays enters the cibarium.

As the fan is abducted, the closed rays are pulled out from between the fully-adducted mandible and the labropalatum as suggested in Fig. 3. Once past the mandible the fan rays open

rapidly to continue filtering.

While browsing on the substrate, a larva of *S. tahitiense* always has its cephalic fans fully adducted, apparently as in Fig. 4. The larva, still attached by its posterior circlet of hooks, bends over and applies its mouthparts to the substrate. Mandibular movements were almost too rapid to observe, but working in unision, they appear to abduct only sufficiently to engage the dorsal articulation axis of rotation "a" (Fig. 37). During adduction the mandibular tip appeared to scrape the substrate, but exactly which structure did scrape was not clear. The maxillae abduct slightly after mandibular abduction begins, and they adduct just prior to mandibular adduction. The mandibles appear to brush over the adoral surfaces of the maxillae as they carry on into the cibarium to full adduction. Consistent browsing around itself by a larva, produces a U-shaped clear area on the substrate with the larva in the open end of the "U". Larvae were never observed to browse behind themselves.

Movement of larval *S. oviceps* mandibles appears similar to that of larval *S. tahitiense* during both filter feeding and/or browsing. Initially, both mandibles abduct dorsally until almost parallel to the extended cephalic fan stems. At this stage, the mandibular tips are clear of and above the labrum. It was this apparently exaggerated mandibular movement that prompted investigation of mandibular articulation. When filter feeding, fans are used alternately and when adducted are along the dorsolateral sides of the labrum (Fig. 23, 24). Adduction of the fan is too fast to observe. The mandibles and maxillae begin adducting as the labrum swells slightly. The mandibles adduct medially to the maxillary lobes (Fig. 21, 22, 30) and make contact with the hypostomial teeth (Fig. 35). The fan abducts slowly and its movement is followed by partial abduction of the mandibles.

The mandibles, instead of adducting medial to the maxillary lobes, often adduct more laterally thereby gathering them and forcing them completely into the cibarium. The palpi are not involved in this movement. Such mandibular movements occur between cephalic fan movements. The labiohypopharyngeal complex is also pushed into the cibarium at these times by the mandibles. The effect is rather startling as the larva appears to swallow its own mouthparts, as is seen on the *S. oviceps* larva's right side shown in Figure 23.

During browsing the cephalic fans are either fully adducted (Fig. 42) or left fully abducted and open (Fig. 43). Occasionally, only one cephalic fan was adducted. Browsing larvae cleared an almost closed C-shaped area on the substrate, often feeding behind themselves.

Activities of two *S. oviceps* larvae were each timed for five minutes. Approximately 20% of the time was spent filter feeding, 26% browsing while the fans were adducted, 13% browsing with the fans abducted and open, and 40% neither filter feeding nor browsing. During browsing, one or two complete mouthpart movements were made per second.

DISCUSSION

A summary of differences in mouthpart structure and feeding behaviour between larvae of *S. tahitiense* and *S. oviceps*, dealt with in this section, is given in Table 2.

Mouthpart Function

Observations made here from larvae of *S. tahitiense* strongly suggest that the mandibles are the most important mouthparts in removing food particles from the cephalic fans.

Food particles collected on the adoral surface of the fan rays may be removed by the mandibular raking bristles (rb) (Fig. 6) and by the proximal adoral brush (pab) (Fig. 10, 11) sweeping over the adoral surface of the fan. However, the mandible appears incapable of cleaning the full width of the closed fan. Certainly, the pectinate, distal adoral brush (dab) (Fig. 7) and the prosthecal brushes (dpb) (Fig. 6) of the mandible sweep only the aboral fan surface

where there are no food particles (Fig. 5, 6).

Table 2. Summary of Differences in Mouthpart Structure and Feeding Behaviour Between Larvae of *S. tahitiense* and of *S. oviceps*.

S. tahitiense	*S. oviceps*
Labropalatum broad Anterior palatal brush well developed	Labropalatum reduced, keel-like Anterior palatal brush reduced
Cephalic fans normal	Cephalic fans reduced
Mandibles normal with well developed adoral brushes and raking bristles. Apical teeth sharp. Prosthecal brushes normal. Articulation dorsoventral, with two axes of rotation	Mandibles shortened, strengthened and heavily sclerotized, adoral brushes reduced, raking bristles absent, but functionally replaced by spinous teeth and mandibular serrations. Apical teeth worn. Distal prosthecal brush slightly reduced. Articulation lateral, with one axis of rotation.
Maxillae normal	Maxillae normal, but appear relatively large in relation to other reduced mouthparts.
Labiohypopharyngeal complex normal.	Labial brushes slightly reduced.
Hypostomial teeth sharp, coadapted to fit mandibular teeth.	Hypostomial teeth worn, closely coadapted to fit mandibular teeth.
Feeding stance normal, body twisted 180° longitudinally during filter feeding.	Feeding stance modified, body twists only to 90° longitudinally during filter feeding.
Cephalic fans fully adducted during browsing.	Cephalic fans often abducted during browsing.

The subtly curved raking bristles (ab) are coadapted to interdigitate with the cephalic fan rays and to perhaps flick along the ray microtrichia (rm) (Fig. 6). The ability of simuliid larvae to filter feed on bacterial suspensions (Fredeen 1964) may be, in part, accounted for by the microtrichia and this suggested cleaning action.

The suggestion that the adoral brush and the raking bristles are important in removing food from the cephalic fans is further strengthened by the fact that *Twinnia biclavata* Stone and *Gymnopais* sp. (near *dichopticus* Stone) larvae, which lack cephalic fans, have the mandibular adoral brush reduced (Chance 1970 and Craig, per. obs. respectively). *Crozetia crozetensis* (Womersley) larvae have highly modified short-rayed cephalic fans, and the adoral brush of the mandible is slightly reduced (Dumbleton 1962, Davies 1965, Craig, pers. obs.).

The apical brush (ab) may be used for scraping the substrate during browsing. This is suggested by the extreme development of this brush on larval mandibles of *Gymnopais* sp. (near *dichopticus*) which, lacking cephalic fans, can only browse for food. However, *Twinnia biclavata* larvae, which also lack fans, do not show such extreme modification of the apical brush

(Craig, pers. obs.).

Simulium oviceps larvae appear to use the apical teeth of the mandibles to scrape the substrate for these show considerable wear (Fig. 25, 35), as I have indicated elsewhere (Craig 1975).

The inwardly-directed hairs of the anterior palatal brush (apb) on the labropalatum (Fig. 12, 13, 14, 26, 31) probably play as great a role in removal of food particles from the fans as do the mandibles. Such was suggested by Chance (1970). Still, even here, at greatest cephalic fan adduction, not all the adoral surface can be cleaned (Fig. 4). Assuming that the anterior palatal brush (apb) is responsible for removal of food from the closed fan, how is the food transferred from that brush to the cibarium? The maxillae do not appear to be involved in cleaning the fan (Fig. 5), but Fig. 13 shows that they could, during adduction, brush food off the anterior palatal brush (apb) toward the cibarium. The dorsal brush of the maxilla could in turn be cleaned by the inwardly-directed hairs of the anterior palatal brush, as the maxilla abducted.

The prosthecal brushes (Fig. 5, 6, 25), although wiping the aboral surface of the closed fan rays, appear to be more important in cleaning the anterior palatal brush. All three prosthecal brushes wipe over the anterior palatal brush during adduction of the mandible and, at full adduction, the proximal prosthecal brush (ppb) can be seen projecting along the cibarium (Fig. 12, 31). Again, these brushes would be cleaned themselves in turn during mandibular adduction by the anterior palatal brush.

Observations on larval *S. oviceps* mouthparts suggest that the adoral sculpted area (sca) of the maxilla (Fig. 30) is not molar in function, but instead resists abrasion of the mandibular apical teeth (Fig. 30). The dorsal brush (db) may also serve such a function. Any food particles collected on the aboral maxillary brush during filter feeding or browsing could be cleaned off by the labial brushes (lb) (see Fig. 13, 14, 20) as the maxillae adduct. The relationship of mandibular teeth to the maxillae suggests that food particles collected on the maxillary brushes could be cleaned off by the apical teeth, particularly the spinous teeth of the mandible (Fig. 3, 4, 5).

Certainly, the apical teeth and spinous teeth of the mandible are not involved in cleaning the anterior palatal brush (apb). Fig. 12, 31 show that these structures do not meet that brush during adduction. However, the raking bristles (rb) of the mandibular distal adoral brush do make contact with the anterior palatal brush as does the main body of the distal adoral brush (not clearly evident in Fig. 12).

Reduction of covering brush and distal adoral brush, plus absence of raking bristles from mandibles of larvae of *S. oviceps*, which have reduced cephalic fans, supports the probable important role of these structures in removal of food particles as indicated for typical cephalic fans of *S. tahitiense*.

Which mandibular structures are used by larvae of *S. tahitiense* to rake particles from their cephalic fans is not known, but the absent raking bristles may be replaced functionally by the spinous teeth (sp) and mandibular serrations (ms), as suggested in Fig. 25 where these structures are situated favourably for such a function.

Modifications, such as strong dorsal ridge, massive sclerotization and perhaps shifted articulations of mandibles of *S. oviceps* larvae appear well suited for an enhanced browsing role.

The other less modified structures, such as apical brush and prosthecal brushes on mandibles of *S. oviceps* larvae suggest that these structures have a more general role in feeding, one not associated with the cephalic fans, or even functions not associated with feeding at all.

The general adoral orientation of hairs and brushes on the mouthparts ensures that food once introduced into the system will, by repeated movements of the mouthparts, be worked posteriorly into the cibarium. Furthermore, the system will be self-cleaning. Mouthparts in

general are integrating structures for taking a relatively dilute food source, the particles in the water, and concentrating it into a bolus in the cibarium.

The general sequence of mouthpart movements suggested here for filter feeding agrees with that proposed by Fortner (1937) and Chance (1970). Kurtak (1973) studied mouthpart movement of simuliid larvae of many species cinephotographically, and his observations agree with most of the sequence proposed here. However, he states clearly (his p. 85) that the mandible wipes over the adoral ("inner surface") of the closed fan. He further observed that the mandible often cleaned the secondary fan (sf) (see Fig. 1 here) of the partly closed cephalic fan.

Kurtaks' observation of the mandible cleaning the adoral surface of the fan is at total variance with observations of Fortner (1937), Chance (1970) and with those presented here.

The film sequence of larval *Simulium pictipes* feeding given by Kurtak (1973, his Fig. 64) shows mainly silhouettes, and although mandible and fan can be identified, their spatial relationship is not clear. Furthermore, typical mandibular structure as illustrated by that of *S. tahitiense* larvae, tends to preclude such movement by the mandibles as there is only the apical brush on the aboral surface of the mandible to wipe the adoral surface of the fan.

I have made extensive high speed macrocinephotographic observations on feeding of larval *S. vittatum* (300 frames per sec at 1/1300 sec shutter speed, versus the 64 fps at 1/300 sec shutter speed of Kurtak) and have not observed such a movement.

Kurtaks' observation that the mandible is sometimes used to clean the secondary fan may be correct. A partly adducted fan could easily bring the secondary fan within reach of the apical structures of the mandible.

Sensory Organs

Palatability of food is probably detected first by the adoral basiconic sensilla (bs) of the maxillae (Fig. 13, 15, 16, 29) as these are the first sensilla with probable gustatory function which make contact with the food. The labial palpal sensilla (Fig. 19, 33) probably further check the food as it is pushed into the cibarium. Maxillary palpal sensilla (Fig. 17) never make contact with filtered food and may be involved in sensing water, or substrate during browsing.

Mandibular-Hypostomial Coadaptation

If the mandibles are adducted while being viewed through the *foramen magnum* it is immediately clear that, as the mandibles rotate on their axes and approach the hypostomium, the profile of their apical teeth changes. Instead of the teeth appearing sharp as is usually figured for simuliid larval mandibles (Fig. 6, 8, 25), they become apparently more rounded in profile (Fig. 39, 40). Furthermore, the mandibular tips travel almost parallel to the hypostomial teeth when they meet as is suggested in Fig. 37. The close coadaptation of the teeth in larval *S. oviceps* appears to be involved in some way in wear of the hypostomial teeth. Recently ecdysed larvae have sharp hypostomial teeth (Craig 1975), but these later become worn (Fig. 35, 36), and in mature 9th instar larvae are often extremely worn in the two places where the mandibles make contact (Fig. 41).

Coadaptation of mandibular and hypostomial teeth in larval *S. tahitiense* is not as close as that in larval *S. oviceps*. However, the outer and apical mandibular teeth, when in contact with the hypostomium, are almost parallel to the lateral hypostomial teeth and the mandibular teeth tips fit between the hypostomial teeth (Fig. 39). It seems clear that the shape of the hypostomium and its teeth are coadapted to allow close contact with the mandibular teeth. Wood, Peterson, Davies and Gyorkos (1963), and Crosskey (1973) have suggested that the hypostomial teeth in larval simuliids are used to cut the silk strand. Observations here of the close coadaptation between mandibular and hypostomial teeth strongly supports their suggestion, but indicates that the mandibles are also involved in cutting.

A close examination of mandibular and hypostomial teeth coadaptation, as done here, might clarify the reasons for the considerable variation in these teeth in larval Simuliidae.

Mandibular Articulation

The double socket of the mandibular dorsomedian articulation is probably widespread in typical larval simuliids as it allows the mandibles more extensive abduction to gather the closed and adducting cephalic fan rays. Couvert (1970) clearly illustrated this double socket for larval *Prosimulium conistylum* Rubtzov, but made no comment on its function.

Changes in plane of mandibular movement of larval *S. oviceps* has been made possible by the narrowing of the labropalatum to its present keel-shape (Fig. 21, 23). Such a narrowing, probably concomitant with reduction of the cephalic fan (Craig 1974), has rotated the original dorsomedial articulation of the mandible to a more medial position almost lateral to the lateral articulation (Fig. 38). This arrangement of articulations allows only an almost vertical plane of mandibular movement, but one closely coadapted to the shape of the labropalatum. This modification may allow more of the mandibular apex to be used for browsing and may also account for the generally linear profile of the hypostomium in comparison to that of larval *S. tahitiense* (Fig. 21, 40, cf 18, 20, 39).

Feeding Behaviour

Feeding behaviour of *S. oviceps* larvae is not strikingly different from that of the more typical *S. tahitiense* larvae. Browsing is an integal part of larval simuliid feeding behaviour (Serra-Tosoi 1967) and *S. oviceps*, having reduced cephalic fans, has modified mandibular and hypostomial teeth for more intensified browsing. However, the length of time larvae spent browsing did not differ greatly from that observed for larval *S. venustum*, (Mokry 1975) and larval *S. vittatum* (Chance, pers. comm., 1977). The only truly unusual feeding behaviour of larval *S. oviceps* is that their cephalic fans can be open while they browse. Such behaviour is precluded for typical simuliid larvae because their cephalic fan rays are too long.

The function of many mandibular structures is still unknown. It is possible that they are involved in other aspects of larval life besides feeding, such as silk manipulation during cocoon formation prior to pupation (Crosskey, in litt, 1976). Certainly, at that time, the mandibles are moved rapidly over the forming cocoon as the larva weaves its body back and forth (Craig, pers. obs.).

The mandibles may also be involved when a larva pulls itself along the silk thread secreted after it detaches. Observation on detached *Simulium vittatum* larvae (Craig, pers. obs.) show that movement up the thread involves rapid, repetitive mandibular morements, plus slower movements of the proleg which is brought up to and into the mouthparts. Larvae can move at about 2 cm per minute up the silk thread using this method.

This study of mouthpart movement and feeding behaviour in closely-related Tahitian simuliid larvae, has not answered the original question of why *S. oviceps* has reduced cephalic fans and modified mandibles. However, the functional relationships of larval simuliid mouthparts have been further clarified.

One possible reason for presence of reduced cephalic fans in larval *S. oviceps* concerns food availability. While collecting *S. oviceps* larvae, I attempted to collect simuliid eggs from the Punaruu river with a plankton net. However, within a few minutes the net clogged with organic material. Perhaps ancestral *S. oviceps* larvae, faced with a rich food supply, could afford reduction of their cephalic fans and yet still filter sufficient food. This suggestion does not explain why larvae of *S. tahitiense* and of *Simulium* sp. (probably *cheesmanae*), occurring in the same habitats as *S. oviceps* larvae, retained the typical cephalic fan. The evolution of Tahitian Simuliidae is more likely correlated with the geological history of the two major parts of the island, Tahiti-iti and Tahiti-nui, but that is outside the scope of this work.

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ABBREVIATIONS

"a" & "b"	Axis of rotation	ma	Median articulation
aab	Aboral apical brush	maa	Mandibular adductor apodeme
ab	Apical brush	ml	Aboral median lobe
abt	Antennal buttress	mnd	Mandible
ama	Mandibular abductor apodeme	mpb	Median prosthecal brush
ami	Aboral mandibular inflexion	ms	Mandibular serrations
ant	Antenna	mxl	Maxillary lobe
ants	Antennal socket	mxp	Maxillary palpus
apb	Anterior palatal brush	ns	Nipple-like sensillum
as	Anteromedian strut	ocp	Occiput
at	Apical tooth	os	Ovoid sensillum
bs	Basiconic sensillum	ot	Outer teeth
cb	Covering brush	pat	Preapical teeth
cf	Cephalic fans	pab	Proximal adoral brush
cs	Cone-shaped sensillum	plg	Proleg
dab	Distal adoral brush	ppb	Proximal prosthecal brush
db	Dorsal brush	ppg	Palpifer
dma	Dorsomedial articulation	ps	Preapical sensilla
dpb	Distal prosthecal brush	rb	Raking bristles
dr	Dorsal ridge	rm	Ray microtrichia
ds	Dichotomous bristles	s	Small sensillum
fs	Fan stem	sa	Spinose area
gs	Globular sensillum	sas	Salivary silk
hyp	Hypostomium	sca	Sculptured area
hypt	Hypostomial teeth	sf	Secondary fan
hypx	Hypopharynx	st	Spinous teeth
la	Lateral articulation	su	Sulcus
lap	Labial palpus	ta	Tormal apodeme
lb	Labial brush	ts	Trichoid sensillum
lcb	Lacinial bristles	tus	Tubular sensillum
lig	Ligular plate	va	Ventrolateral articulation
lp	Labropalatum		

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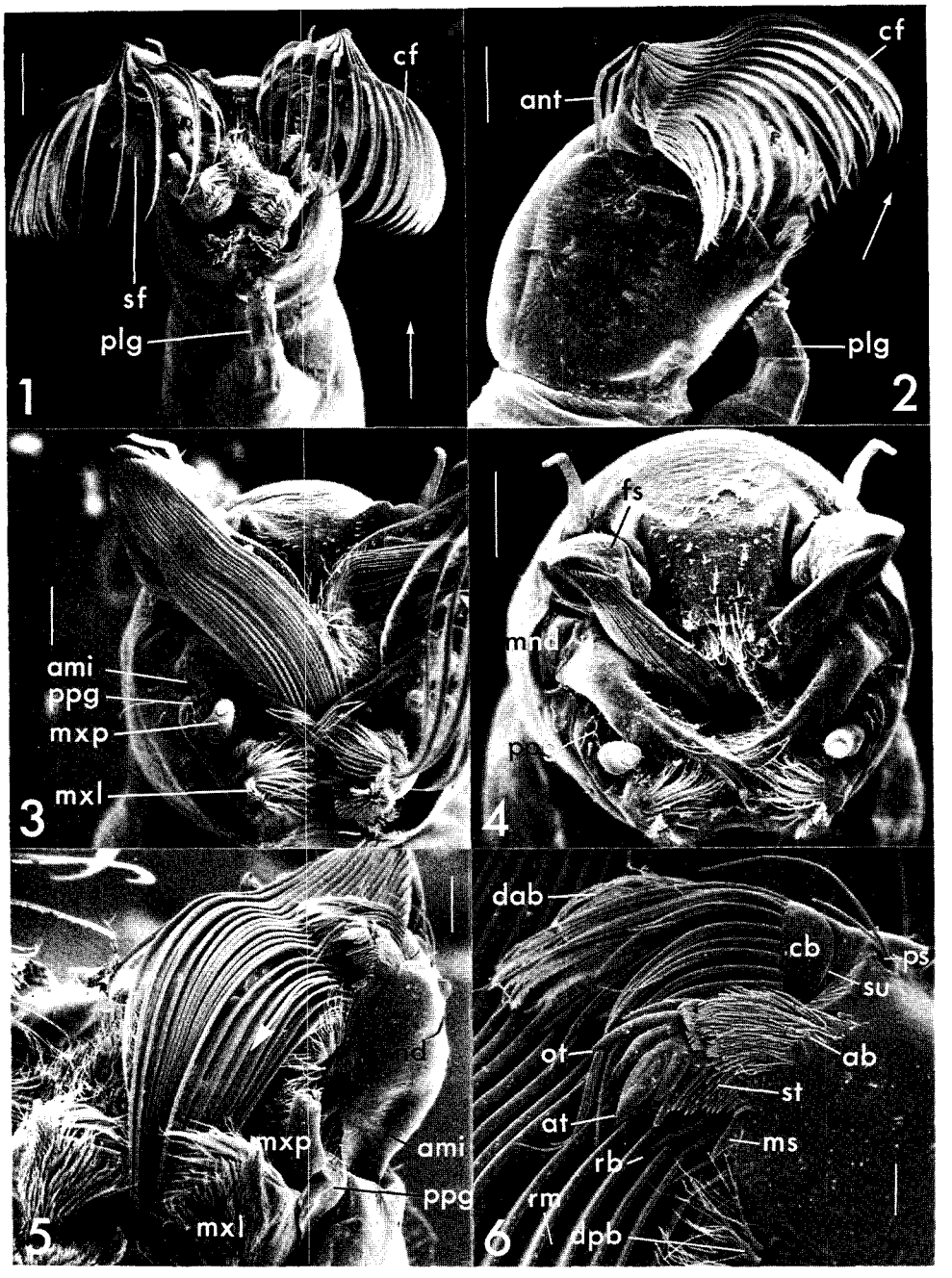
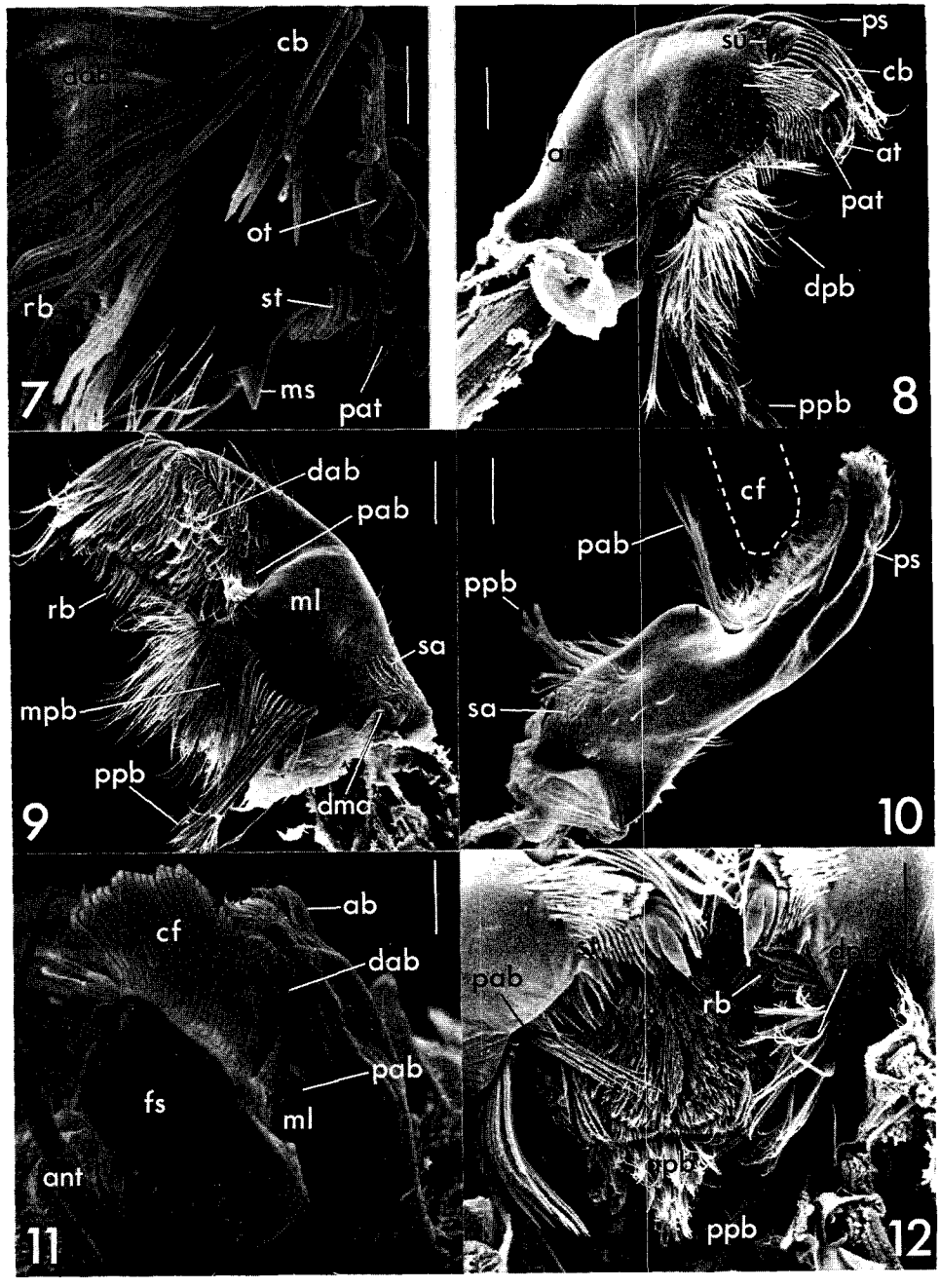
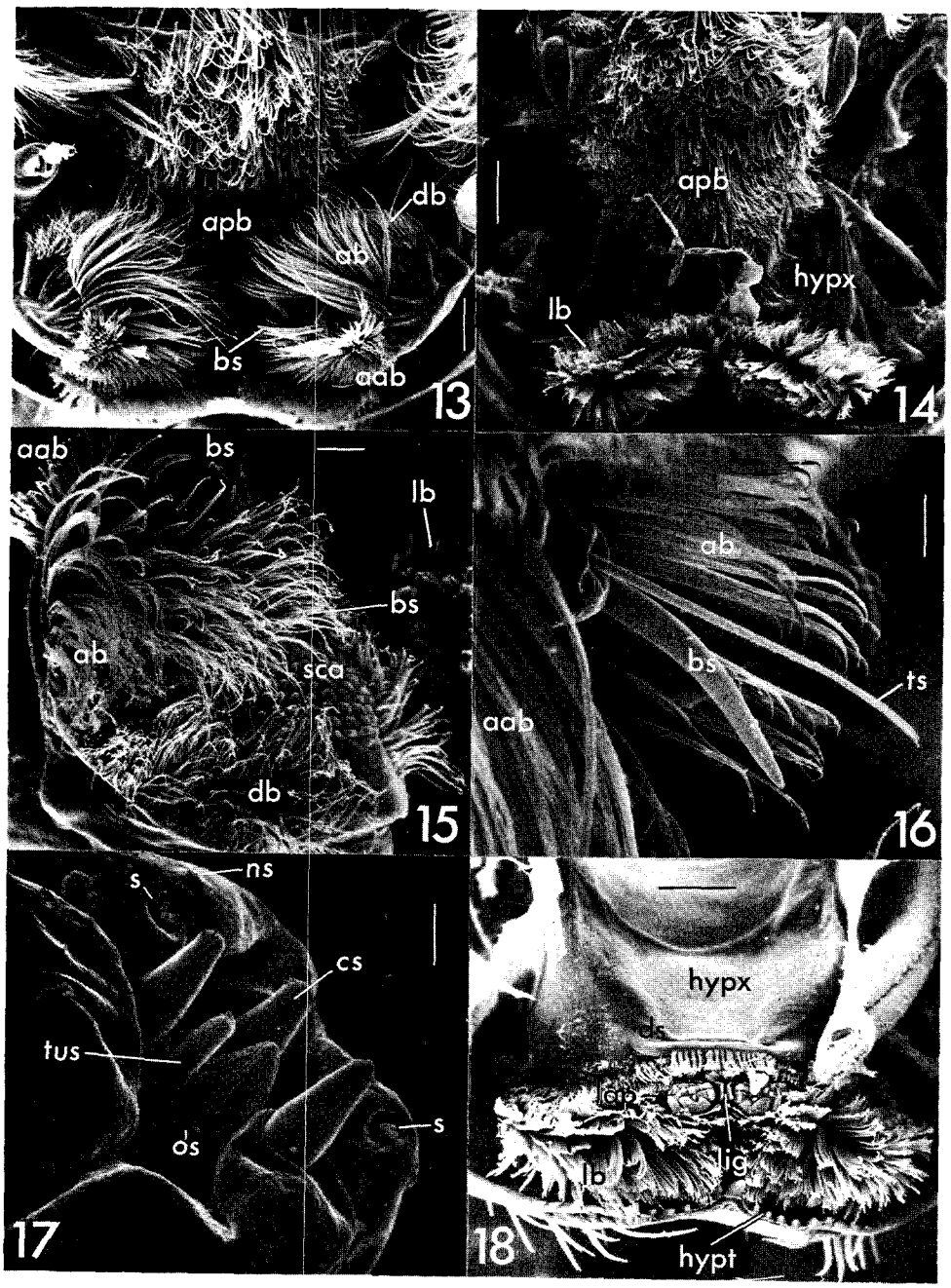


Fig. 1-20. Larval *Simulium tahitiense*. Fig. 1. Anterior view, cephalic fans (cf) fully abducted and open. Arrow indicates direction of water flow. Scale 200 μm. Fig. 2. Same, lateral view. Scale 200 μm. Fig. 3. Anterior view of right cephalic fan closed and adducted as in normal filter feeding. Scale 100 μm. Fig. 4. Anterior view of both cephalic fans adducted to fullest extent. Scale 100 μm. Fig. 5. Anteroventral view of left mandible (mnd) adducting over aboral surface of closed, adducted cephalic fan. Arrow indicates direction of movement. Scale 50 μm. Fig. 6. Tip of left mandible showing close coadaptation of raking bristles (rb) to rays of closed cephalic fan. Scale 20 μm.



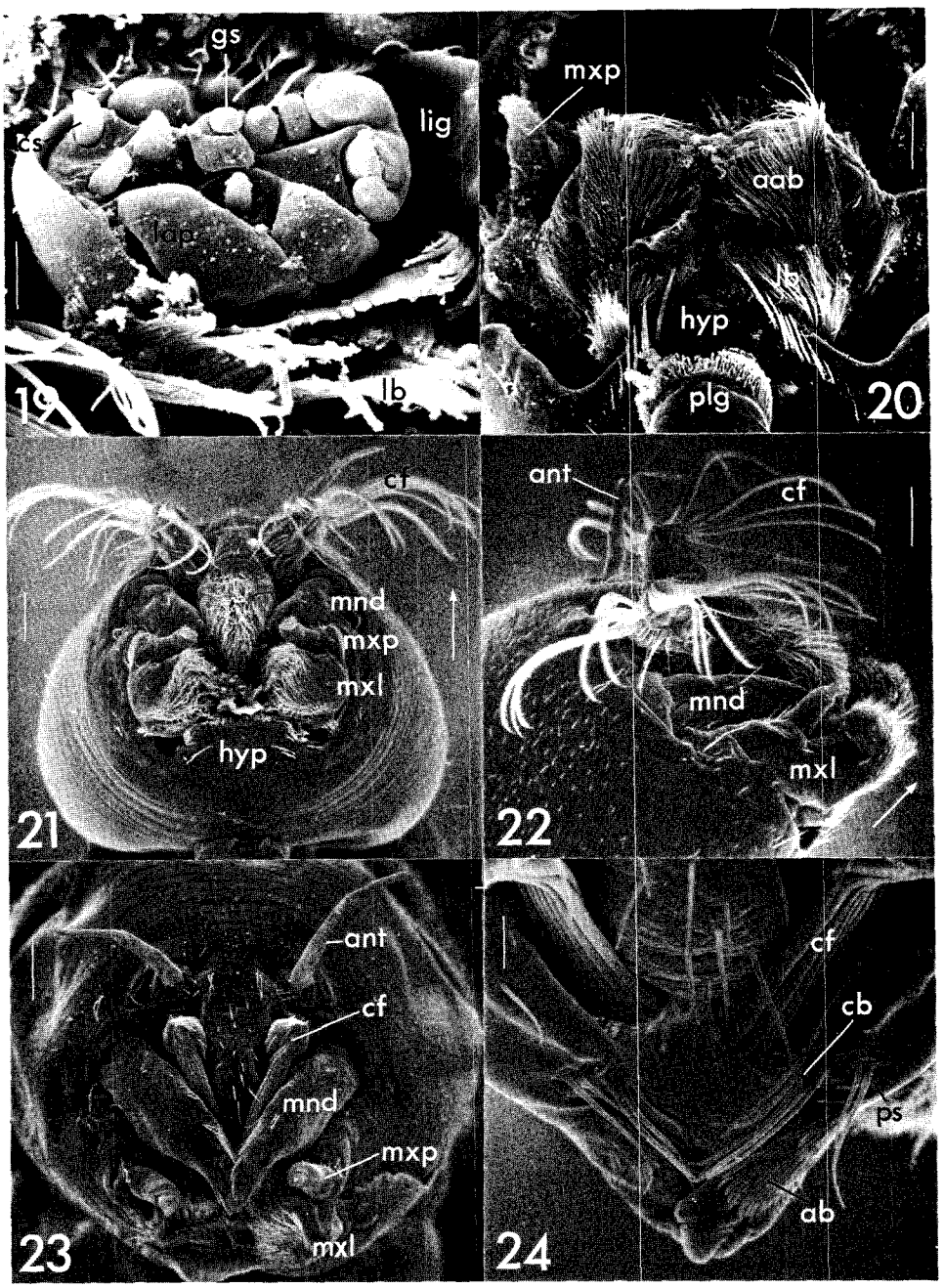
Larval *Simulium tahitiense* (con't).

Fig. 7. Apical view, adoral surface of left mandible. Scale 10 μm. Fig. 8. Aboral surface of right mandible. Scale 50 μm. Fig. 9. Adoral surface of right mandible. Scale 50 μm. Fig. 10. Dorsal surface of right mandible. Scale 50 μm. (dotted line indicates position of adducted cephalic fan). Fig. 11. Dorsal view of right mandible and adducted cephalic fan showing co-adaptation of closed fan rays to adoral median lobe (ml) and proximal adoral brush (pab). Scale 50 μm. Fig. 12. Ventral view of anterior palatal brush (apb) and mandible (Dissected specimen). Scale 50 μm.



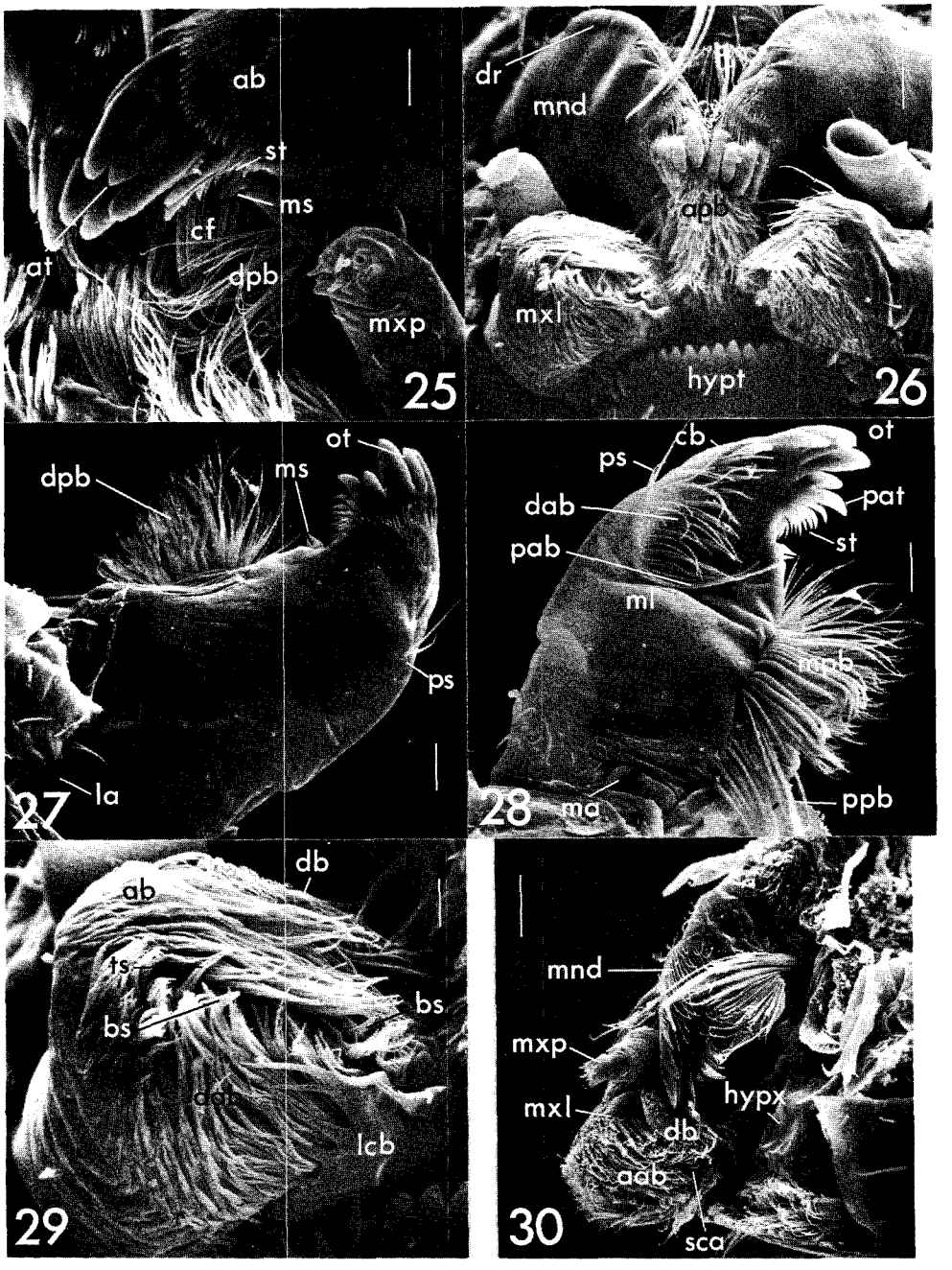
Larval *Simulium tahitiense* (con't).

Fig. 13. Anterior view of anterior palatal brush (apb) and maxillae. Scale 50 μm. Fig. 14. Anterior view of anterior palatal brush, hypopharynx (hypx) and labial brushes (*lb*) (Dissected specimen). Scale 50 μm. Fig. 15. Dorsal view of adoral surface of left maxillary lobe. Scale 20 μm. Fig. 16. Distal sensilla of maxillary lobe. Scale 10 μm. Fig. 17. Adoral view of maxillary palpus apical sensilla. Scale 2 μm. Fig. 18. Anterior view of hypophyarynx, labial palpi (lap) and hypostomial teeth (hypt). Scale 50 μm.



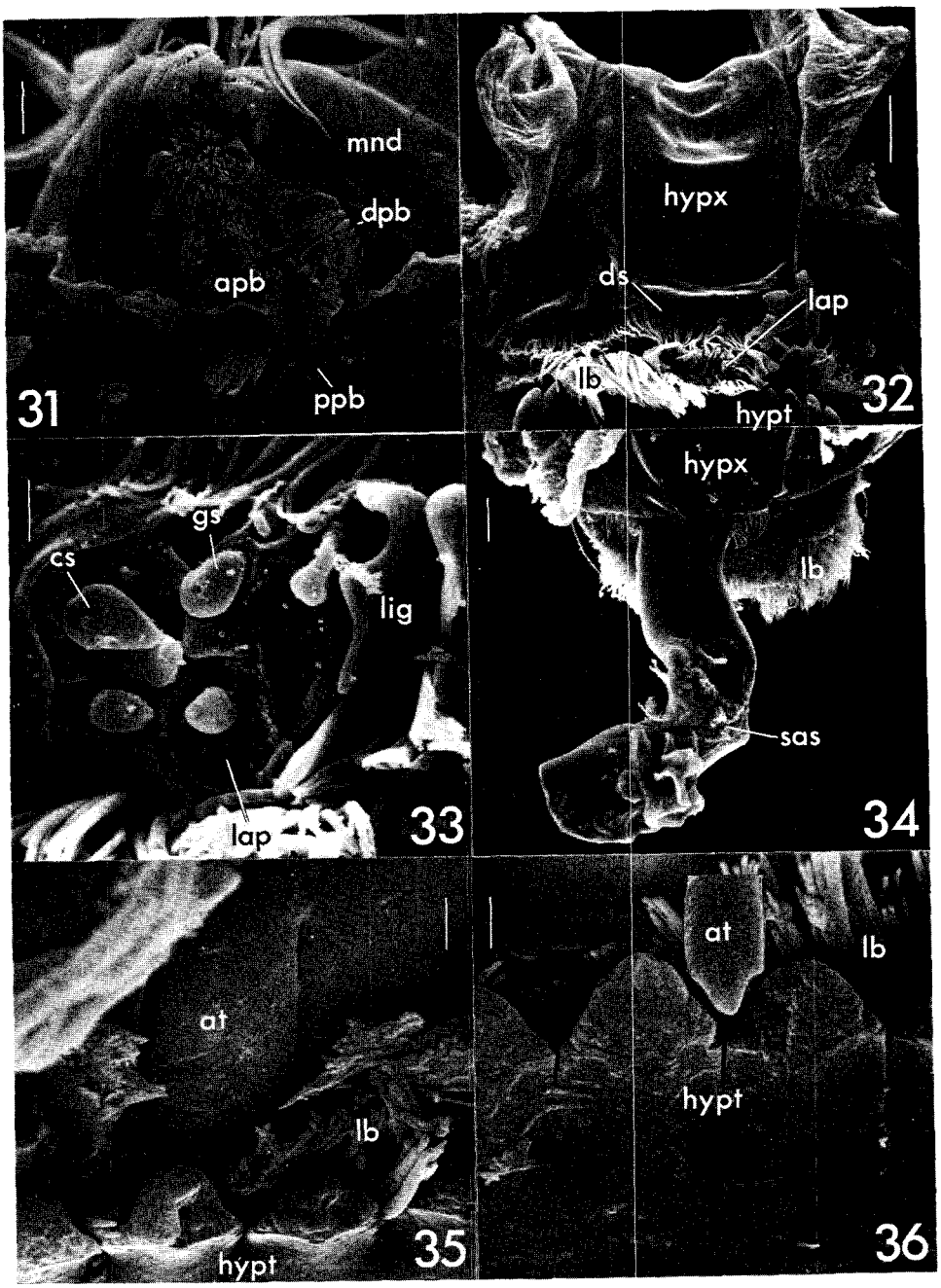
Larval *Simulium tahitiense* (con't).

Fig. 19. Labial palpi sensilla. Scale 5 μm. Fig. 20. Ventral view of maxillary lobes, labial brushes and hypostomium (hyp). Scale 50 μm. Fig. 21 - 38. Larval *Simulium oviceps*. Fig. 21. Anterior view, cephalic fans fully abducted and open. Arrow shows direction of water flow. Scale 50 μm. Fig. 22. Same, lateral view. Scale 50 μm. Fig. 23. Anterodorsal view of adducted cephalic fans. Scale 50 μm. Fig. 24. Dorsal view showing relationship of partly adducted mandible tips to the fully adducted cephalic fans. Scale 20 μm.



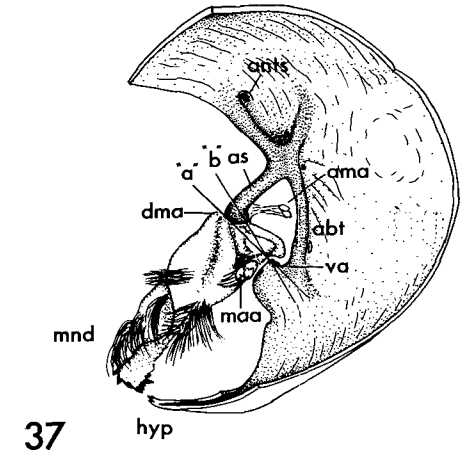
Larval *Simulium tahitiense* (con't).

Fig. 25. Lateral view of adducted cephalic fan rays and mandibular tip. Scale 10 μm. Fig. 26. Anterior view of relationship between adducted mandible and anterior palatal brush (apb). Scale 20 μm. Fig. 27. Aboral surface of left mandible. Scale 20 μm. Fig. 28. Adoral surface of left mandible. Scale 20 μm. Fig. 29. Anteromedial view of maxillary lobe. Scale 10 μm. Fig. 30. Dorsolateral view of relationship of fully adducted mandible and maxillary lobe. (Dissected specimen.) Scale 50 μm.



Larval *Simulium tahitiense* (con't).

Fig. 31. Ventral view showing relationships of mandibular prosthecal brushes (ppb, dpb) to the anterior palatal brush. (Dissected specimen.) Scale 20 μm. Fig. 32. Anterodorsal view of hypopharynx. Scale 20 μm. Fig. 33. Labial palpus sensilla. Scale 2 μm. Fig. 34. Salivary silk strand (sas) emerging from salivary gland opening under the hypopharynx (hypx). Scale 20 μm. Fig. 35. Anterior view of coadaptation of mandibular apical tooth and hypostomial teeth. Scale 5 μm. Fig. 36. Ventral view of hypostomial teeth (Insert of apical tooth of mandible, not to scale, shows close coadaptation in shape). Scale 2 μm.



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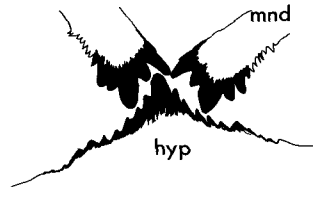

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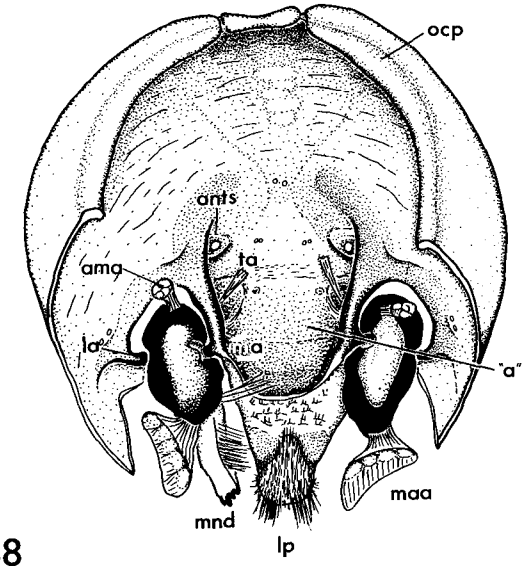

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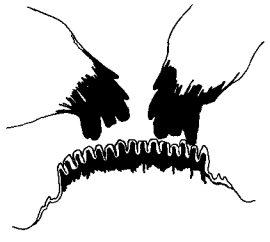

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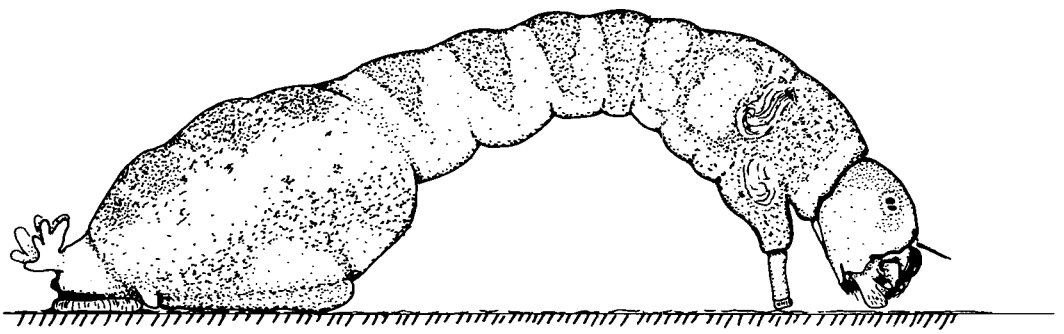
Fig. 37. *Simulium tahitiense*. Posterolateral internal view of mandibular articulation. Head cut dorsoventrally; labrum removed. Scale 0.1 mm. Fig. 38. *Simulium oviceps*. Posteroventral internal view of mandible articulation. Head cut horizontally. Scale 0.1 mm. Fig. 39. *Simulium tahitiense*. Posterior view of hypostomial teeth and fully adducted mandibular apical teeth. Scale 0.05 mm. Fig. 40. *Simulium oviceps*. Same. Fig. 41. *Simulium oviceps*. Hypostomium of late 9th instar larva showing wear of teeth. Scale 0.05 mm.



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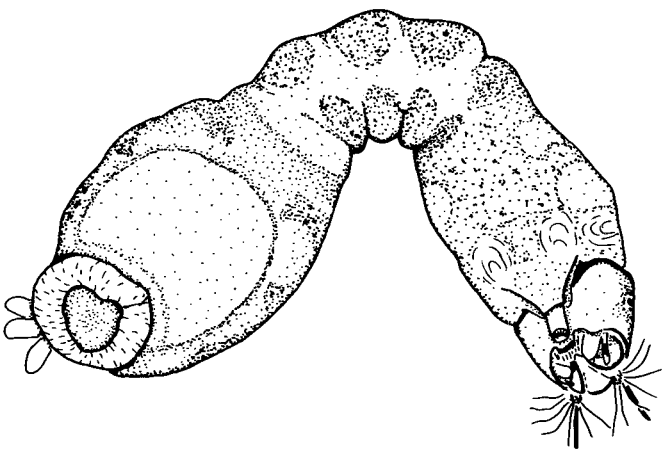

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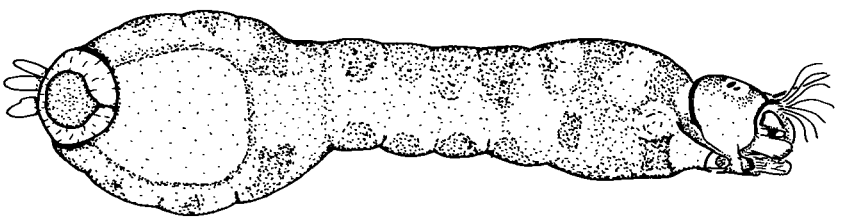

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Fig. 42-44. Larval *Simulium oviceps*. Fig. 42. Lateral view of typical larval stance during browsing (fans adducted). Scale 1.0 mm. Fig. 43. Ventral view of larva browsing (cephalic fans abducted). Fig. 44. Ventral view of larva filter feeding.