

Chapter 12

Setae and Microtrichia: Structures for Fine-Particle Feeding in Aquatic Larvae

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INTRODUCTION

Fine organic material is the most abundant food source in aquatic ecosystems and can be categorized on the basis of particle size: ultra-fine particulate organic matter (UFPOM, 0.5–50 μm), fine particulate organic matter (FPOM, 50–1,000 μm), and coarse particulate organic matter (CPOM, >1,000 μm) (Cummins and Klug, 1979). Dissolved organic matter (DOM) is of molecular dimensions. Organic particle distribution in freshwater ecosystems is a function of particle size. Smaller particles remain suspended, while larger ones are loosely deposited. Particles may also become attached to the substratum. Both particle size and location influence the structures and mechanisms for successful feeding.

The functional feeding group (FFG) classification of Cummins (1973, 1974) provides a basis for comparing feeding behavior in aquatic environments. Although this classi-

fication encompasses feeding activities that utilize a wider range of food types than the fine material under consideration here, the FFG classification of specifically fine particle feeders has been further refined (McShaffrey and McCafferty, 1988) (Table 1).

Three recent approaches to FFGs, using the ultrastructure of feeding appendages, are of particular interest from a structural perspective. (1) A morpho-behavioral approach is exemplified by the work of McShaffrey and McCafferty (1986, 1988, 1990, 1991) and Bae and McCafferty (1991). They observed and described the feeding behavior of several North American Ephemeroptera, distinguished the sequential movements of individual structural units, and linked the mechanisms of structure to morphology at an ultrastructural level. (2) In a morpho-ecological approach, Palmer (1991) used the ultrastructure of larval simuliid feeding appendages to discriminate closely related,

TABLE 1. A Functional Feeding Group (FFG) Classification of Fine-Particle Feeders Based on That of McShaffrey and McCafferty (1988).

| FFG | Type | Food | Structures used |
|------------|--|---|--|
| Filterers | Passive net Passive setal Active | Suspended UFPOM and FPOM Suspended UFPOM and FPOM Deposited UFPOM and FPOM, which has been actively suspended | Silk nets Setae |
| Collectors | Gatherers Brushers Scrapers | Loosely deposited UFPOM and FPOM Loosely deposited UFPOM and FPOM Organic material attached to a substrate | Body parts other than setae, e.g., leg setae Body parts such as chitinous maxillary scraping bars |

UFPOM, ultra-fine particulate organic matter, 0.5–50 μm ; FPOM, fine particulate organic matter, 50–1,000 μm .

morphologically similar species that live in different habitats and therefore utilize different food resources. In this example, larval feeding structures provided an ecologically meaningful basis for the morphological discrimination of closely related species. (3) Using a morpho-mechanistic approach, Dahl et al. (1987) considered the mechanical implications of filter feeding by small culicid larvae. They developed a functional, systems-based (Rountree, 1977) model of feeding morphology and the mechanisms for particle flow and retention and analyzed the interaction between structure, behavior, and abiotic conditions in suspension feeding (e.g., feeding under conditions of low Reynold's number [Vogel, 1981]). A similar approach to simuliid and oligoneurid filter feeding was followed by Braimah (1987a,b).

The structural similarity of setae and microtrichia associated with the feeding habits of particular FFGs is identifiable in several aquatic insect genera, families, and orders from a variety of localities worldwide. In this chapter, the aim is to present evidence that there is a morphological basis for the ecologically identified FFGs: passive filterer (Figs. 1–11), active filterer and gatherer (Fig. 12), brusher (Figs. 13–24), and scraper (Fig. 25). The data presented here are static, and from a structural and functional perspective further morpho-behavioral and morpho-mechanistic research would be fruitful.

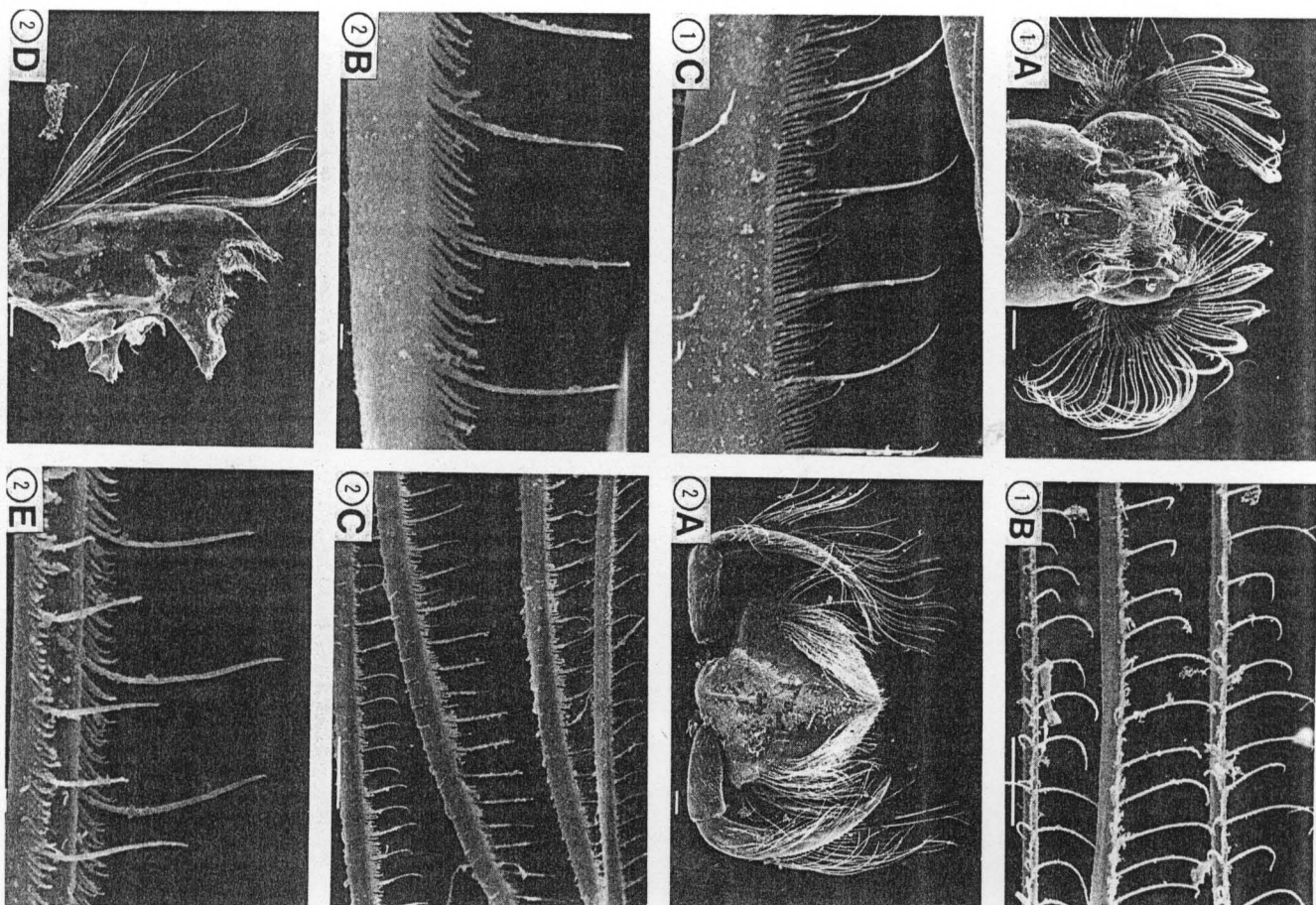
SETAE: THE BASIS OF FINE PARTICLE FEEDING

Setae, bare or with a variety of patterns of microtrichia, are fundamentally character-

istic of fine-particle feeding (McShaffrey and McCafferty, 1986, 1988, 1990; Braimah, 1987b; Dahl et al., 1987; Bae and McCafferty, 1991; Palmer, 1991; Palmer et al., 1993). From the literature, and from a study of mouthparts from the aquatic larvae of South African Diptera (Simuliidae) and Ephemeroptera (Oligoneuridae, Baetidae, Heptageniidae, Leptophlebiidae, Tricorythidae, Caenidae), three categories of setae may be distinguished: stout setae, fine setae, and comb setae (Table 2).

Stout setae have no microtrichia. Examples occur on the inner margin of oligoneurid maxillae (Fig. 10J) and in rows at the base of the setal series that comprise leptohebiid and heptageniid brushes (Figs. 17B, 18B, 19B, 20B, 21B, 22B, 23, and 25A).

Fine setae may be with or without microtrichia. Long fine setae without microtrichia are found on the forelegs of a species within the Caenidae (Palmer et al., 1993). Short, curved, fine setae without microtrichia are found dorsally on the apical joint of oligoneurid labial palps (Figs. 10C,D, 11D,E), where they appear to serve the same abrading function as the stout setae in a lep-



Figs. 1, 2. Arrays of setae used by passive setal filterers to feed on fine suspended organic particles characteristically have one or two rows of subequal or unequal microtrichia. These are exemplified by the cephalic fan (Fig. 1A) and fan setae (Fig. 1B,C) of *Simulium gairdneri* (Simuliidae: Diptera); and the labium (Fig. 2A), labial setae (Fig. 2B,C), mandible (Fig. 2D), and mandibular setae (Fig. 2E) of *Tricorythus discolor* (Tricorythidae: Ephemeroptera). 1C, 2B, 2E. Bars = 1 μm ; 1B, 2C, bars = 10 μm ; 1A, 2A, 2D, bars = 100 μm .

TABLE 2. A Descriptive Classification of Setal Types Based on Data From the Literature and on a Study of South African Diptera and Ephemeroptera

| Setal type | Microtrichia |
|-------------|---|
| Stout setae | None |
| Fine setae | Without microtrichia With microtrichia |
| | Feathery Pectinate Equal Subequal or unequal |
| Comb setae | Variable |

tophlebiid or heptageniid setal brush (Figs. 13-16).

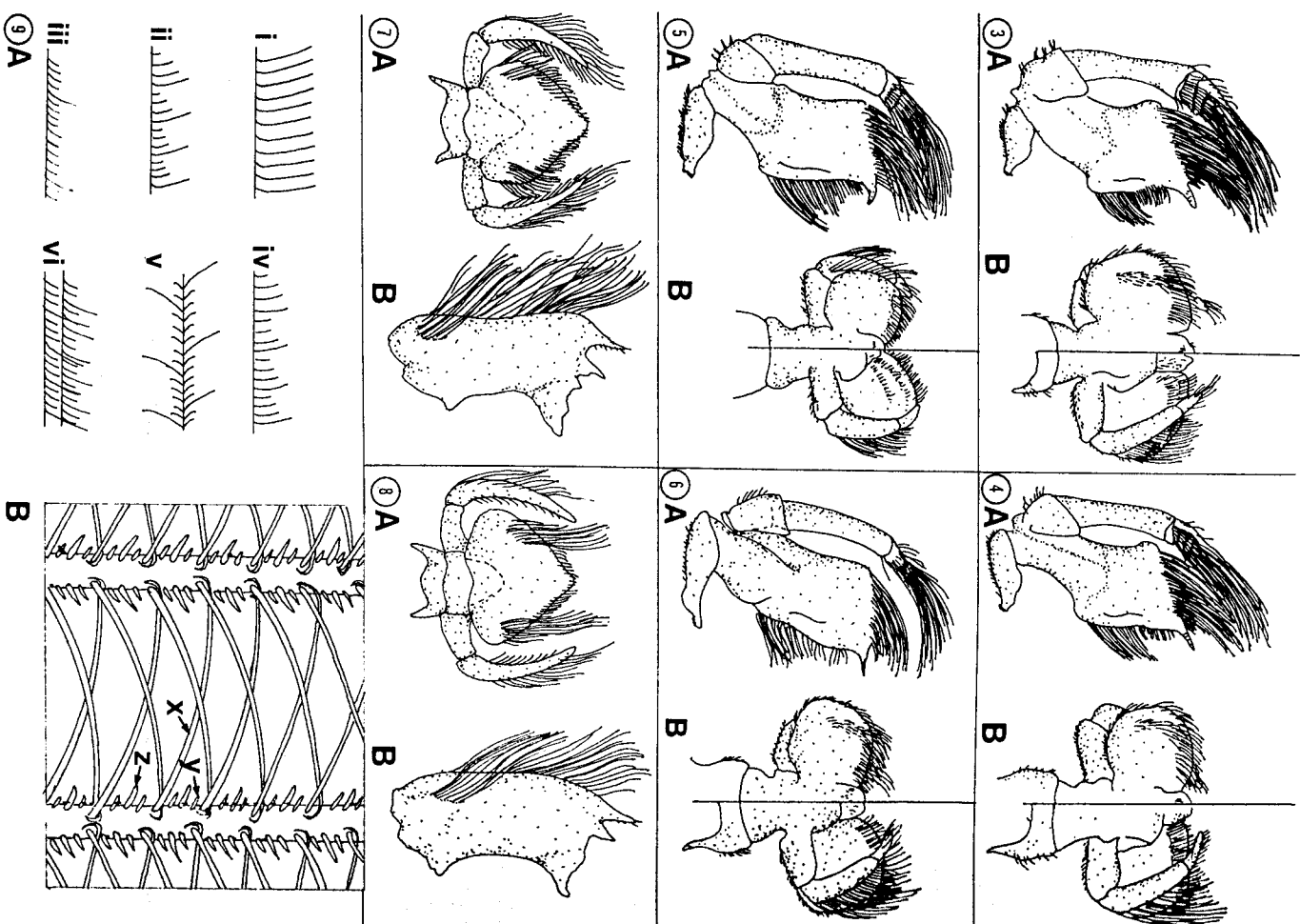
Microtrichia on fine setae may be feathery or pectinate. Feathery microtrichia are long and irregular. Examples occur in the Oligoneuriidae, on the dorsal labial surface (Figs. 10A,B, 11J,MK) and hypopharynx (Figs. 10G,H, 11F,G). There are two forms of fine setae with pectinate microtrichia. Equal microtrichia are evenly spaced, of equal length, and may occur in one or two rows. These are ubiquitous and are found on various mouthpart appendages of all fine-particle feeders. Equal microtrichia may be longer ($>3 \mu\text{m}$) or shorter ($<3 \mu\text{m}$) (Palmer et al., 1993). Filterers usually have longer microtrichia (Bae and McCafferty, 1991) (Figs. 10F, 11L), and gatherers shorter ones (Palmer et al., 1993) (Fig. 12). Pectinate setae

with short microtrichia occur on the ventral surface of oligoneuriid labia (Fig. 11I), while the anterior setae of a brush (Figs. 17B, 18B, 19B, 20B, 21B, 22B, 23, and 25A) have microtrichia that are curved. Pectinate microtrichia may also be subequal or unequal. In this case setae have long microtrichia interspersed with shorter ones (Figs. 1B,C, 2B,C,E, 9A,B, 10K) or have shorter microtrichia at the base of the longer ones (Figs. 11B,C). These setae are exclusively characteristic of feeding by passive setal filtration.

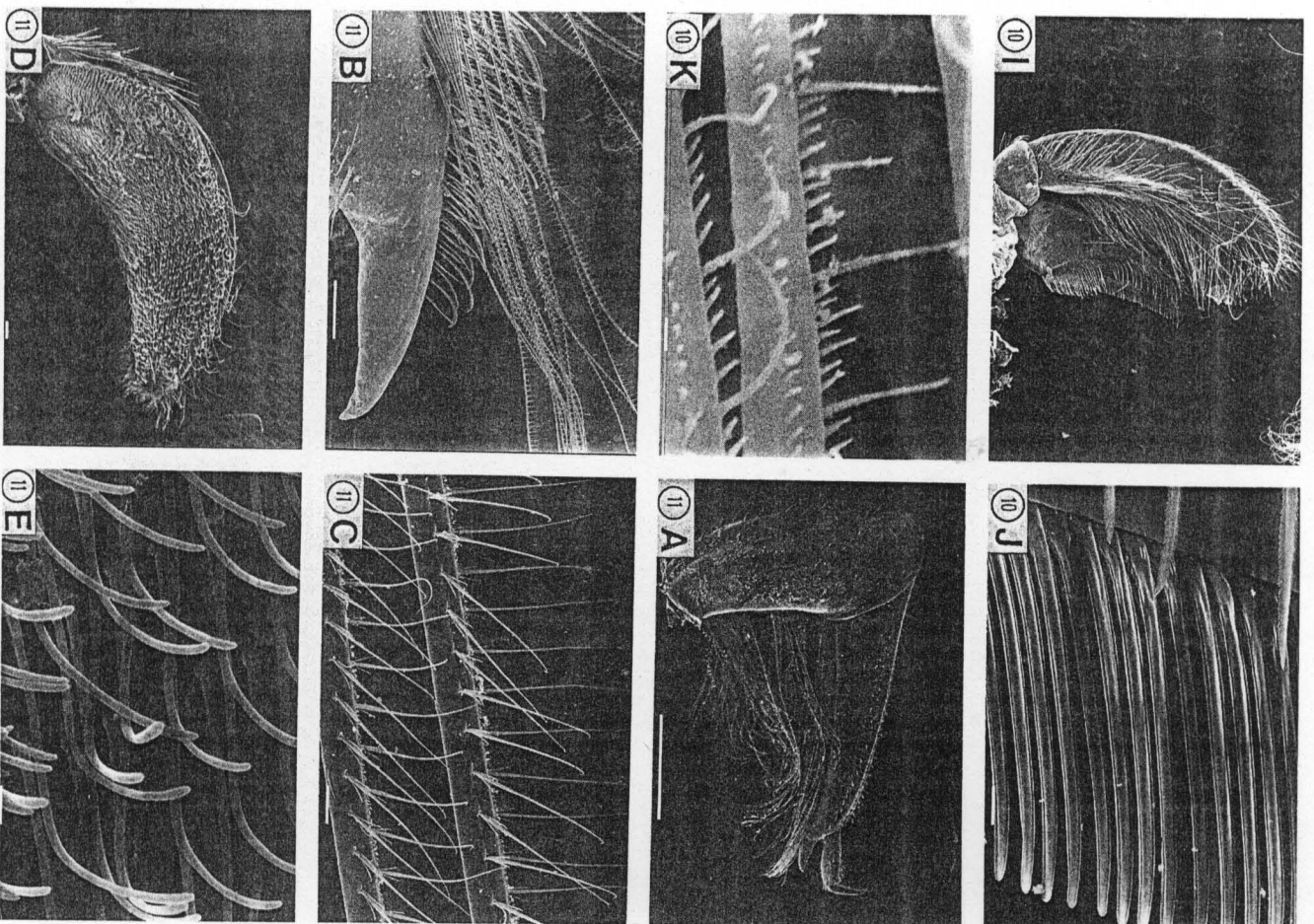
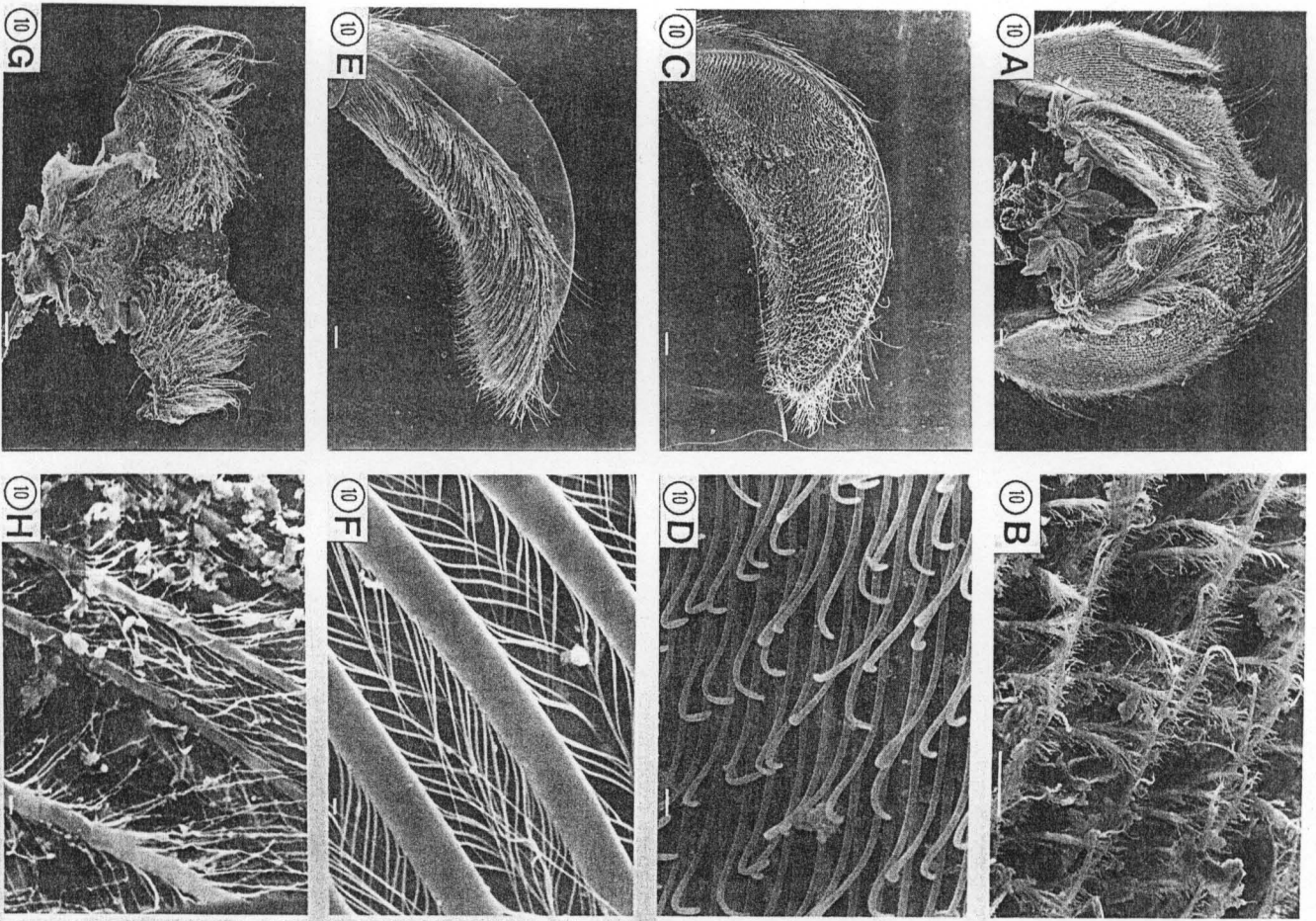
The third setal type is comb setae. They are associated with fine setae in most fine-particle feeders studied or illustrated and seem to be a necessary structural adjunct. There are no behavioral descriptions of the function of combs, though it is easy to speculate that they remove particles that collect on fine setae. Several of the combs illustrated here form a row at the base of leptohebiid maxillary brushes (Figs. 19A, 20A, 21A); these are also apparent in light microscopic drawings (Figs. 13-16). Combs are interspersed between feathery setae on oligoneuriid labia (Fig. 11K) and at the tip of the filtering leg (Fig. 11B). Combs have been recorded on the paraglossae of the heptageniid *Afromuris harrisoni*, and on the maxillary palps of tricothyrid and caenid larvae (Palmer et al., 1993).

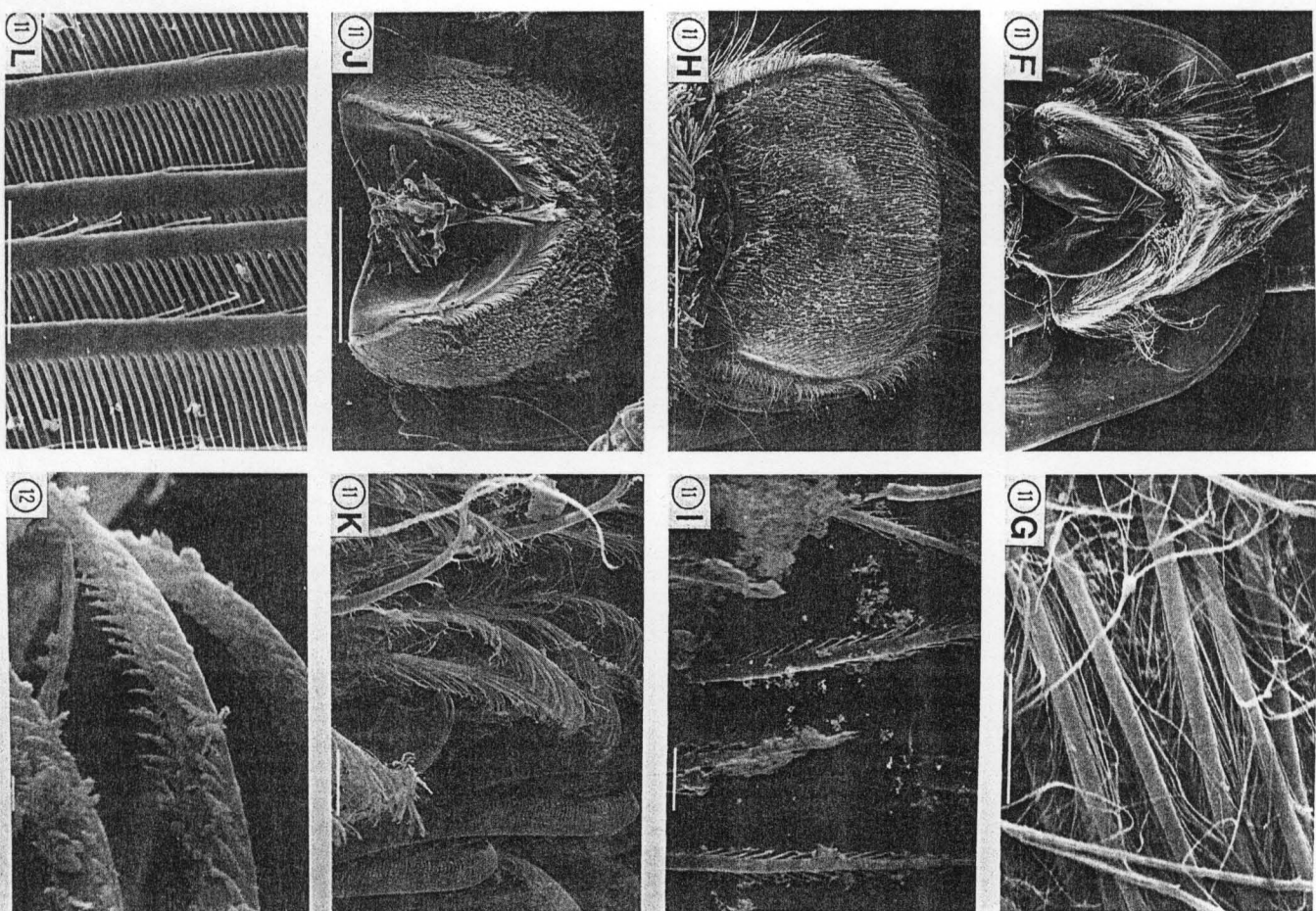
SETAL COMBINATIONS CHARACTERISTIC OF FFCS

Functional groups will be considered in sequence from those that utilize suspended material and inhabit high velocity habitats (passive filterers) down a velocity gradient to those feeding in low velocity habitats on loosely deposited material (active filterers, brushers, and gatherers). Organisms that remove tightly attached organic material that does not wash away in a current (scrapers) are found under a wide range of velocity conditions. Of the passive filterers, only setal filterers will be considered, since net filterers such as hydropsychid caddisfly larvae do not utilize structural appendages for feeding.



Figs. 3-9. Leptohebiidae characteristically have a series of setae that form a brush (see Figs. 13-16), but at least four South African species have arrays of filtering setae: *Hemania maculipennis* (Fig. 3), *Hysler planumini* (Fig. 4), *Hemania thelma* (Fig. 5), and *Neelamella ephraidi* (Fig. 6). (Figs. 3-6 redrawn from Dominguez and Flowers, 1989, where maxilla labium is in B, dorsal is left, and ventral is right). Drawings of tricothyrid filtering setae are included for comparison (Figs. 7, 8). Fig. 9. Setae from South African Simuliidae (drawn from Palmer, 1991). A: Six possible microtrichial patterns: (i) one row of equal microtrichia; (ii) one row of subequal microtrichia; (iii) one row of unequal microtrichia; (iv) one row of unequal microtrichia in two planes; (v) one row of unequal, reduced microtrichia; and (vi) two rows of unequal microtrichia with a lateral fringe. B: A diagrammatic view of the ventral aspect of two cephalic fan setae of *Simulium hesli* (setal pattern type vi, A). Each seta has two rows of long microtrichia (x), with curved tips that hook around the base of microtrichia of adjacent setae. Long microtrichia are flanked by short microtrichia (y) that curve to the rear and hold tips of microtrichia from adjacent setae in position, forming a coupling network. Groups of short peg-like microtrichia (z) alternate with long microtrichia.





Passive Setal Filterers

Passive setal filtering occurs in at least the Diptera (Simuliidae and Culicidae) and Ephemeroptera (Tricorythidae, Oligoneuridae, Leptophlebiidae, and Potamanthidae) (Figs. 1–11). In all cases the structural unit of filtering is an array of setae equipped with one or two rows of equal or subequal microtrichia. (While subequal and unequal setae occur exclusively in passive filterers, not all passive filterers have them.)

Simuliidae use setal cephalic fans for passive filter feeding (Currie and Craig, 1987; Fig. 1). Palmer (1991) describes six categories of increasingly complex microtrichial pattern: from a single row of equal peg-like microtrichia to two rows of unequal microtrichia, with a lateral fringe (Fig. 9A,B). The unequal setae of *Simulium gatense* (Fig. 1B,C) are structurally indistinguishable from the labial and mandibular setae of two South African tricorythid mayflies, *Tricorythus discolor* (Fig. 2B,C,E) and *Tricorythus reticulatus* (Palmer et al., 1993), and the maxillary setae of the oligoneurid *Oligoneuropsis*

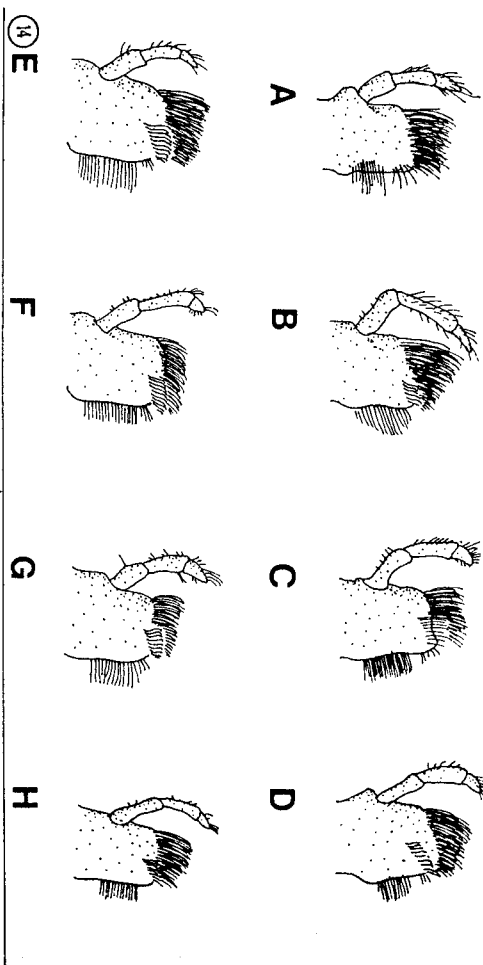
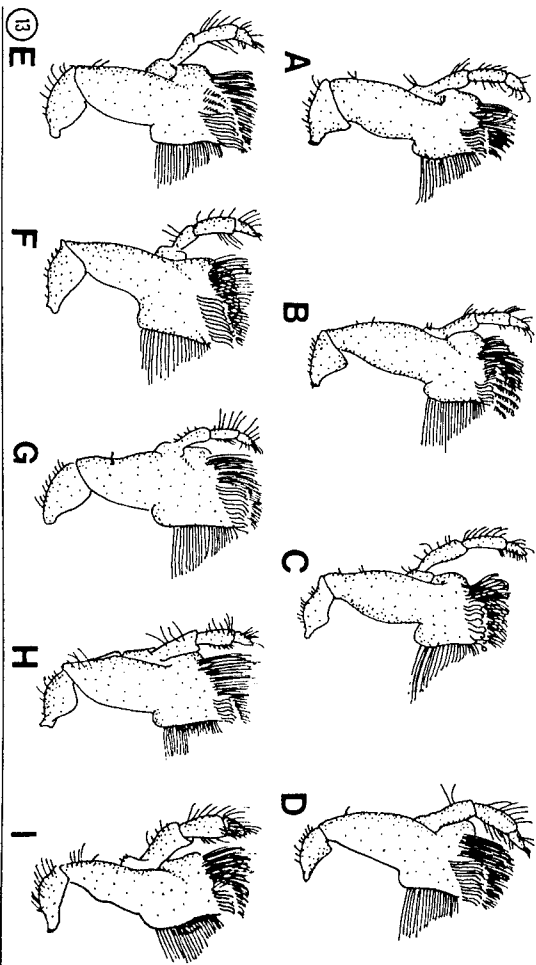
sp. (Fig. 10K). Bae and McCafferty (1991) show similar micrographs for the potamanthid mayfly *Anthopotomus myops*, as does Braimah (1987b) for the simuliid *Simulium bivittatum* and the oligoneurid *Isonychia campestris*. The leg setae of two South African Oligoneuridae (*Oligoneuropsis* sp. and *Elasoneuria* sp.) are also subequal, but the shorter microtrichia occur at the base of the longer ones (Fig. 11C).

In addition to subequal setae, all the passive filterers studied had an array of other setae on various mouthpart appendages, most commonly pectinate setae. Dahl et al. (1987) show that culicid passive filterers use pectinate setae to feed. South African Oligoneuridae have a wide array of setal types (Figs. 10, 11), the functions of which are as yet unknown.

In the literature, many organisms described as filterers are not accompanied by micrograph illustrations. Figures 3–8 show light microscopic drawings of a range of ephemeropteran filterers. Figure 7A,B are drawings of Figure 2A,D, respectively, and Figure 8A,B are from micrographs of Palmer et al. (1993). They are included to show their similarity to a series of drawings of the labia and maxillae of four South American Leptophlebiidae (Figs. 3–6). Several leptophlebid genera from New Zealand, Australia, South Africa, and South America (Figs. 13–16) are brushers. In contrast, these four genera from an area at the junction between Brazil, Argentina, and Paraguay are described as filterers (Dominguez and Flowers, 1989) (Figs. 3–6). Detailed phylogenies of the Ephemeroptera and of the Simuliidae within the Diptera would indicate where passive filtration structures have arisen as independent adaptive features. Even without a phylogenetic framework, the FFG category passive setal filterer is a useful ecological description that applies to several taxonomic groups.

Active Setal Filterers

The most comprehensively described and illustrated active filterers are the Potoman-



thidae (Bae and McCafferty, 1991). They are characterized by mouthparts with prolific, mainly pectinate, setae. Active filterers in the ephemeropteran families Caenidae and Baetidae have also been described (Palmer et al., 1993).

Brushers

The most characteristic brushers are the Leptophlebiidae (Figs. 13-23). The term "brusher" was coined and defined by McShaffrey and McCafferty (1986), morphologically described by (Palmer et al., 1993), and is the equivalent of the term "browser" used by Winterbourn et al. (1984) and Dahl et al. (1987). Brushers are structurally characterized by a series of setae that form a brush.

In the case of Leptophlebiidae (Figs. 13-23) and Heptageniidae (Fig. 25A), the brush comprises a series of setae from stout setae at the base to fine pectinate setae with curved microtrichia anteriorly. As with the filterers, the line drawings (Figs. 13-16) include both species for which micrographs are available (Fig. 14B,D-H) and several for which they are not. The drawings illustrate the consistency of gross leptophlebid maxillary brush structure, as the micrographs (Figs. 17-23) do for the ultrastructure. Dahl et al. (1987) describe and illustrate culicid brushers. Currie and Craig (1987) describe brushing and

scrapping in simuliids, and Figure 24 shows a series of simuliid maxillary setae strongly reminiscent of an ephemeropteran brush and possibly the structural basis for brushing in this dipteran family.

Gatherers

The mouthparts of gatherers are generally less setose (Palmer et al., 1993), and the setae that are present are simple pectinate setae, usually with short microtrichia (Fig. 12). Gatherers use other body parts, such as legs, to bring food particles to the mouth. Setae on the mouthparts possibly function in particle retention rather than particle acquisition.

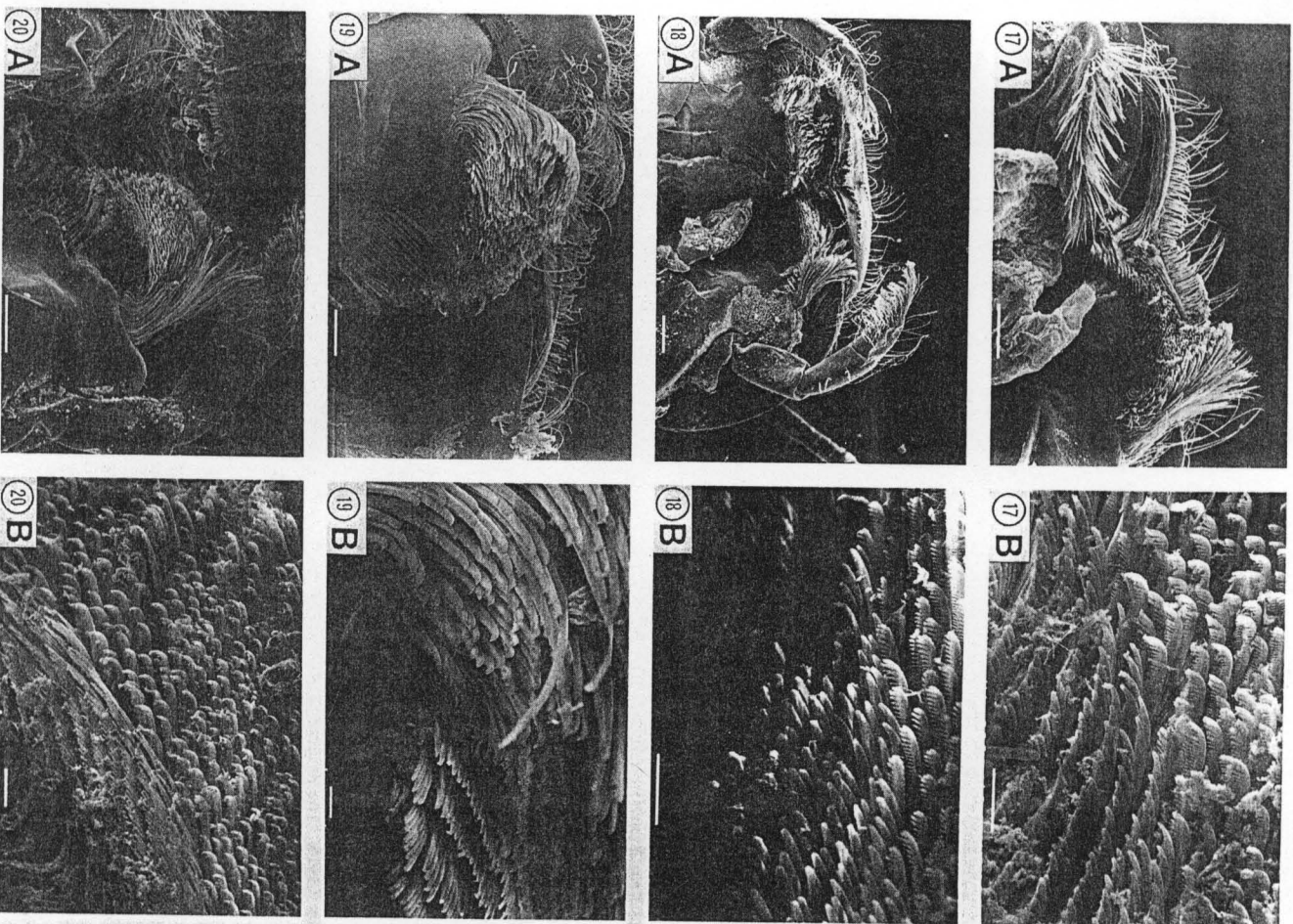
Scrapers

Scrapers feed on tightly attached organic material. The heptageniid *Afromurus harrisoni*, in addition to labial palp brushing (Fig. 25A), also uses chitinous scraping bars on its maxillae to remove tightly attached material (Fig. 25B). Similarly, the North American heptageniid *Rithrogena pellucida* also feeds by a combination of brushing with labial palp brushes and scraping using scraping setae on the maxillary palps (McShaffrey and McCafferty, 1988). *Adenophlebia auriculata* (Palmer et al., 1993) has comb setae at the base of the brush that are structurally similar to these scraping setae. The baetid *Baetis harrisoni* is a gatherer with scraping setae at the apex of the paraglossae (Palmer et al., 1993).

CONCLUSIONS

Stream dwelling insect larvae are essentially opportunistic feeders (Cummins and Kluge, 1979) and display remarkable flexibility in feeding behavior (McShaffrey and McCafferty 1986, 1988, 1991). A FFG designation refers at best to the most frequent behavioral pattern, which may change seasonally or with food availability. What has been demonstrated here is an ecological, guild-based classification of aquatic larvae that has a consistent morphological basis, across both a wide geographic range and at least two insect orders.

Figs. 13-16. The maxillae of southern hemisphere leptophlebid brushers, from New Zealand (Fig. 13), South Africa (Fig. 14), Australia (Fig. 15), and South America (Fig. 16) are structurally uniform. Fig. 13. A: *Austroclima sepi*. B: *Mutillius lunia*. C: *Cryptophlebia anklandensis*. (A-C, redrawn from Towns and Peters, 1979a.) D: *Isotantulus abditus*. E: *Archioscolus philippii*. (D,E, redrawn from Towns and Peters, 1979b.) F: *Adiophlebioides cromwelli* (redrawn from Towns and Peters, 1978). G: *Zephlebia versicolor*. H: *Neozephlebia scia*. I: *Acanthophlebia cruentata*. (G-I, redrawn from Towns, 1983.) Fig. 14. A: *Euphlebia bicolor* (redrawn from Crass, 1947). B: *Aptonyx tricuspidatus*. C: *Aptonyx tubularis* (redrawn from Barnard, 1932). D: *Adenophlebia peringilla*. E: *Adenophlebia auriculata*. F: *Cassinophlebia calida*. G: *Choroterpes nigrescens*. H: *Choroterpes elegans*. Fig. 15. A: *Nebosiphlebia humulata* (redrawn from Dean, 1988). B: *Nyngara burnii*. C: *Bibuhnera kadluna*. (B,C, redrawn from Dean, 1987.) A: *Equiphlebia* sp. (redrawn from Dominguez, 1988). B: *Massartella brenti* (redrawn from Pescador and Peters, 1990). C: *Pemphlebia burrii* (redrawn from Pescador and Peters, 1991).



Figs. 17-25. The setal series constituting a brush. The maxillary brush of several South African brushers is quite distinctive, with rows of stout setae at the base changing

anteriorly to rows of fine pectinate setae. Fig. 17. *Choroterpes nigriscens*. Fig. 18. *Adenophlebia auriculata*. Fig. 19. *Casimiphlebia calida*. Fig. 20. *Adenophlebia peringulata*.

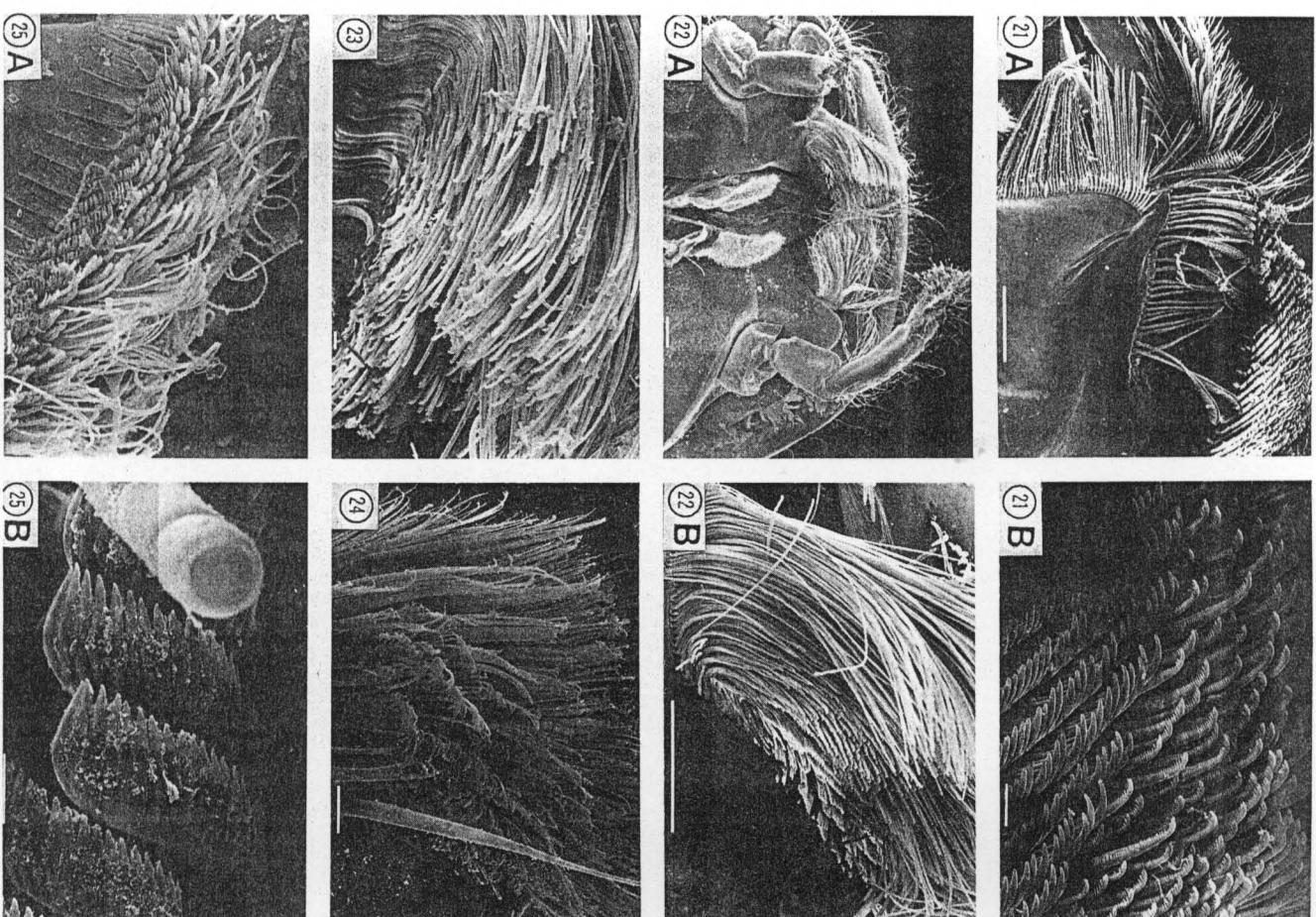


Fig. 21. *Adenophlebia peringulata*. Fig. 22. *Adenophlebia sylvatica*. Fig. 23. *Apironyx incuspidatus*. Fig. 24. *Apironyx harrisoni*. Fig. 25A. *Apironyx harrisoni*.

bars (Fig. 25B). 17B, 18B, 19B, 20B, 21B, 23, 24, 25A, 25B, bars = 10 μ m; 17A, 18A, 19A, 20A, 21A, 22A, 22A, 22A, bars = 100 μ m.

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