

MORPHOLOGY AND CLASSIFICATION OF DECAPOD  
CRUSTACEAN LARVAL SETAE: A SCANNING ELECTRON  
MICROSCOPE STUDY OF *DISSODACTYLUS CRINITICHELIS*  
MOREIRA, 1901 (BRACHYURA: PINNOTHERIDAE)

*Gerhard Pohle and Malcolm Telford*

A B S T R A C T

Setae of the three zoeae, megalopa and first crab instar of *Dissodactylus crinitichelis* are described in detail from laboratory reared specimens. Scanning electron microscopy showed that setae are morphologically more complex and diverse than previously thought. More than thirty distinct setal types were observed. Of these, fifteen are plumodenticulate, equipped with distal denticules and proximal setules. An attempt has been made to accommodate this diversity within a unified system of classification by combining two previously existing schemes, which required some minor modifications. The proposed criteria for classification include such shaft characteristics as length/width ratio, location and conspicuousness of annulus, shape of tip, presence (or absence) and position of pore as well as the distribution and type of setules and denticules. On a basis of morphology some functions of setae can be inferred. It is suggested that complex setae, such as some plumodenticulate types, might perform multiple functions. Other cuticular structures are described and illustrated, including two cuticular organ complexes of unknown function, found in all examined stages.

Setae have been widely used in differentiating species and stages of crustacean larvae. Criteria most often used are setal counts and positions, with little or no regard to their particular structure. Gonor and Gonor (1973) have warned that this may be questionable because of significant individual variability, which becomes apparent in larger samples. However, if setae of larvae were distinct in type, they might still provide an important diagnostic character. Furthermore, a more detailed knowledge of setal structure is a necessary primary step toward a better understanding of the much neglected area of setal functions.

To date most research on crustacean setae has been done at the light microscope (LM) level. The detailed studies of Thomas (1970) and Fish (1972) on adult crayfish and isopod setae show that setal structure is complex and that differentiation of many different kinds is possible. Subsequent LM studies on portunid larvae (Bookhout and Costlow, 1974; 1977; Shinkarenko, 1979) have recognized the differential features of setae in larvae. All these works show the limitations of LM in discerning diagnostic morphological details, such as presence or absence and position of pores. The scanning electron microscope (SEM) is an ideal tool to overcome these difficulties. Thomas (1971), Farmer (1974) and Drach and Jacques (1977) have done pioneering SEM studies on adult crustacean setae. SEM research on larvae in general and larval setae in particular, however, has been neglected.

*Dissodactylus crinitichelis*, a small parasitic pinnotherid crab, is used in this paper to characterize and classify larval and first crab instar setae by preliminary LM and subsequent SEM analysis. It is hoped that this will lead to a more unified and widely applicable vocabulary and classification of setae, while at the same time providing greater precision in making larval descriptions (Pohle and Telford, 1981).

## MATERIALS AND METHODS

*Collection and Culture.*—Specimens of *D. crinitichelis* larvae and first crab instars were obtained from laboratory culture as described by Pohle and Telford (1981).

*Specimen Preparation and Examination.*—Literature on preparation of larvae for SEM is very scant (Scotto, 1980) and therefore methodology has been explained in detail here. Freshly molted specimens of each instar were immobilized by chilling for several minutes before fixation for 12–16 h in 2% glutaraldehyde, buffered to pH 8.5 with 1 M sodium cacodylate in Millipore-filtered seawater (0.22  $\mu\text{m}$ ). Subsequently, specimens were rinsed and stored in buffered and filtered sea-water. For SEM, specimens were gradually transferred to distilled water and, if necessary, cleaned with a dilute detergent solution for several days before rinsing.

Appendages were dissected using tungsten wire electrolytically sharpened in 10% KCL. To reach and separate them with minimum damage, the carapace was removed. Zoeae were arranged in profile, megalopae and first crab instars dorsal side up, and the carapace lifted dorsally with a hooked needle where the abdomen enters the cephalothorax. The carapace was gently pulled away while pushing the abdomen in the opposite direction with a straight microneedle. A dissecting needle was then used to hold down the specimen by piercing the cardiac area, while a straight blade-like needle was used to separate appendages starting from the most posterior. These were teased away by working only at their points of attachment, avoiding setose areas.

Whole specimens or dissected appendages were mounted in distilled water on aluminum stubs, frozen in liquid nitrogen and freeze-dried in a Speedvac-Pearse Tissue Dryer. Stubs were sputter coated with gold in a SEMPREP 2 (Nannotech Thin Films Ltd., Cambridge, England), before scanning with a Cambridge 180 SEM.

Larval setae of at least 10 specimens were examined under the LM. For SEM investigation a minimum of 4 to 5 specimens were used.

## RESULTS

### Setal Terminology

Various names have been applied to sensilla-type cuticular outgrowths, including hairs, bristles, spines and setae among others, with little agreement as to precise meaning; compare, for example, Fish (1972), Farmer (1974) and Thomas (1970). The latter author limited himself to two definitions which have been adopted here: all more or less hair-like cuticular outgrowths will be referred to as setae if they possess a basal socket; more massive structures, arising directly from the cuticle, are defined as spines and will not be considered in this report. Setae will be categorized by name and, if possible, alphanumeric rank; e.g., plumose setae (TYPE 4a). Figure 1 illustrates a hypothetical plumodenticulate (TYPE 13) seta and basic terminology used here. Setal categories TYPES 1, 6–8 and 10 of Drach and Jacques (1977), which were not observed in *D. crinitichelis*, have been omitted.

Development of the basal socket varies considerably from very conspicuous and elaborate (e.g., TYPE 3a, Fig. 2A) to barely visible (e.g., TYPE 3b, Fig. 2B).

The remaining terminology deals with the shaft and its outgrowths. The shaft is separated into two parts by an annulus, a ring- or joint-like discontinuity. The proximal and distal shaft portions are referred to as pre- and post-annular, respectively. The annulus varies in position and conspicuousness so as to be useful in setal classification. For example, on the plumose natatory setae (TYPE 5b) of zoeae it is prominent and located half-way or beyond the length of the shaft (Fig. 2C). Schlotterbeck (1976) referred to these setae as two-segmented in *Pachygrapsus crassipes*. Plumodenticulate cuspidate setae (TYPE 13-xi) have a near basal, much less conspicuous annulus (Fig. 4E). When present, pores are located post-annularly, either terminally or subterminally, depending on setal type.

Setal shaft outgrowths can be divided into two broad categories, setules and denticules (Fig. 1). The former, also known as barbules (Reaka, 1975), are gen-

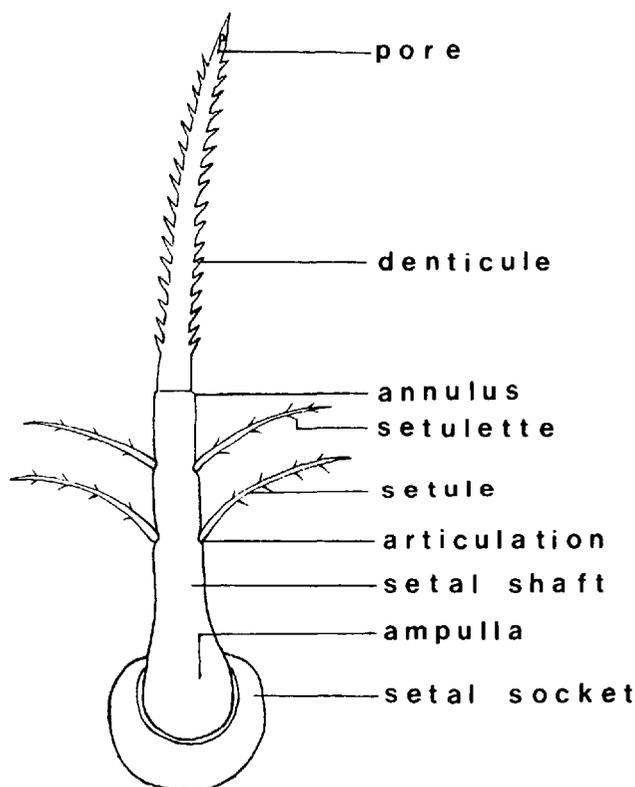


Figure 1. Diagram of a hypothetical plumodenticulate seta (TYPE 13), illustrating some of the basic setal terminology used in this paper.

erally flatter, longer and more flexible than denticules. They may occur along the entire shaft length. Setules emanate from the shaft either in two opposite rows (plumose setae, TYPE 4 and 5) or from around the entire shaft (pappose setae, TYPE 9). They vary in density from sparsely distributed to extremely dense, so as to make the shaft and annulus almost invisible. Setules are articulated at their base on the shaft. They vary in length from short and digitate to long and flexible (Figure 1). Small lateral branches on setules have been referred to as setulettes.

In contrast to setules, denticules arise directly (no articulation) from the shaft. These thorn- or tooth-like extensions are most often encountered post-annularly. Several terms have been used to identify denticules of different forms, such as "serrae" and "serrulae" (Thomas, 1970), "dents" and "épines" (Drach and Jacques, 1977). Although these terms imply differences in size and shape, we were unable to distinguish them from the descriptions provided. We have employed the one term, denticules, for these structures, supplemented with additional descriptions when necessary. Similarly, the term scales ("écailles" of Drach and Jacques, 1977), refers to forms intermediate between setules and denticules. We have discarded it in favor of qualifying descriptions. To avoid confusion with existing alphanumeric classification, setae with both setules and denticulations have been lumped into the plumodenticulate category TYPE 13, followed by Roman numeric subcategories.

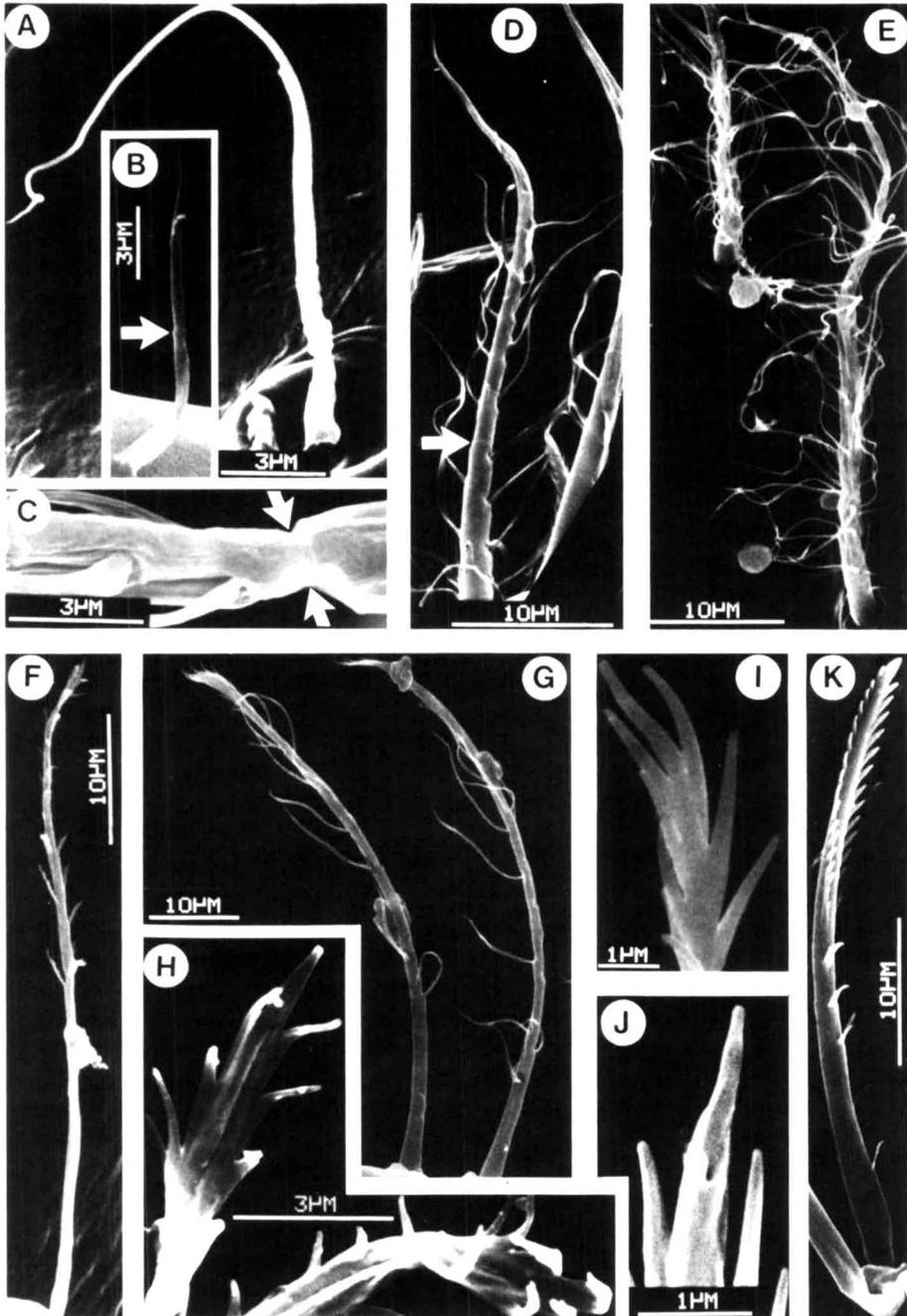


Figure 2. SEM of *D. crinitichelis* setae. A, simple seta (TYPE 3a); B, simple seta (TYPE 3b); C, plumose natatory seta (TYPE 5b); D, plumose seta (TYPE 4b); E, pappose seta (TYPE 9b); F to K are plumodenticulate setae: F, TYPE 13-i; G, TYPE 13-ii; H, tip of TYPE-13iii; I, tip of TYPE 13-i; J, tip of TYPE 13-iii; K, TYPE 13-iii. Arrows indicate the position of annuli in figures 2 to 6.

## Setal Types

*Simple Setae* (TYPE 3).—Without evident outgrowths from shaft under LM, although SEM sometimes shows a very small protruberance. TYPE 3a. Thin, smooth, of varying length; sharp-tipped, without pore; often bent distally, anchored proximally in prominent socket (Fig. 2A). Dorsolateral on carapace, abdominal somites (not telson) of zoeae. TYPE 3b. Length/width ratio (L/W) ~15. As TYPE 3a but socket inconspicuous, shaft shorter with blunt tip and terminal pore (Fig. 2B). Proximal segments of endopodite of maxilliped 1 in zoeae; carapace, abdomen and scaphognathite blade of megalopa and first crab instar.

*Plumose Setae* (TYPE 4).—Feather-like, annulus inconspicuous (Fig. 2D); two opposite rows of long, flexible setules along almost entire length; mostly with setulettes (Fig. 4K). Pore absent. TYPE 4a. Sparsely plumose. (L/W ~22–24). On coxopodite of maxillule in megalopa. TYPE 4b. (L/W ~20). With more setules on smooth, tapering shaft; tip flexible (Fig. 2D). Coxopodite of maxilla, beginning in first zoea; fringing carapace, branchiostegite in megalopa and first crab instar. TYPE 4c. (L/W ~15). With more inflated base, dense array of setules. Form palisade on scaphognathite margin in all stages; singly as border setae on maxillule in zoeae 2 and 3. TYPE 4d. (L/W ~ 25–125). Similar to 4b but shaft can be much longer, setules of extreme length (often almost as long as shaft itself). Distal segments of endopodite of maxilliped 3 in megalopa and first crab instar.

*Plumose Natatory Setae* (TYPE 5).—With extremely long shafts, very conspicuous annuli. TYPE 5b. (L/W ~ 45–50). With single, prominent annular indentation halfway or beyond on shaft (Fig. 2C), possibly serving as an articulation, for flexibility during the recovery stroke. Exopodites of maxillipeds 1 and 2, all zoeal stages.

*Pappose Setae* (TYPE 9).—(L/W ~ 28–30). With long, flexible setules, irregularly around shaft, sparse (9a) to very dense (9c) as in TYPE 4 setae. Tips sharp, flexible, lacking pore. Sparsely pappose setae (9a) form short row beneath eyes and hepatic regions of first crab instar; with average setule density (9b) more common, as on basal segment of antennule, proximal endopodite segment on maxilliped 3 of megalopa and first crab instar (Fig. 2E); densely pappose (9c) only on mandibles of megalopa and first crab instar.

*Plumodenticulate Setae* (TYPE 13).—Length variable; two types of shaft outgrowths; setules proximally (usually pre-annular) and denticules distally, i.e., post-annularly.

TYPE 13-i. (L/W ~ 25–110): Long to extremely long, slender; with almost straight, non-tapering shaft; short, digitate setules on middle third (Fig. 2F); distal third with two dense rows of denticules. Tip flat, without pore (Fig. 2I). Megalopa, first crab instar, on border of maxillule and distally on epipodite of maxillipeds 1 and 3.

TYPE 13-ii. (L/W ~25–50): Similar to 13-i but with long, flexible setules on second quarter of shaft, extending further distally (Fig. 2G and 2H). Megalopa, first crab instar, on merus of ambulatory legs and medially on epipodite of maxilliped 3.

TYPE 13-iii. (L/W ~15–20): Very smooth (Fig. 2K) with relatively short, sparsely digitate setules (similar to Fig. 4I) possibly occurring beyond annulus (Fig. 2K); post-annular shaft portion robust, with two distinct rows of sharp denticules. Tip pointed, subterminal pore (Fig. 2J). Basipodite of maxilliped 1 and distal segments of endopodite of maxilliped 2 in megalopa and first crab instar.

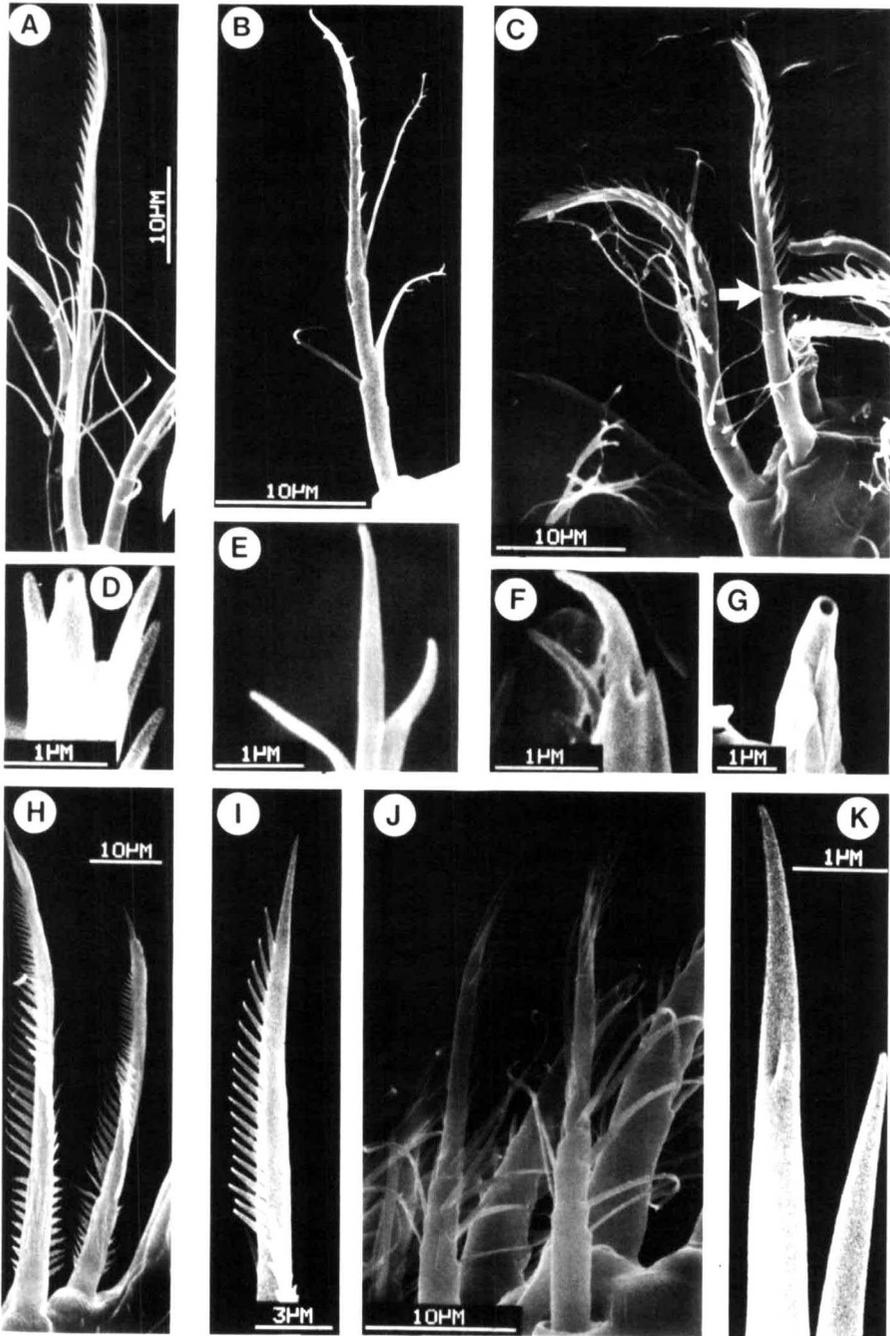


Figure 3. SEM of *D. crinitichelis* plumodenticulate setae. A, TYPE 13-iv; B, TYPE 13-v; C, TYPE 13-vi (left) and 13-vii (right); D, tip of TYPE 13-iv; E, tip of TYPE 13-v; F, tip of TYPE 13-vi; G, tip of TYPE 13-vii; H, TYPE 13-viii; I, tip of TYPE 13-viii; J, TYPE 13-ix; K, tip of TYPE 13-ix.

TYPE 13-iv. (L/W ~20–25): Smooth, slender, with long, flexible setules along first half of shaft (Fig. 3A). Post-annular region densely denticulated in two rows. Tip blunt, with clearly visible terminal pore (Fig. 3D). Endopodite of maxillules, maxillae and maxilliped 1, all zoeal stages.

TYPE 13-v. (L/W ~15–20): More delicate, usually no more than two pairs of long, flexible setules proximally (setulettes present); two rows of narrow, widely spaced denticules (compare to 13-iii and 13-iv) (Fig. 3B). Tips sharp, without pore (Fig. 3E). Aboral edge of maxillary basipodite in zoeal stages, characteristically directed towards adjacent mouthparts.

TYPE 13-vi. (L/W ~15–20): With many long, flexible setules, often loosely arranged in four rows, extending beyond annulus (Fig. 3C, left seta). Two dense rows of denticules extend to pointed tip with subterminal pore (Fig. 3F). Zoeal stages, on basipodite of maxilla; coxopodite maxilliped 1, megalopa.

TYPE 13-vii. (L/W ~15): Located in zoeae between preceding two setal types. Annulus more prominent, setules relatively short; extensively adorned with long denticules, often also present pre-annularly (Fig. 3C, right seta). Tip blunt with terminal pore (Fig. 3G).

TYPE 13-viii. (L/W ~15): Robust, tapering, occurring exclusively on telson of zoeae (Fig. 3H). Elaborate sockets allow considerable movement. Setules stiff, pointed, digitate, shorter proximally, extending two thirds along shaft beyond annulus. Two dense rows of sharp denticules with confluent bases. Tip very sharp, lacking pore (Fig. 3I).

TYPE 13-ix. (L/W ~13): Smooth, slender, with very straight, narrow base. Two rows of long, flexible setules (with setulettes); denticules long, sharp (Fig. 3J). Tip very pointed, bearing minute slit-like pore (Fig. 3K). Subterminally on basipodite of maxillules, coxopodite of maxillipeds 1 in zoeal stages 2, 3.

TYPE 13-x. (L/W = 11 or less). Stout; setules irregularly arranged, graded from short, flexible, with few setulettes proximally, to long, broad setules with more setulettes medially (Fig. 4A); annulus distal (Fig. 4B); very stout denticules graded in size. Tip sharp, subterminal pore (Fig. 4C and 4D). Only on coxopodite of maxillules, in all stages. "Graded multidenticulate" setae of Bookhout and Costlow (1974); in successive stages setules gradually lost, proximal shaft portions naked in post-larval instars (Fig. 4B).

TYPE 13-xi. (L/W = 7 or less): Shaft with inflated base or ampulla (Fig. 4E), near basal annulus. Setules irregular, long, flexible; two rows of very stout denticules. With terminal pore. "Plumodenticulate cuspidate" setae of Bookhout and Costlow (1974). As in 13-x, setules gradually lost in subsequent stages (compare Fig. 4E with 4F and 4G); setae then referred to as denticulate cuspidate (Fig. 4G). Exclusive to basipodite of maxillules in all stages.

TYPE 13-xii. (L/W ~20–25): Superficially resemble TYPE 13-iv, with long, flexible setules, blunt tip with terminal pore. Distinctive, slender, widely spaced denticules in three rows, not two (Fig. 4H). Proximal on basipodite of maxillipeds 1, 2 in all zoeae.

TYPE 13-xiii. (L/W ~20–25): Similar to 13-xii, but one row of very short, rigid, digitate setules (Fig. 5A) with prominent flexible attachment on setal shaft (Fig. 4I). Subterminal on endopodite of maxilliped 2 in zoeal stages.

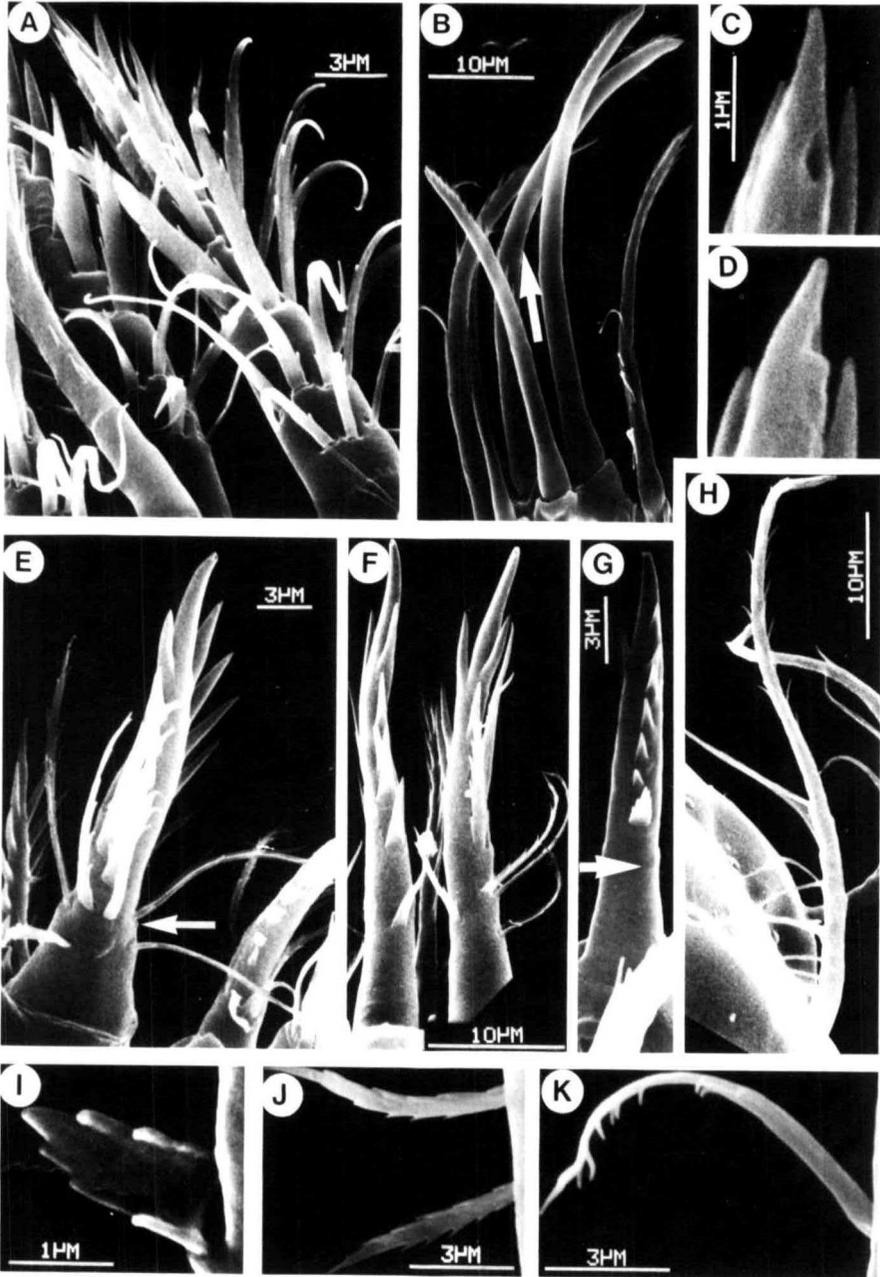


Figure 4. Plumodenticulate setae of *D. crinitichelis*. A, TYPE 13-x in first zoea; B, TYPE 13-x in megalopa; C and D, tips of TYPE 13-x; E, TYPE 13-xi in first zoea; F, TYPE 13-xi in third zoea; G, TYPE 13-xi in first crab instar; H, TYPE 13-xii; I, short digitate setule showing basal articulation; J, longer intermediate setule type; K, long setule with setulettes of plumose seta.

TYPE 13-xiv. (L/W ~18): No more than one pair of setules proximally, very delicate denticules distally, often adhering to shaft, almost indistinguishable (Fig. 5B). Tip round, relatively blunt, without pore. All zoeal stages proximally on basipodite of maxilliped 2.

TYPE 13-xv. (L/W ~25–30): Another sparsely plumodenticulate seta with barely visible denticules and setules, latter occasionally absent (Fig. 5C and 5D). Tip pointed but with minute terminal pore (Fig. 5E). Basipodites of maxillipeds 1, 2 of zoeae.

*Serrate Setae* (TYPE 11).—Shaft stout, without setules, naked pre-annularly. Denticules of different size, usually forming two V-shaped rows. TYPE 11c. (L/W ~8). Very stout, denticulations of mixed size arranged in sickle-shaped fashion (Fig. 5G). In *Dissodactylus crinitichelis* only single row of serrations present (Fig. 5F), instead of usual two (Thomas, 1970; Bookhout and Costlow, 1974; 1977). Tip with apical pore (Fig. 5H). Megalopa and first crab instar, opposing each other on dactylus and propodus of chelipeds. TYPE 11a. (L/W ~10–17). “Serrulate” (Thomas, 1970), “finely serrate” setae (Bookhout and Costlow, 1977) with very small, closely spaced serrations (denticulations of a kind) on tapering shaft (Fig. 5I). Tip snout-like, pore terminal (Fig. 5J). Pereiopods in post-zoeal stages, especially around dactyls of walking legs (Fig. 6E). Similar seta found singly on palp of maxilliped 3 among plumed setae in megalopa and first crab instar.

*Cuspidate Setae* (TYPE 2).—Massive, cone shaped. TYPE 2d. (L/W ~5–7). With naked, relatively short pre-annular shaft portion, prominent annular ring. Tapered shaft post-annularly with small, irregular denticules (Fig. 6a). Inconspicuous terminal pore. Pereiopods of first crab instar.

*Proboscate Setae*. Preliminarily assigned to TYPE 16. (L/W ~10).—Stout, superficially resembling simple (3b) or serrulate (11a) setae, but with one or two setules close to prominent near basal annulus and one or two pairs of minute denticules appressed against shaft (Fig. 6B). Post-annular shaft curved distally, with distinct terminal pore on blunt snout-like tip. Among palisade of plumose setae (9b) on coxopodite of maxillule in zoeae and on proximal palp segment of maxilliped 3 in megalopa and first crab instar.

*Aesthetascs* (TYPE 31). (L/W ~20–40).—Specialized setae only found on antennule. Thin-walled, smooth, non-tapering shaft of varying length (Fig. 6C and 6D). Tip blunt to round, no pore found (Fig. 6F).

#### Other Cuticular Outgrowths

*Cincinnuli*. (L/W ~1).—Short rounded shaft, extending distally into flattened hood with digitate margin oriented at right angle to shaft (Fig. 6G). Exclusively on endopodites of pleopods (appendix interna) in megalopa. In pairs, usually interlocking with another cincinnulus pair, linking right and left pleopods (Fig. 6H).

*Denticulettes*, *Spinules*.—Minute (1–2  $\mu\text{m}$  long), very sharp processes occurring in groups (Fig. 6I). Most abundant on telson and mandible in zoeae; more sparsely on first antennular segment (postlarvae) and most other appendages. Not found on endopodites of maxillules, maxillae, maxillipeds (in zoeae) and antennae.

*Microtrichia*. (L/W ~40).—Extremely small, slender, flexible hair-like out-

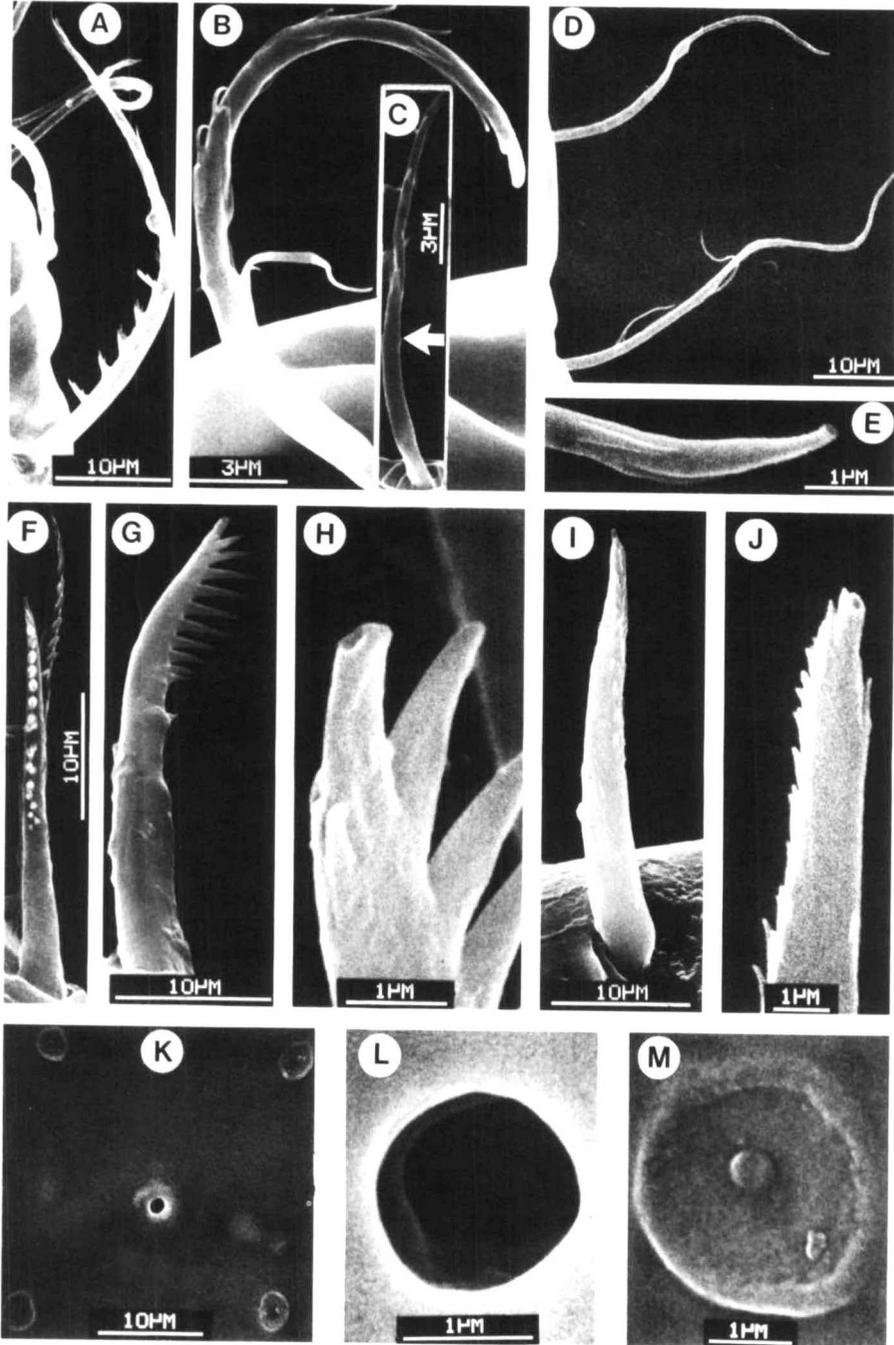


Figure 5. SEM of *D. crinitichelis* sensillae. A to E are plumodenticulate setae: A, TYPE 13-xiii; B, TYPE 13-xiv; C and D, TYPE 13-xv; E, tip of TYPE 13-xv; F and G, serrate seta (TYPE 11c); H, tip of TYPE 11c; I, serrulate seta (TYPE 11a); J, tip of TYPE 11a; K, cuticular organ complex; L, central pore of cuticular organ; M, one of four lateral structures of cuticular organ.

growths (Fig. 6J), usually aggregated on surface of endites of maxillules and maxillae in zoeae only.

*Internal Cuticular Outgrowths*.—At least three different seta-like outgrowths occur in the gastric mill: (i) robust, straight, naked peg-like structures, possibly with terminal pore; (ii) simple, flat hair-like outgrowths, applied against surface (Fig. 6K); (iii) longer, flat structures with short lateral branches (Fig. 6K).

*Cuticular Organ Complex*.—A peculiar, previously undescribed organ complex was found frontally, in the center of the carapace, about midway between the eyes and dorsal spine in all zoeal stages (Fig. 5K). It consists of a central pore (Fig. 5L), surrounded by four equidistant ring-like cuticular elevations which bear a nipple-like structure in the center (Fig. 5M). Immediately posterior to the dorsal spine a similar organ was found with two additional cuticular elevations flanking the central pore. Both organs were also seen on the carapace of the megalopa and first crab instar in corresponding positions.

Isolated pores without any associated structures have also been found in *D. crinitichelis* on appendages and the body surface of zoeae. Such "sensory pores" (Laughlin and Neff, 1976) are known to occur in the zoea of *Rithropanopeus harrisi*.

## DISCUSSION

### Setal Morphology

#### *Micromorphology of Setal Shafts*

The annulus is an important diagnostic feature on setal shafts (Thomas, 1970). In *D. crinitichelis*, under the LM, this structure was only visible on plumose natatory setae (TYPE 5b) of zoeae. When using SEM annuli became apparent on almost all the setae examined. The presence of annuli has been shown by Reaka (1975) to be due to the mode of setal formation. Setae are partly invaginated before evertion shortly after ecdysis. The deepest point of invagination is at the point of flexure, represented by the annulus. The degree to which each seta is invaginated determines the characteristic position of the annulus: the deeper the invagination, the longer the pre-annular portion and more distal the annulus, and vice versa. Thus all setae should have an annulus due to its formation in seta-genesis. This distinguishes them from spines which lack both annulus and socket. It remains to be explained, however, how multi-ringed setae are formed, such as the ones (TYPE 5a) found by Drach and Jacques (1977).

Another valuable, distinctive feature of setal shafts is the tip. SEM micrographs showed that many setae of *D. crinitichelis* bear pores. The position, or absence, of a pore was related to shape of the tip. Setae with terminal pores have more or less blunt tips, whereas subterminal pores are found on pointed tips. Pores vary in size and shape: stout proboscate setae (16), for example, have large round terminal pores (Fig. 6B), while finely pointed plumodenticulate setae (13-vii) have minute, more slit-like, subterminal pores (Fig. 3K).

On some setae pores could not be found. These include all plumose (TYPE 4 and 5), pappose (TYPE 9), simple (TYPE 3a) and plumodenticulate setae (TYPE 13-i, -ii, -v, -viii, -xiv), which have very long, slender post-annular shaft portions. Thomas (1970) was of the opinion that all setae of the crayfish, *A. pallipes*, possess pores. However, despite a separate SEM study of setal tips (1971), Thomas was unable to show pores on setae similar to the pore-less types found in *D. crinitichelis*. Drach and Jacques (1977) examined the setae of six natant and six

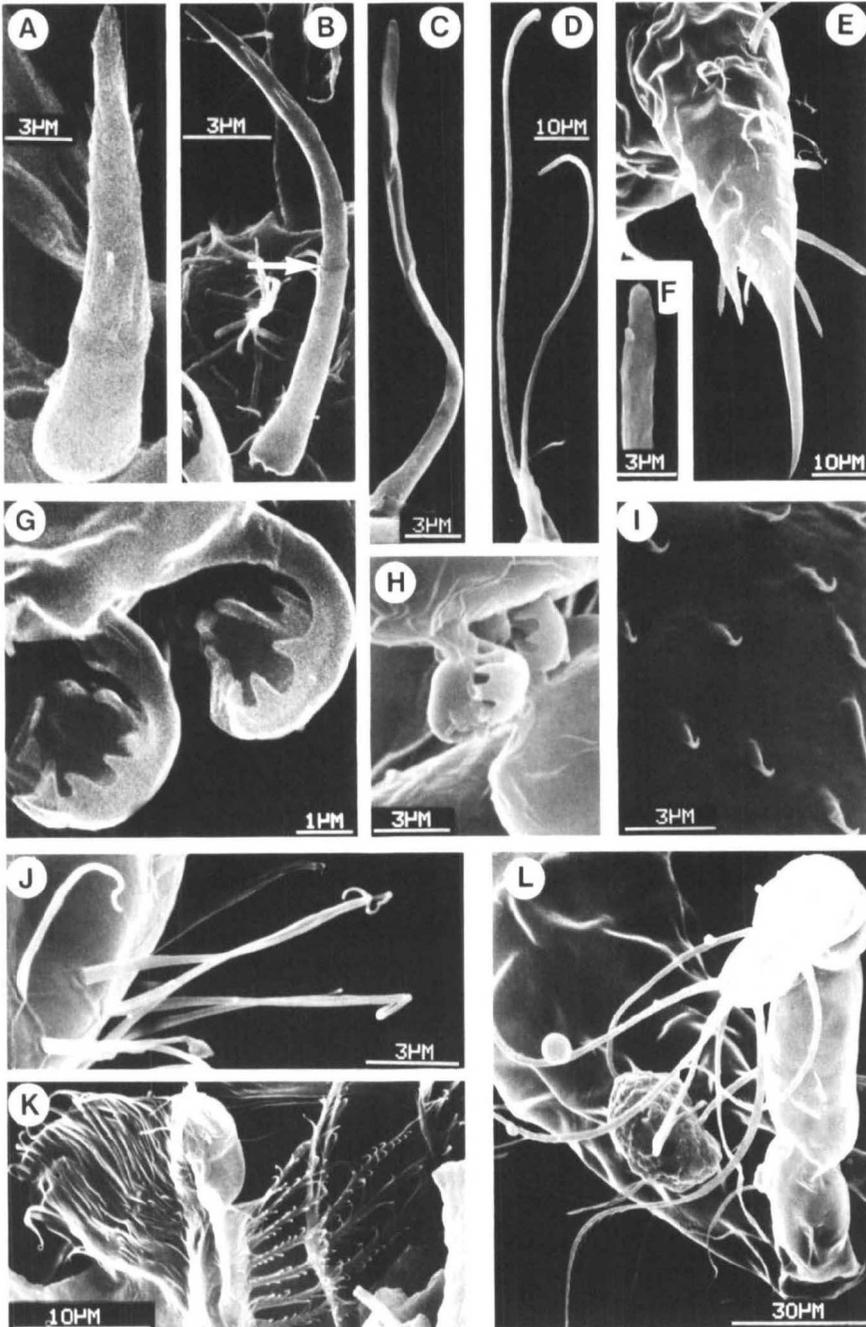


Figure 6. Various cuticular outgrowths of *D. crinitichelis*. A, cuspidate seta (TYPE 2d); B, proboscate seta (TYPE 16); C, short form of aesthetasc; D, long aesthetascs; E, bifid dactyl of megalopa walking leg with serrulate setae (TYPE 11a); F, tip of aesthetasc; G, cincinnuli of megalopa pleopods; H, two pleopods of megalopa hooked up via two cincinnuli pairs; I, a group of denticulettes; J, microtrichia of zoeal stages; K, two cuticular outgrowths of megalopa gastric mill; L, first maxilliped of zoea with plumodenticulate setae (TYPE 13-iv) on distal segment carrying a possible food particle.

reptant decapod crustaceans by SEM and also found numerous setae devoid of pores. It seems, therefore, that some crustacean setae, including several of *D. crinitichelis*, do not have any pores.

Antennules of *D. crinitichelis* and other crustaceans bear special types of setae (aesthetascs, TYPE 31), known to be chemosensory in function (Laverack, 1964; Weel and Christofferson, 1966; Ache and Case, 1969; Shephard, 1974). They have end-pores in crustaceans such as *A. pallipes* (Thomas, 1970) and the lobster *Panulirus argus* (Laverack and Ardill, 1965). However, in other crustaceans, such as the crabs *Cancer* (Ghiradella et al., 1970) and *Paragrapsus gaimardii* (Snow, 1973) pores have not been found. It appears now (Guse, 1979) that the aesthetascs of some crustaceans, including *Neomysis integer*, have a porous cuticle distally instead of a single pore. It seems likely that this is also the situation in *D. crinitichelis*.

Shafts of aesthetascs vary with respect to numbers of annuli. Fish (1972) could not find an annulus in *Eurydice pulchra*, nor could we in *D. crinitichelis*. Thomas (1970) reported a single one in *A. pallipes*. In contrast, aesthetascs of *Cancer* (Ghiradella et al., 1970), *Paragrapsus gaimardii* (Snow, 1973) and *Pagurus alaskensis* (Snow, 1974) have multiple periodic annulations along most of the shaft length. Thus, aesthetascs can be easily distinguished on the basis of pores and annuli alone.

#### *Micromorphology of Setal Shaft Outgrowths*

One technical distinction has been made and is adopted here: setae with denticles only are serrate or serrulate, those with a second type of outgrowth (discussed below) plumodenticulate. Such setae have been reported with two V-shaped rows of denticles post-annularly (Thomas, 1970; Fish, 1972; Farmer, 1974). Recently, however, Factor (1978) found "triserrate setae" on larval lobsters. In *D. crinitichelis* unusual serrate setae on the chela show only a single row of denticulations and some plumodenticulate setae (13-xii, -xiii) have three rows. Denticles, therefore, do not always occur in two V-shaped rows, as previously supposed.

Setae with setules are more complex than previously thought. While denticule-like structures are direct and continuous extensions from the shaft wall, setules are articulated at their bases (Figs. 4A, 4E, 4F), thus allowing for increased flexibility to prevent breakage. Setules vary considerably in length and width from short, almost denticule-like (Fig. 4I), to a somewhat longer intermediate form (Fig. 4J), to very long and flexible (Fig. 4K). In extreme cases (TYPE 4d), setules can be almost as long as the shaft itself. Setule type is usually constant for a given seta but a few, TYPES 13-x and 13-xi, characteristically have setules graded in length. Setulettes occur on most setules, forming short, straight digits on small stiff setules (Figs. 3H and 4I) to long, often hook-like structures on long setules of plumose setae (Fig. 4K). On occasion setulettes may seem to be absent (e.g., Fig. 2D) but it is more likely that these delicate structures are then applied against the setule, possibly during preparation. Setules and setulettes were frequently seen interlocking with those of adjacent setae of the same type (4b), suggesting a screening function.

Most setae with setules retained these outgrowths throughout development. However, some setal types, including the graded multidenticulate and plumodenticulate cuspidate setae (TYPE 13-x and 13-xi), gradually lost all their setules during subsequent molts, until only denticles were left on the shafts in the megalopa or first crab instar. Bookhout and Costlow (1974) observed the same

on plumodenticulate cuspidate setae in larvae of *Portunus spinicarpus*. Other setae which appear smooth but show minor outgrowths with SEM (TYPES 13-xiv, 13-xv and 16) could be explained by this reduction of setules or, if derived from simple setae, by development of outgrowths (Menzies, 1956; Farmer, 1974).

### Setal Classification

Despite variability in morphology there are clear, characteristic patterns, which allow for definition of distinct setal types. It is important, therefore, that these morphological complexities be recognized in a unified setal classification system. The systems of Thomas (1970) and Drach and Jacques (1977) provide the best terminology and classification to date, but neither is adequate alone. We have incorporated *D. crinitichelis* setae into the latter scheme, with some proposed modifications. At the same time, we have relied primarily on the terminology of Thomas (1970), which seems most widely accepted and has already been applied to larval setae of lobsters (Factor, 1978) and portunid crabs (Bookhout and Costlow, 1974; 1977; Shinkarenko, 1979).

Thomas (1970), who was the first to recognize setal diversity, found at least 20 distinct types in *A. pallipes*. These were divided into 5 subcategories, four of which included precisely described setae which were assigned separate names. The remaining division of plumodenticulate setae was not categorized in this manner. Some differences were recognized but, unlike other setae, not in the nature of their tips. The subsequent SEM study on setal tips (Thomas, 1971) did not include plumodenticulate setae.

Based on a variety of adult reptant and natant crustaceans, Drach and Jacques (1977) proposed an alternative alphanumeric classification scheme, without using complex terminology. It is based on the presence or absence of 15 setal features, devised to include existing as well as new types yet to be discovered. Basic types (e.g., plumose) are given Arabic numerals and variations (e.g., pores, length and density of outgrowths) are put into alphabetic subcategories (e.g., TYPE 4a, 4b etc.)

Many setal types can be placed in the alphanumeric categories of Drach and Jacques (1977), while still accommodating the terminology of Thomas (1970). Setal types with two kinds of shaft outgrowths were placed in TYPE 13, subdivided as 13a–13e, according to form of outgrowths (épines, dents, écailles, barbules). The highly diverse plumodenticulate setae of *D. crinitichelis* do not fit these subdivisions. To avoid confusion whilst retaining the basic system, plumodenticulate setae have been put into provisional Roman numeral subdivisions of TYPE 13 (13-i to 13-xv), according to such criteria as L/W ratio, annulus, pore and shaft outgrowths.

Other modifications involve additional subdivisions for distinct variations. This includes plumose seta TYPE 4d and pappose setae TYPE 9a to 9c, the latter subcategories corresponding to increasing setule density. The plumose natatory setae of *D. crinitichelis*, with a single large annulus, were given a separate rank (TYPE 5b) to distinguish them from TYPE 5a which has multiple annuli (Drach and Jacques, 1977).

### Setal Functions

Functions of setae cannot be determined with certainty based on morphological and behavioral findings alone; they should be supported by physiological evidence. Such research, in crustacea, has mainly concentrated on antennules, long suspected as a site of chemoreception (Slifer, 1970). Aesthetascs are now estab-

lished as setal chemosensors on these appendages. For most other setae physiological evidence is very poor. Morphology, behavior and location of setae have been used collectively to make inferences about possible functions. Interpretation in some cases is plausible, in others controversial (compare Thomas (1970), Fish (1972), Farmer (1974) and Shinkarenko (1979)). One of the more convincing examples includes plumose setae which often interlock via setules and setulettes to form a palisade. In *D. crinitichelis* such setae lack pores and, presumably, a chemosensory function. The structural arrangement strongly suggests a screening function of some kind. On the other hand, the long setules of plumose natatory setae on maxillipeds of zoeae could functionally increase the surface area available for thrust in locomotion.

Another good example is found on the pleopods of the abdomen in the megalopa, which are used exclusively for locomotion. The observed synchronization of pleopod pairs during swimming seems to be maintained by highly modified paired setae (Fig. 6G). These cincinnuli (Drach and Jacques, 1977), unlike most other setae, are not innervated by nerve fibers (Tombes and Foster, 1979), suggesting a mechanical function instead. Fish (1972) described them as "couplers," ensuring simultaneous movement and therefore increased effectiveness of single pleopod pairs in creating a water current. In *D. crinitichelis* megalopae cincinnuli were found interlocking tightly (Fig. 6H), thus supporting this theory.

Other setae, such as the serrulate type, have very large, conspicuous end-pores (Fig. 5J), while the remaining shaft portion is relatively devoid of outgrowths. Serrulate setae (TYPE 11a) are found on all pereopods in the megalopa and first crab instar, especially on the dactyls of walking legs where 4 or more are distributed in a fan-like fashion (Fig. 6E), their tips and pores pointing toward the substratum. Such an arrangement implies a chemosensory function. Experiments by Laverack (1963) on the dactyls of walking legs of *Carcinus maenas*, *Portunus puber* and *Homarus vulgaris* support this interpretation, which has subsequently been confirmed (Shelton and Laverack, 1970). Serrulate setae (TYPE 11a) found on *D. crinitichelis* pereopods, correspond closely to the sensory setae of *Homarus gammarus* (Shelton and Laverack, 1970).

Findings in this study suggest that while some setae have a single function, others, such as certain plumodenticulate setae, could have as many as three. Setules could act as screens or brushes, depending on length and density. Denticules, depending on size and shape, could be used for cleaning, grasping, transferring (Fig. 6L) or abrading food. Those setae with pores could also act as chemosensors. Plumodenticulate setae TYPE 13-iv with conspicuous terminal pores (Fig. 3D), which are found on the endopodites of maxillules and maxillae, for example, have been observed in live zoeae and their use seems to suggest some form of testing of material combined with food transfer and possibly abrasion (Shinkarenko, 1979). Other plumodenticulate setae have very fine tips, lacking pores and could act as mechanoreceptors (reviewed by McIver, 1975). The unusual position of TYPE 13-v setae, on the basipodite and in later zoeal stages on the coxopodite of the maxillule, seems to suggest this. They are oriented almost at right angles to other setae and directed towards adjacent mouthparts, thus possibly functioning as inter-limb coordinators (Fryer, 1960). There is evidence for mechano-sensitive structures in *Artemia salina* (Lent, 1977) which are likely responsible for coordinating metachronal limb movements.

On other appendages multiple functions may be performed by several setae. Different setal types which appear in associations (Thomas, 1979) are variously known as "companion setae" (Laverack, 1964) and "accessory setae" (Snow, 1974). Similar setal relationships occur in *D. crinitichelis*. For example, often a

proboscate seta (TYPE 16) with a large terminal pore is closely associated with a palisade of poreless plumed setae of one kind or another. The former seta could be chemosensory, while the latter ones fulfill a screening function. Three strikingly different plumodenticulate setae (TYPE 13-v, -vi and -vii; see Figs. 3B and 3C) are present in specific positions and orientations on the basipodite of the maxillule. Such an arrangement could represent a sophisticated setal complex which performs a multitude of functions as a unit. Evidence to this effect would help determine the "whole-animal significance" (Snow, 1974) of various setae.

#### ACKNOWLEDGMENTS

This work was supported by the Natural Sciences and Engineering Research Council of Canada through Operating Grant #A4696. We thank Mr. E. Lin, Department of Zoology, University of Toronto, for technical assistance in SEM and Dr. Finn Sander, Director, for use of facilities at Bellairs Research Institute, Barbados.

#### LITERATURE CITED

- Ache, B., and J. Case. 1969. An analysis of antennular chemoreception in two commensal shrimps of the genus *Betaeus*. *Physiol. Zool.* 42: 361-371.
- Bookhout, C. G., and J. D. Costlow, Jr. 1974. Larval development of *Portunus spinicarpus* reared in the laboratory. *Bull. Mar. Sci.* 24: 20-51.
- . 1977. Larval development of *Callinectes similis* reared in the laboratory. *Bull. Mar. Sci.* 27: 704-728.
- Drach, P., and F. Jacques. 1977. Système sétifère des Crustacés Décapodes. Principes d'une classification générale. C. R. Acad. Sc., Paris, Sér. D 284: 1995-1999.
- Factor, J. R. 1978. Morphology of the mouthparts of larval lobsters, *Homarus americanus* (Decapoda: Nephropidae), with special emphasis on their setae. *Biol. Bull.* 154: 383-408.
- Farmer, A. S. 1974. The functional morphology of the pereopods of *Nephros norvegicus* (L.) (Decapoda: Nephropidae). *J. Nat. Hist.* 8: 121-142.
- Fish, S. 1972. The setae of *Eurydice pulchra* (Crustacea: Isopoda). *J. Zool. London.* 166: 163-177.
- Fryer, G. 1960. The feeding mechanism of some atyid prawns of the genus *Caridina*. *Trans. R. Soc. Edinb.* 64: 217-244.
- Ghiradella, H. T., J. Cronshaw, and J. Case. 1970. Surface of the cuticle on the aesthetascs of *Cancer*. *Protoplasma* 69: 145-150.
- Gonor, J. J., and S. L. Gonor. 1973. Variations in appendage setal counts in zoea larvae of four porecellanid crabs (Decapoda, Anomura) from Oregon. *Crustaceana* 25: 245-252.
- Guse, G.-W. 1979. Feinstruktur der Aesthetasken von *Neomysis integer* (Leach) (Crustacea, Mysidacea). *Zool. Anz.* 203: 170-176.
- Laughlin, R. B., and J. M. Neff. 1976. SEM observations on sensory structures of the zoea *Rithropanopeus harrasi*. *Am. Zool.* 16: 214.
- Laverack, M. S. 1963. Aspects of chemoreception in crustacea. *Comp. Biochem. Physiol.* 8: 141-151.
- . 1964. The antennular sense organs of *Panulirus argus*. *Comp. Biochem. Physiol.* 13: 301-321.
- , and D. J. Ardill. 1965. The innervation of the aesthetasc hairs of *Panulirus argus*. *Quart. J. Microscop. Sci.* 106: 45-60.
- Lent, C. M. 1977. The mechanism for co-ordinating metachronal limb movements between joined male and female *Artemia salina* during precopulatory behaviour. *J. Exp. Biol.* 66: 127-140.
- McIver, S. B. 1975. Structure of cuticular mechanoreceptors of arthropods. *Ann. Rev. Ent.* 20: 381-397.
- Menzies, R. J. 1956. A study of the microscopic structure of isopod setae. *Ann. Mag. Nat. Hist., Ser. 12*, 9: 698-700.
- Pohle, G., and M. Telford. 1981. The larval development of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae) in laboratory culture. *Bull. Mar. Sci.* 31: 753-773.
- Reaka, M. L. 1975. Molting in stomatopod crustaceans. I. Stages of the molt cycle, setagenesis, and morphology. *J. Morph.* 146: 55-80.
- Schlotterbeck, R. E. 1976. The larval development of the lined shore crab, *Pachygrapsus crassipes* Randall, 1840 (Decapoda, Brachyura, Grapsidae) reared in the laboratory. *Crustaceana* 30: 184-200.

- Scotto, L. E. 1980. Studies on decapod crustacea from the Indian River region of Florida. XIV. A method for rapid preparation of brachyuran larvae for scanning electron microscopy. *Crustaceana* 38: 99-101.
- Shelton, R. G. J., and M. S. Laverack. 1970. Receptor hair structure and function in the lobster *Homarus gammarus* (L.). *J. Exp. Mar. Biol. Ecol.* 4: 201-210.
- Shepherd, P. 1974. Chemoreception in the antennules of the lobster, *Homarus americanus*. *Mar. Behav. Physiol.* 2: 261-273.
- Shinkarenko, L. 1979. Development of the larval stages of the Blue Swimming Crab, *Portunus pelagicus* L. (Portunidae: Decapoda: Crustacea). *Austr. J. Mar. Freshwater Res.* 30: 485-503.
- Slifer, E. H. 1970. The structure of arthropod chemoreceptors. *Ann. Rev. Ent.* 15: 121-142.
- Snow, P. J. 1973. Ultrastructure of the aesthetasc hairs of the littoral decapod, *Paragrapsus gaimardii*. *Z. Zellforsch.* 138: 489-502.
- . 1974. Surface structures of the antennular flagella of the hermit crab *Pagurus alaskensis* (Benedict): A light and scanning electron microscope study. *J. Morph.* 144: 195-216.
- Thomas, W. J. 1970. The setae of *Astropotamobius pallipes* (Crustacea: Astacidae). *J. Zool., London*, 60: 91-142.
- . 1971. Electronmicroscope studies of crayfish setae (*Astropotamobius pallipes*). *Experientia* 27: 1454-1455.
- . 1979. Setal relationships and their significance in *A. pallipes*. *Experientia* 35: 1309-1311.
- Tombes, A. S., and M. W. Foster. 1979. Growth of appendix masculina and appendix interna in juvenile *Macrobrachium rosenbergii* (De Man) (Decapoda, Caridea). *Crustaceana, Suppl.* 5: 179-184.
- Weel, P. B. van, and J. P. Christofferson. 1966. Electrophysiological studies on perception in the antennulae of certain crabs. *Physiol. Zool.* 39: 317-325.

DATE ACCEPTED: April 10, 1981.

ADDRESS: Department of Zoology, University of Toronto, Ontario, M5S 1A1, Canada.