

GILL-CLEANING MECHANISMS OF THE MUD LOBSTER *THALASSINA ANOMALA* (DECAPODA: THALASSINIDEA: THALASSINIDAE)

Zenon B. Batang and Hiroshi Suzuki

A B S T R A C T

The gill-cleaning mechanisms of the mud lobster *Thalassina anomala* were examined. The gill complement consists of 12 arthrobranchs and 5 podobranchs, both having cylindrical flattened filaments. Morphological inference suggested passive gill-cleaning mechanisms involving various setal systems; multidenticulate setae (on scaphognathite, setobranch, distal epipod), pappose setae (on coxae, proximal epipod), serrate setae (short setal tufts on limb coxae), and plumose setae (on carapace fringe). Smooth setae were found on the thoracic epimeron (inner wall of the branchial chamber) and inner branchiostegal margin. Small lamellar protrusions on the pereopodal arthroidium were noted bearing dense pappose setae. The multidenticulate scaphognathite and epipodal setae were serrate distally. The digitate scale setules of multidenticulate setobranch, epipodal, and scaphognathite setae shared similarities: (1) digitation pattern gradually changes distally from angular to linear, (2) proximal setules incline toward the base while distal setules incline toward the tip with overlapping inclinations in a transition zone, and (3) setule density increases distally on the setal shaft. The multidenticulate scaphognathite setae have a V-form spiral arrangement on the distal part of the shaft, which is atypical in decapods. Aquarium observations did not show active gill cleaning by thoracic limbs, but general body grooming and respiratory reversal were observed. The phyletic relationships of gill-cleaning mechanisms, with notes on branchial morphology, are discussed.

Grooming mechanisms vary among decapod taxa, and predominantly involve the third maxillipeds, pereopods, or other setiferous thoracic processes which prevent fouling of body surfaces, cephalothoracic appendages, embryos, and gills (Bauer, 1975, 1977, 1978, 1979, 1981, 1989; Hindley and Alexander, 1978; Martin and Felgenhauer, 1986; Pohle, 1989a, b; Fleischer *et al.*, 1992; Nickell *et al.*, 1998; Suzuki and McLay, 1998). Grooming behaviors are closely related in function, but usually differ in structural morphology (Bauer, 1977, 1981, 1989). Grooming has been regarded as a conservative systematic character denoting phyletic affinity and adaptive value in decapods (Bauer, 1981, 1989; Martin and Felgenhauer, 1986; Suzuki and McLay, 1998). Most grooming structures are characterized by the presence of setal systems whose diverse forms and lesser-known functions invite further scrutiny (Jacques, 1989; Watling, 1989; Fleischer *et al.*, 1992; Felgenhauer, 1992).

The respiratory process in decapod crustaceans draws water into the branchial chamber and predisposes the gills to deleterious fouling by particulate debris and epizootes (Bauer, 1989, 1998). Fouling of gills may seriously affect respiration and ion regulation (Bauer, 1981, 1989; Martin and Felgenhauer,

1986). Therefore, decapods have evolved a variety of gill-cleaning mechanisms to counter fouling pressures. These mechanisms include setiferous thoracic epipods (penaeids, nephropids, palinurids, and brachyurans), pereopods (carideans, stenopodids, thalassinids, and anomurans), epipod-setobranch complex (carideans) or setobranchs only (axiids and astacids), scaphognathite setae (atyiid carideans), and branchiostegal setae (astacids) (Bauer, 1981, 1989, 1998; Suzuki and McLay, 1998). An antifouling function has also been attributed to the compound fringe setae on limb articles and carapace (Bauer, 1981, 1989). Respiratory reversal, or the back-flushing of respiratory water from the branchial chamber, has been similarly recognized as gill-cleaning activity in decapods (Bauer, 1989), while the newly reported phenomenon of "limb rocking" (Bauer, 1998) may have been overlooked in other species. Limb rocking refers to intentional agitation of limbs thus jostling the setobranchs and setiferous epipods in the crayfish *Procambarus clarkii* Girard, 1852 (see Bauer, 1998).

In the Thalassinida Burkenroad, 1981, gill-cleaning mechanisms are less well known relative to other reptant taxa, with few and scattered references to axiids, upogebiids, and callianassids (Martin and Felgenhauer, 1986;

Bauer, 1989; Nickell *et al.*, 1998). Pereiopodal gill brushing has been found in calianassids and upogebiids, and setobranchs in axiids. Though thalassinids generally exhibit uniform subterranean habit and burrow-adapted morphology (Scholtz and Richter, 1995), variations in gill form are well recognized (Nash *et al.*, 1984; Astall *et al.* 1997). The group has widespread geographic distribution ranging from deep-sea to supralittoral zones of mangrove swamps (Labadie and Palmer, 1996) and their cosmopolitan range has been attributed to their morphological and behavioral adaptability (Nickell *et al.*, 1998). Thalassinids undergo active bioturbation which can have substantial geochemical impact through the redistribution of nutrients, trace metals, and radionuclides (Whitehead *et al.*, 1988; Ziebis *et al.*, 1996). Their fossorial habit presupposes constant exposure to fouling pressures and hypoxia, though various respiratory adaptations of the group to hypoxic, or even anoxic, conditions have been noted in Astall *et al.* (1997). Antifouling implications of burrowing behavior has also been suggested (Bauer, 1989). The systematic position of thalassinids remains unsettled and the taxon has been formerly grouped with the Anomura (Martin and Abele, 1986) or excluded from them (Scholtz and Richter, 1995). Based on gill-cleaning and body-grooming characters, Bauer (1989) concluded a thalassinid origin of the anomurans.

The mud lobster *Thalassina anomala* Herbst, 1804, or mangrove lobster to some authors (Yunker and Scura, 1985; Pillai, 1990), inhabits the eulittoral and supralittoral zones of mangrove swamps in estuarine tropical shores (Pillai, 1990). The species is a deposit feeder which can stand prolonged emersion despite its subterranean habit. It usually creates complex burrow systems that can reach 2 m deep and forms conical mounds on the ground surface which can significantly alter substrate topography (Pillai, 1992). The biomechanics of its chelae has been studied in relation to feeding, digging, and aggressive encounters (Pillai, 1990).

Here, we present aspects of thalassinid grooming behavior by describing the gill-cleaning mechanisms of the mud lobster based on morphological inference and aquarium observations. Emphasis is given to the ultrastructure and distribution of setiferous processes which are conceivably involved in

gill cleaning. A synthesis of thalassinid gill-cleaning mechanisms is subsequently discussed.

MATERIALS AND METHODS

Mud lobsters were collected from mangrove swamps in Lombok Island, Indonesia, and Amami-oshima, southern Japan, in March and May 1998, respectively, by excavating burrows. Specimens were preserved in 70% alcohol. Body size was expressed in carapace length (CL: dorsomedial distance between the tip of the rostrum and the posterior edge of the carapace). Following dissection of the branchial chamber by cutting off the branchiostegites, the position, structure, and branchial formula of the gills were noted. Gross morphological observations of the branchial chamber, using larger specimens (CL > 5.0 cm), were conducted by light microscope (Nikon SMZ-U) with camera lucida.

The ultrastructures of gill-cleaning processes were observed by scanning electron microscope (SEM). For SEM preparation, branchiostegites were cut off and the entire cephalothorax halved longitudinally. Samples were dehydrated in 2-h series of ethyl alcohol (EtOH: 80%, 90%, 95%, 100%, 100%), later replaced with 2 mixtures (1:1, 2:1) of tri-butyl alcohol (t-BuOH) and EtOH, and 2 final changes of absolute t-BuOH. Samples in absolute t-BuOH were refrigerated overnight after which they were freeze-dried (VFD-21 t-BuFreeze Dryer), mounted on aluminum stubs, and coated on gold-palladium complex using EIKO IB3 Ion Coater and viewed on SEM (Hitachi S-4100H).

Visual observation of live specimens in the laboratory was conducted to determine species-specific behavior of gill cleaning. Single specimens were placed in a glass aquarium filled with brackish water and graded sediments, predominantly white fine sands, to ensure visual clarity. The aquarium was aerated continuously and the specimen fed with commercial crustacean food. Observation was done 3–5 h daily within a week and all signs of body-grooming activities, as defined by Bauer (1981), were recorded. Gill nomenclature follows Astall *et al.* (1997) where gills assigned to a thoracic somite are labeled according to associated thoracic appendages. For brevity, maxillipeds 1–3 and pereopods 1–5 are indicated by M1–M3 and P1–P5, respectively. The description of setal systems is based on Felgenhauer (1992) and Watling (1989).

RESULTS

Branchial Morphology

The mud lobster *T. anomala* has paired arthrobranches (anterior and posterior) articulating on the arthrodium of M2–P4 (Figs. 1B, 2, Table 1). Podobranchs arise singly from the coxae of M2–P3. Podobranchs are well developed on M2–P2, rudimentary on P3, and lost on P4. Setiferous epipods are present on M2–P4, increasing in length posteriorly, with the P4 epipod being twice as long as the M2 epipod. The setiferous epipods originate on the same base as the podobranchs (Fig. 2), both projecting posteriorly, and filling the ventral periphery of the branchial chamber.

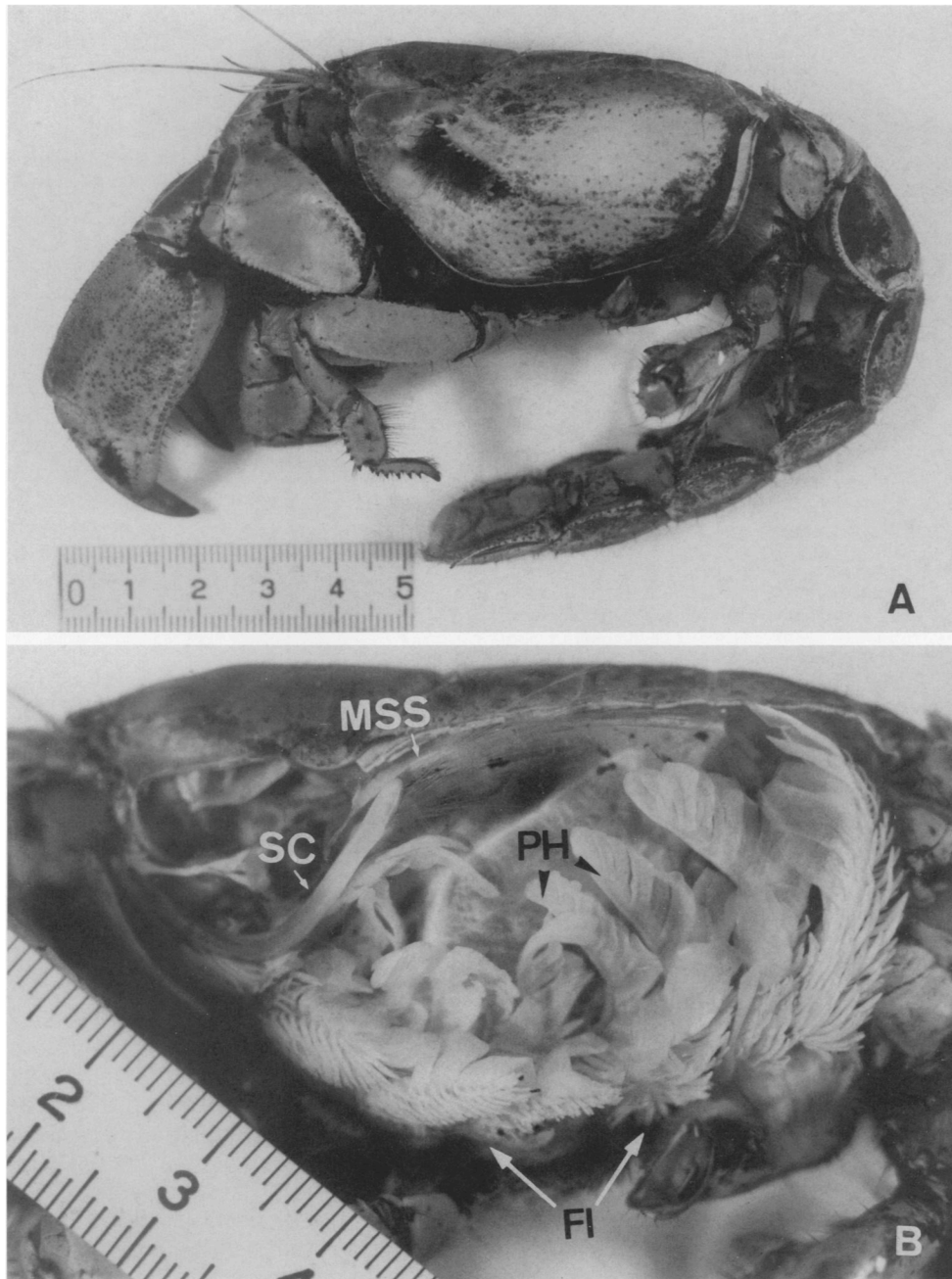


Fig. 1. *Thalassinia anomala* Herbst, 1804. External (A) and internal (B) view of the branchial chamber showing phyllid (PH) and filamentous (FI) gills and the posterior edge of scaphognathite (SC) bearing long multidenticulate setae (MSS). Scale number in cm.

Overall, the mud lobster has 12 arthrobranches and 5 podobranchs (rudimentary podobranch on P3 included) in the gill chamber. Pleurobranches are lacking. Gills and an epipod are absent on P5.

The gills of *T. anomala* consist of two filament forms, cylindrical (filamentous type) and compressed (phyllid type) (Figs. 1B, 2). Both filament forms cooccur in all arthrobranches and podobranchs. The phyllid fila-

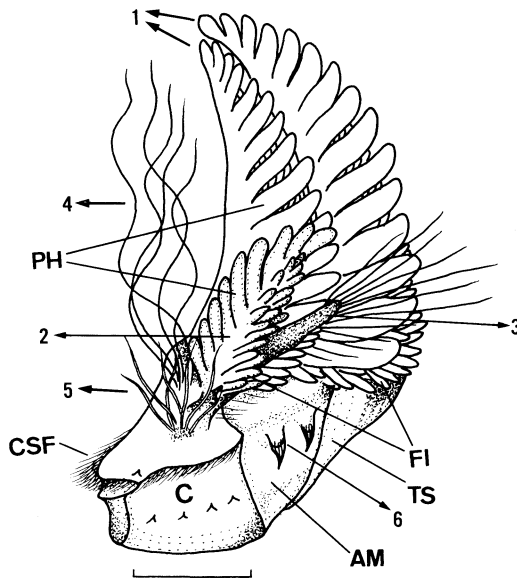


Fig. 2. Schematic diagram of the branchiae and setiferous processes associated with the second pereopod of *Thalassina anomala* Herbst, 1804. Left is anterior part. 1, arthrobranchs (anterior and posterior); 2, podobranch; 3, epipod; 4, setobranch setae; 5, outer short coxal setae; 6, arthrodial lamellae bearing setae; PH-phylloid gill filaments; FI-filamentous gill filaments; TS-thoracic sternite; CSF-coxal setal fringe; C-coxa. Scale: 5 mm.

ments are longer but obviously have thinner cuticle than the filamentous filament. The latter filaments are enveloped in transparent epithelial sheaths. Within the branchial chamber, the phylloid filaments of arthrobranchs project upright, filling most of the branchial space, while the filamentous type protrude numerous on the basal section of the gill shaft and, together with the podobranchs, form stacks of filaments guarding the ventral periphery of the branchial chamber (Fig. 1B).

Gill-cleaning Processes and Setal Systems

Scaphognathite Setae.—A long scaphognathite arises from the second maxilla, extending posteriorly into the anterior branchial chamber (Fig. 1B). The posterior end of the scaphognathite is ornamented with long setae (Fig. 3A, B) bearing digitate scale setules (Fig. 3C). The multidenticulate scaphognathite setae (MSS), following Suzuki and McLay (1998), project from supracuticular sockets on the scaphognathite margins and extend as far as the phylloid filaments of P4 gills, which arch posteriorly following the marginal curvature of the branchial chamber. In

addition, the dorsodistal margin of the tip of each scaphognathite bears four short smooth setae with hooked tips (Fig. 3B). Both setal types on the scaphognathite lack an annulus.

The scale setules of the MSS differ in digitation pattern and inclination along the setal shaft. The digitation pattern is angular proximally and gradually becomes linear on the distal part of the setal shaft. The angular digitate scales are randomly distributed on the proximal part of the setae and incline toward the setal base (Fig. 3E). The linear digitate scale setules become denser distally and incline toward the setal tip (Fig. 3F). The distal scale setules form V-shaped generative lines on the shaft, which appear to spiral at low magnification (Fig. 3C). The mixture of oppositely inclined scales (transition zone) generally occurs midlength along the setal shaft. The MSS taper and become serrated distally (Fig. 3D).

Coxal Setal Systems.—Four setal types arising on thoracic coxae are distinguished; long and short setal groups on the dorsolateral surface of the coxa, the setal fringe on coxal margins, and the setal tufts on arthrodial lamellae (Fig. 2).

The dorsolateral setae are found in two distinct locations on M3 and P1–P4, an inner group of long multidenticulate setae (Figs. 2, 4) and an outer group of short annulate serrate setae (Figs. 2, 5A–F). Both setal groups lie close to the epipodal base, with decreasing setal density posteriorly. The coxal surfaces do not show prominent papillar or tubercular formation, or setobranchs in the sense of Borradaile (1907), which abound in carideans and astacids (Bauer, 1981, 1998). By virtue of their morphology and location, we term the long multidenticulate setae “setobranch setae.” These setobranch setae insert into gill filaments (Figs. 4A, 6A) and their digitate scale setules imply a gill-cleaning function (Bauer, 1981, 1998). The setae arise from basal sockets on the coxa (Fig. 4-1), thus allowing them to move flexibly when jostled. The digitate scale setules of the setobranch setae also vary in shape and orientation along the shaft (Fig. 4). One twentieth of the setal length from the base is naked and without an annulus (Fig. 4-1), after which scale setules appear and incline proximally (Fig. 4-2). A transition zone of setule inclination spans a region nearly equal to one-fifth

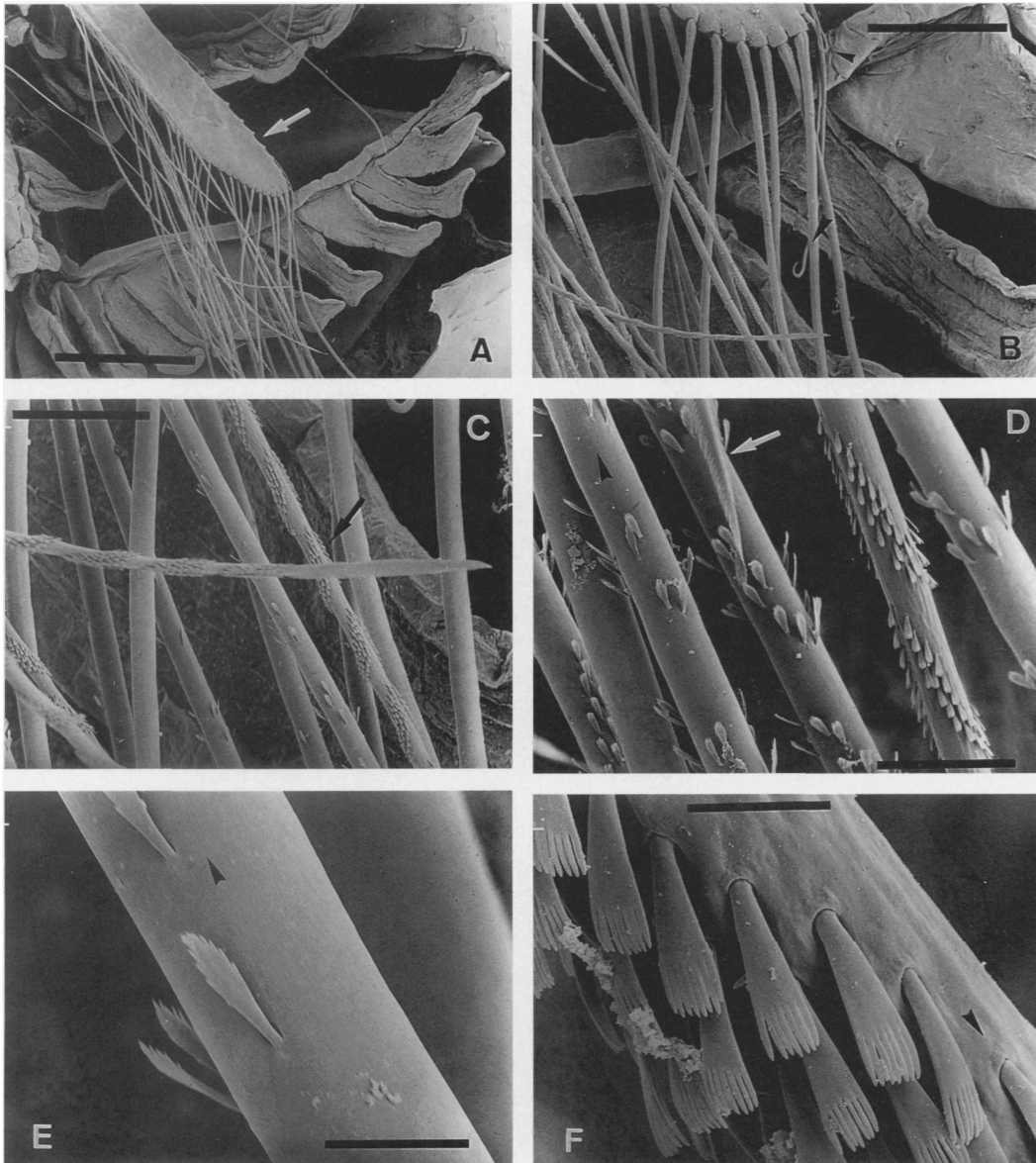


Fig. 3. *Thalassina anomala* Herbst, 1804. A, posterior edge of scaphognathite (arrow) with multidenticulate setae; B, proximal view of multidenticulate scaphognathite setae (MSS) and smooth setae with hooked tips (arrowheads); C, V-form arrangement of scale setules on distal part of MSS showing spiral appearance (black arrow); D, MSS scale setules and serrate tip (white arrow); E, proximal scale setules of MSS showing digitation pattern (angular type) and inclination (arrowhead points to base of seta); F, distal MSS scale setules with linear digitation pattern and inclination to setal tip (arrowhead points to tip of seta). Scale bars: A = 749 μm ; B = 231 μm ; C = 86 μm ; D = 43 μm ; E = 10 μm ; F = 4 μm .

of the setal shaft (Fig. 4-3 to 4-5), thereafter the scale setules incline distally until the setal tip (Fig. 4-6 to 4-8). Setule density increases from base to tip.

The outer short setae (Fig. 5A) are serrate and project from cuticular sockets (Fig. 5B) on the coxal surface. The proximal part of the

seta is naked (Fig. 5C) and bears an annulus (Fig. 5D), followed by a linear series of spiniform serrules which is interrupted by a short naked trunk halfway along the length (Fig. 5E). The spiniform serrules branch out in two opposite generative lines along the shaft and are oriented toward the setal tip (Fig. 5F). The

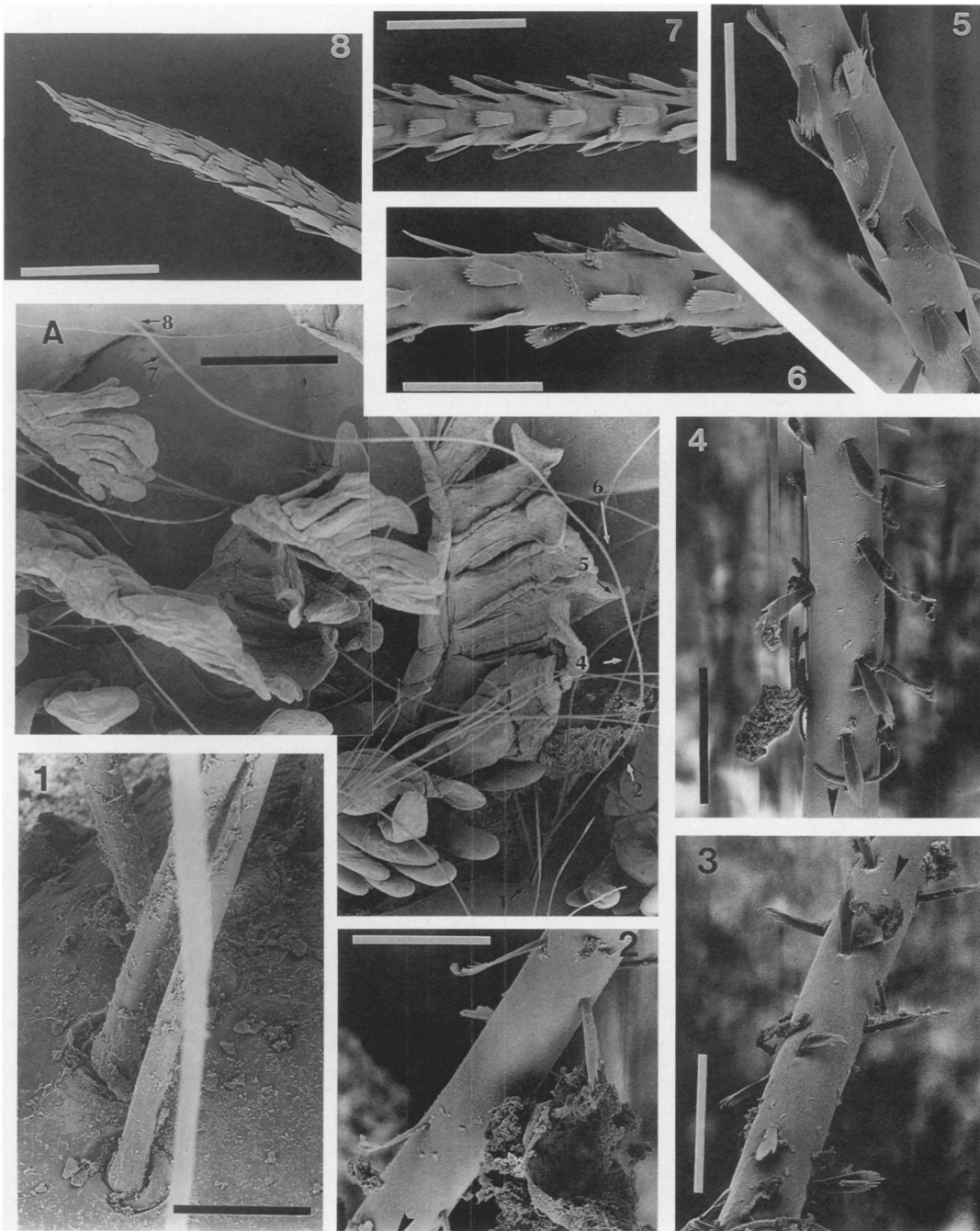
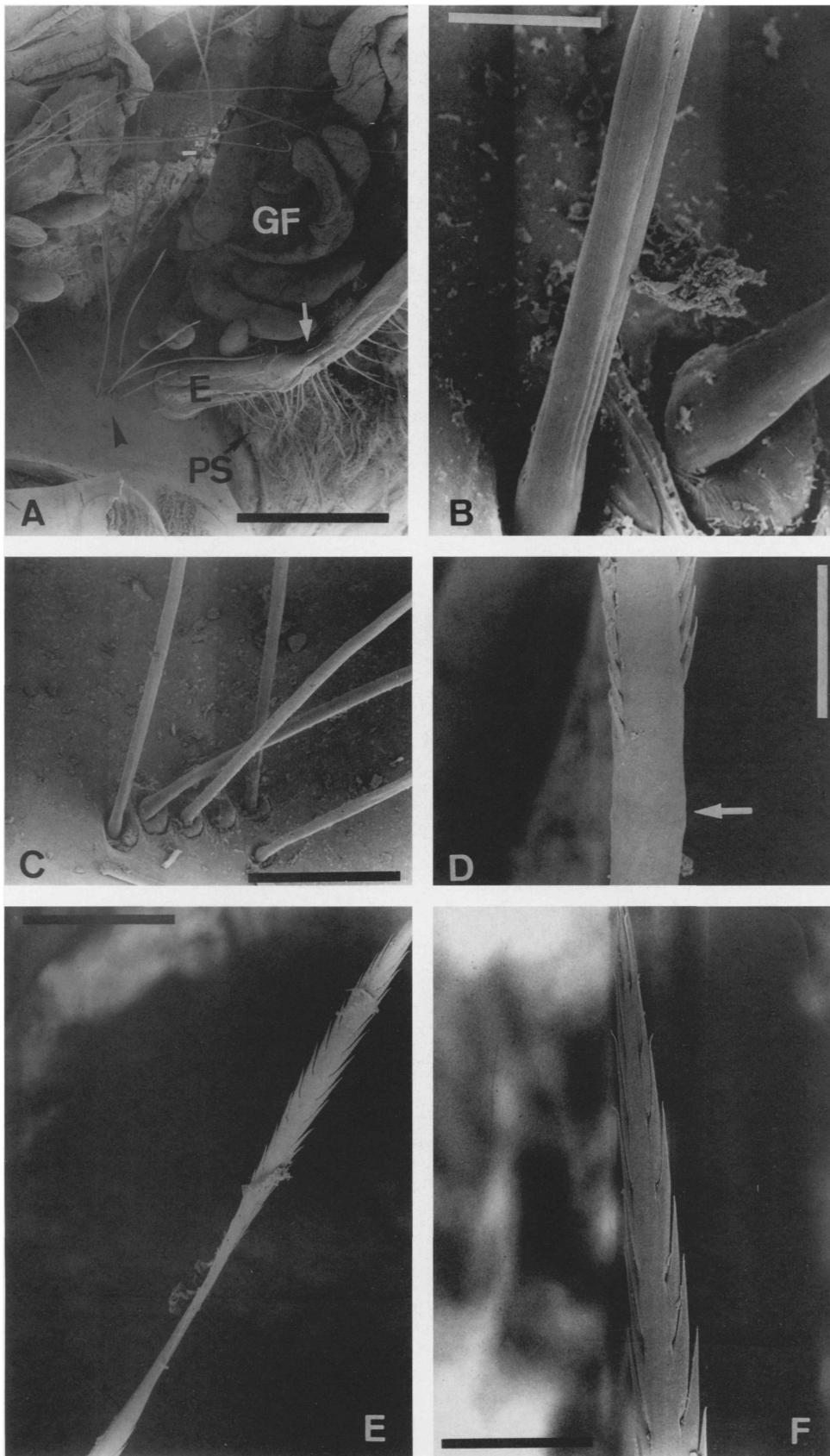


Fig. 4. *Thalassina anomala* Herbst, 1804. A, multidenticulate setobranche setae on coxa, with magnified sections (1-8) of setal shaft. Arrows point to approximate position of magnified sections. Arrowheads in 2-7 point toward base of seta. Scale bars: A = 784 μm ; 1 = 70 μm ; 2-4 = 23 μm ; 5, 6 = 22 μm ; 7, 8 = 20 μm .

Fig. 5. *Thalassina anomala* Herbst, 1804. A, outer tuft of serrate setae on coxa (arrowhead) of fourth pereiopod. Note small lobular protrusion (white arrow), gill filaments (GF) of arthrobranch, and proximal pappose setae (PS) on basal part of epipod (E); B, C, base of serrate setae showing naked proximal part and sockets; D, annulus (arrow); E, naked trunk interrupting serrate part; F, spiniform serrules on distal part of seta. Scale bars: A = 737 μm ; B = 230 μm ; C = 120 μm ; D = 23 μm ; E = 59 μm ; F = 22 μm .



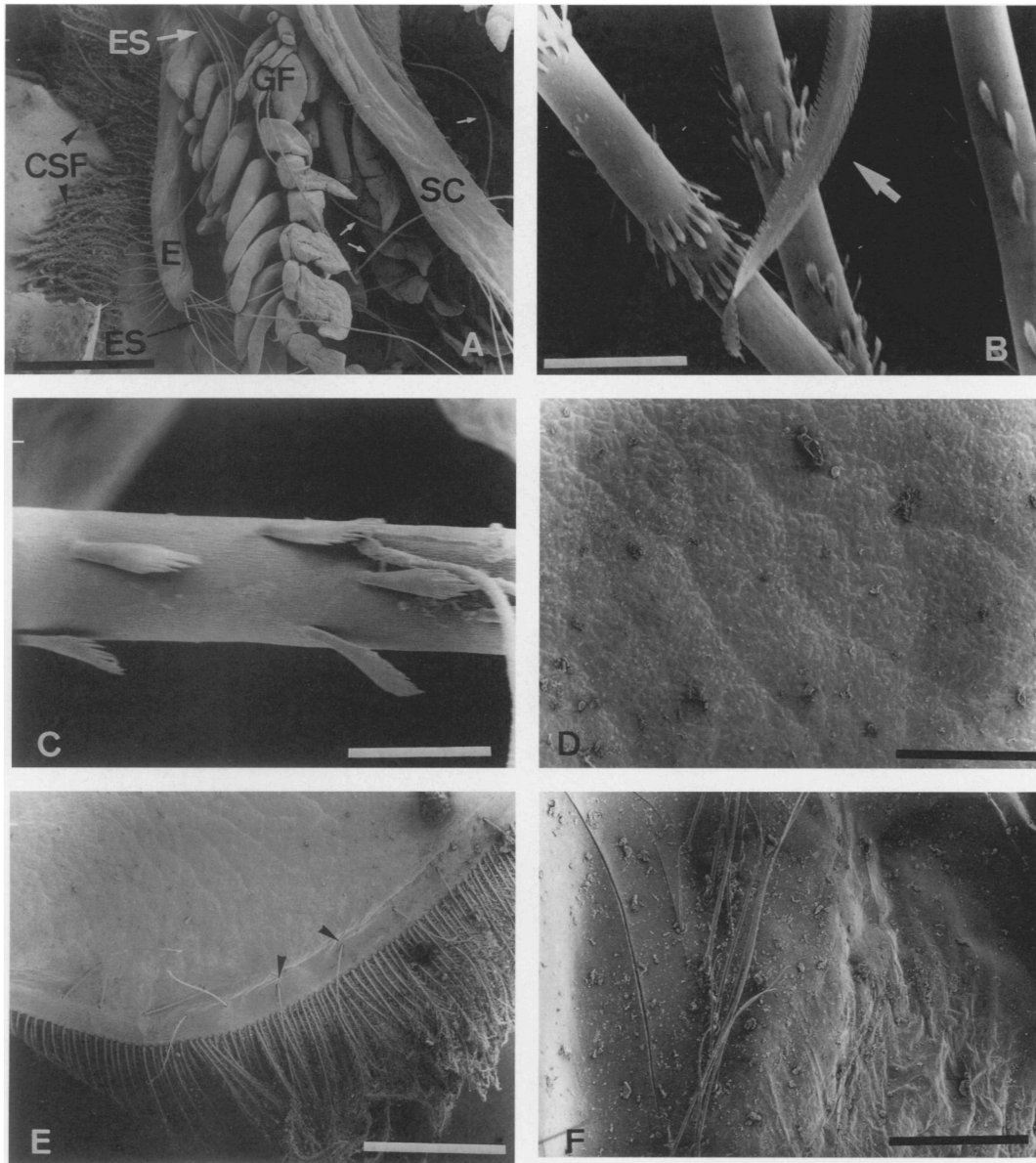


Fig. 6. *Thalassina anomala* Herbst, 1804. A, setiferous epipod (E) on coxa of first pereiopod. Left is ventral part. Note multidenticulate epipodal setae (ES) inserted into gill filaments (GF) of podobranch. White arrows point to setobranch setae inserted through gill filaments; B, digitate scale setules and serrate tip of multidenticulate setae on distal end of epipod; C, magnified view of setal shaft with digitate scale setules; D, inner surface of branchiostegite; E, inner margin of branchiostegite showing subterminal smooth setae (arrowheads pointing to setal base) and terminal plumose carapace fringe setae; F, smooth setae on grooved surface of thoracic epimera. CSF-coxal setal fringe; SC-scapognathite. Scale bars: A = 750 μm ; B = 30 μm ; C = 10 μm ; D = 150 μm ; E = 717 μm ; F = 299 μm .

serrate coxal setae are on the average about one-tenth of the length of the setobranch setae. The spiniform serrules give the seta a comblike appearance which contrasts with the typical setulation of plumose or plumodenticulate setae (Watling, 1989).

Posterior to the arthrobranch articulation on P2–P4, two small lamellar processes extend from the arthrobranchial membrane whose distal margins bear pappose setae (Fig. 2). The margins of the coxae also have dense pappose setae, herein called coxal setal fringe (CSF)

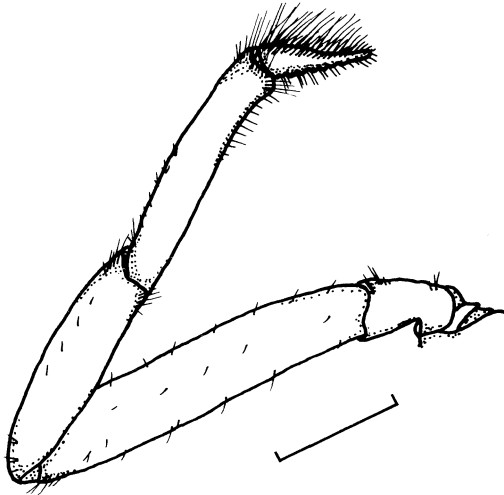


Fig. 7. Left fifth pereopod of *Thalassina anomala* Herbst, 1804. Scale: 5 mm.

(Fig. 6A), which form a setal network around the limb bases. The CSF and the setae on the arthrodial lamellae may have an antifouling function by serving as a filter screen for inhalant water entering the branchial chamber.

Setiferous Epipods.—The setiferous epipods bear a few pappose setae near the base, followed by multidenticulate setae with serrate tips (Figs. 2, 5A, 6A, B) which extend until the posterior edge where they are longest. The posterior edge of each epipod bears 12 long setae. The podobranchs articulate on the inner basal part of the epipods. Proximal to the point of articulation of the podobranch there is a small lobular protrusion from the proximodorsal surface of the epipod. This lobe is also present on the P4 epipod where the podobranch is lost (Fig. 5A). The scale setules of multidenticulate epipodal setae show similarity in digitation and inclination with those of MSS setules, but do not exhibit the V-form arrangement on the distal part of the shaft. The multidenticulate setae on the posterior end of the epipod insert into and intertwine with the filaments of the podobranchs and the basal part of the arthrobranchs lying posterior to the epipod.

Branchiostegal Setae.—The inner branchiostegal surface lacks setae (Fig. 6D), except for a line of singly protruding, widely spaced smooth setae on the inner margins of the branchiostegite. The carapace fringe has dense plumose setae which may serve as a fil-

ter screen for inhalant respiratory water (Figs. 1A, 6E).

Epimeral Setae.—The thoracic epimeron (inner wall of the branchial chamber) has grooved surfaces which are lined with short smooth setae (Fig. 6F). The microgrooves extend ventrally down the limb bases and most likely channel the inflow of respiratory water into the branchial chamber. Direct involvement in gill cleaning by epimeral setae is not impossible, but is virtually limited to scraping of the phylloid filaments upon contact with the epimeral surface.

Aquarium Observations

In aquarium observations spanning 23 h, no active gill-cleaning behavior involving the thoracic limbs was observed. However, grooming of other body parts was regularly exhibited by M3 (on antennae and antennules, autogrooming), P3 (mostly on meral-carpal laterals of M3, P1, and P2), P4 (on meral-carpal laterals of P3 and the lateral side of the carapace, including the hepatic groove setae located anterolaterally), and P5 (ventral side of the abdomen and telson). *Thalassina anomala* exhibited reversed respiratory flow as indicated by intermittent expulsion of a debris-laden, brownish stream behind the carapace. This activity was accompanied by repeated contraction of the branchiostegite while the animal was at rest. Limb rocking was not observed.

Though the P5 of certain upogebiids and callianassids (Bauer, 1989), as well as porcellanid and lithodid anomurans (Pohle, 1989b; Fleischer *et al.*, 1992) was used for gill cleaning, that of *T. anomala* (Fig. 7) was used mainly for walking and for grooming the ventral side of the abdomen and telson. In this process, the abdomen stretches horizontally or curls down ventrally while the pair of P5 simultaneously reach backward and scrub the underside of the abdominal pleura, telson, and pleopods using the pad of dactylar setae. The dactyl of P5 tapers distally and is fringed mostly with multidenticulate setae having brushlike tips. The achelate P5 of *T. anomala* articulates on a movable sternite, allowing for easy anteroposterior mobility. This suggests a morphological advantage for abdominal grooming and, possibly, for limb maneuvering within burrows. The P5 is more

cylindrical than the other pereopods, which exhibit lateral compression.

DISCUSSION

There are three basic gill types in the decapods: dendrobranchiate, phyllobranchiate, and trichobranchiolate. The dendrobranchiate gill has paired lateral branches arising from the central gill axis, with secondary rami protruding from the lateral branch. The trichobranchiolate gill has serial filamentous branches arranged around the central axis, without secondary rami. The phyllobranchiate gill has flat lamellar branches set in two rows and separated by a longitudinal furrow. Thalassinids have both phyllobranchiate and trichobranchiolate gills, and one gill form not fitting either category has been termed thalassinobranchs (Martin and Abele, 1986). In some genera of thalassinids, the trichobranchiolate gill filaments may be extremely flattened (phylloid type) or cylindrical (filamentous type) (Astall *et al.*, 1997). Both phylloid and filamentous filaments cooccur in a single gill axis in *Thalassinia anomala*. Bate (1888) noted this bimorphic gill structure of *T. anomala* and speculated that the phylloid filaments occur in that part of the branchial chamber where respiratory circulation is more "quiescent."

Variations in gill form have caused classificatory confusion in thalassinids (Astall *et al.*, 1997). The gill form of the mud lobster seems intermediate between the purely filamentous gills of *Calocaris macandreae* Bell, 1853, and *Upogebia* spp., and the phylloid gills of *Callianassa subterranea* Montagu, 1808, and *Jaxea nocturna* Nardo, 1847, all thalassinid species previously examined by Astall *et al.* (1997). In the genus *Ambiaxius* Sakai and de Saint Laurent, 1989, which is closely related to *Calocaris* Bell, 1853, the gills lack lateral branches and have been reduced to a single lobe or lamella (Kensley, 1996). Trichobranchiolate gills are viewed to have evolved into phyllobranchiate gills in thalassinids (Martin and Abele, 1986; Suzuki and McLay, 1998). Bate (1888) conjectured that the filamentous "trichobranchial filaments" and compressed "phyllobranchial plates" of the mud lobster had a common origin.

In thalassinids examined by Astall *et al.* (1997), the filamentous and phylloid gill forms were structurally trichobranchiolate, although cuticular differences were recognized. The thinner cuticular membrane of phylloid

filaments reportedly increases the efficiency of gas exchange and, among thalassinids, the larger gill areas of deposit feeders have been interpreted as an adaptation to hypoxic conditions within burrows (Astall *et al.*, 1997). Though burrow life seems to impose serious respiratory limitations, Bauer (1981) proposed that burrowing in itself is an antifouling mechanism through exoskeletal abrasion and substrate smothering, which limit epizoic growth.

Bauer (1981, 1989) classified grooming behaviors into active (direct) and passive (indirect) types based on whether the functional mechanism is intentional or incidental, respectively. Active gill cleaning in decapods has been attributed to pereopodal brushes and the passive mechanisms to setiferous processes arising from thoracic limb bases, e.g., setiferous epipod and epipod-setobranch complexes with few references to posterior scaphognathite setae and branchiostegal setae (Bauer, 1981, 1998). Active and passive mechanisms are believed to be mutually exclusive (Bauer, 1981; Suzuki and McLay, 1998), with the exception of hippolytid carideans where both passive and active mechanisms cooccur in many genera. In the Thalassinida, axiids have setobranchs but do not brush their gills with pereopods, while callianassids and upogebiids perform active brushing but lack setobranchs (Bauer, 1981).

By inference from morphology, the setal systems of *T. anomala* may have filtering or gill-cleaning functions. Bauer (1981, 1989) noted a distinction between the filtering mechanisms, which prevent particles from reaching and fouling the gills, and the passive grooming or cleaning mechanisms, which indirectly scrape the gill surfaces. In *Thalassinia anomala*, a filtering function is ascribed to the pappose setae on the limb bases and the plumose setae on the branchiostegal fringe. Passive gill cleaning is attributed to the multidenticulate and serrate setae on the scaphognathite, coxal surfaces, and epipods. Multidenticulate, serrate, pappose, and plumose setal types are all considered typical grooming and antifouling structures in decapods (Bauer, 1989; Pohle, 1989b; Fleischer *et al.*, 1992).

Astall *et al.* (1997) demonstrated that the branchial ventilation pattern in thalassinids generally follows the posterior-anterior flow route where scaphognathite beating draws respiratory water into the branchial chamber

primarily via the ventrolateral margins of the carapace. Minor inhalant routes also take place between the limb bases where pappose setae densely line the coxal margins. Thus, the inhalant stream is likely filtered by fringe setae before it is circulated through the gill chamber. Bauer (1979) noted the filtering function of setal screens and suggested a mesh size lower limit beyond which respiratory flow may be severely impeded. The mud lobsters showed severe fouling of carapace fringe setae with fine debris.

Reversal of respiratory flow is common in decapods and is aimed at back-flushing detrital materials from the branchial chamber (Martin and Felgenhauer, 1986; Bauer, 1989). Wilkins and McMahon (1972) suggested a mechanism whereby branchiostegal fringe setae may trigger a respiratory reversal in homarid lobsters. Bauer (1979) noted that tightly closed branchial chambers likely exhibit strong respiratory reversals to clean the gills. The plumose setae bordering the scaphognathites of certain thalassinids are thought to increase the efficiency of current generation in the branchial chamber (Nickell *et al.*, 1998). Carapace movements associated with the back-flushing of branchial water are recognized in brachyurans (Maitland, 1992). McMahon and Wilkins (1983) previously noted the respiratory and ionoregulatory implications of respiratory reversal.

In the mud lobster, as in other decapods (Bauer, 1981, 1989), gill cleaning results from the incidental agitation of setal systems during movement of surfaces, such as limb coxae and scaphognathites. Setobranch and epipod setae passively scrape on gill surfaces during limb movement and scaphognathite setae are jostled as the scaphognathite beats vigorously during branchial ventilation (Bauer, 1981, 1989; Suzuki and McLay, 1998). When jostled, multidenticulate scaphognathite setae (MSS) probably scrape on phylloid gills and the inner branchiostegal surface. Hence, MSS may intensively clean these parts due to the constant scaphognathite action during respiration. In *Jaxea nocturna*, Nickell *et al.* (1998) recognized the functional significance of scaphognathite and coxal setae in gill cleaning and that these setae reportedly eliminate the necessity of active pereopodal brushing.

Suzuki and McLay (1998) noted that MSS first appeared in carideans, subsequently was

lost in intervening sister groups, and reappeared in homarids, astacids, and thalassinids (axiids, laomediids, and callianideids). These setae were considered as an ancestral state of the Pleocyemata, and a synapomorphy of the carideans, on the one hand, and the group of homarids, astacids, thalassinids, and brachyurans, on the other. MSS have been lost in anomalans which exclusively clean the gills by the fifth pereopods.

The setobranch setae of mud lobsters resemble those found in carideans, axiids, and astacids by the possession of digitate scale setules (Bauer, 1981, 1989, 1998). Martin and Felgenhauer (1986) noted striking convergences among setal types, citing the identical setae in aeglids and hermit crabs. The grooming setae on the fifth pereopods of porcellanid and lithodid anomurans also showed certain similarities (Pohle, 1989b; Fleischer *et al.*, 1992). Nickell *et al.* (1998) noted the multidenticulate setae on the maxillipedal coxae of *J. nocturna* which were termed "setobranchs" by several authors. Homologous grooming setae in the crayfish were termed "coxopoditic setae" by Huxley (1880) and "setobranchs" by Taylor and Taylor (1992). Originally, the term setobranch referred to setiferous tubercles or papillae on the coxa (Borradaile, 1907), but several authors have used it in referring to the setae arising from the papilla (Bauer, 1979). Though lacking any prominent tubercle on the coxa, we consider the long multidenticulate coxal setae in the mud lobster as setobranch setae by virtue of functional morphology. These setobranch setae closely resemble the MSS and such structural similarity was also observed in *J. nocturna* (Nickell *et al.*, 1998). In the fresh-water crayfish *Procambarus clarkii*, Bauer (1998) experimentally demonstrated that the multidenticulate setobranch setae truly function in gill cleaning. However, setobranch setae may be efficient only in countering particulate fouling but not parasite infestation of gills.

Scale setules give the setae a brushlike character (Bauer, 1989; Watling, 1989; Nickell *et al.*, 1998). We thus relate the opposing inclination and distinctive arrangement of scale setules of multidenticulate setae to scrubbing efficiency. Scaphognathite pumping agitates the setal shaft, conceivably strongest at the distal part, and causes scraping of gill surfaces. This may justify the pre-

ponderance of scale setules more distally on the setal shaft. In *Thalassinia anomala*, the V-form arrangement of digitate scale setules on MSS is very atypical and has not been recorded in other species. Pohle (1989b) described the brush setae on the grooming fifth pereopods of some lithodid crabs which consist of two rows of pointed denticules located ventrally and dense digitiform setules located dorsally on the setal shaft. This peculiar ornamentation of the brush setae, which have scraping and rasping functions, is also attributed to increasing the efficiency of grooming (Pohle, 1989b).

Among thalassinids, *T. anomala* joins the axiids in having passive gill-cleaning mechanisms. The absence of pereopodal gill cleaning in both is probably constrained by the tightly fitting carapace which prevents insertion of thoracic limbs (cf. Nickell *et al.*, 1998; Bauer, 1989). However, related thalassinid-like callianassids and upogebiids have lost setobranchs and setiferous epipods, and have developed active gill-cleaning mechanisms primarily through the use of the fifth pereopods (Bauer, 1981). This indicates that *T. anomala* and axiids are ancestral to callianassids and upogebiids (cf. Bauer, 1981; Nickell *et al.*, 1998). Konishi (1989) has concluded that the upogebiids display an "intermediate condition" between the primitive axiids and advanced laomediids, based on morphological diagnosis of larval specimens. If the phylloid gills are considered a recent differentiation of trichobranchiate gills, as speculated by Bate (1888), then gill form does not seem to correlate with the type of gill-cleaning mechanisms in thalassinids. Suzuki and McLay (1998) similarly concluded the absence of association between gill types and gill-cleaning mechanisms among the major decapod groups. The occurrence of active and passive gill cleaning in thalassinids may indicate the phyletic transition from purely passive (gill cleaning) in astacids and the purely active mechanisms in anomalans.

ACKNOWLEDGEMENTS

We are very grateful to Raymond T. Bauer, Colin L. McLay, and Gerhard Pohle for their critical reading of the manuscript. The mud lobsters from Amami-oshima, Japan, were collected by Motoharu Nakamura. We thank the Faculty of Sciences, Kagoshima University (KU) for the use of their scanning electron microscope. The students at the Marine Biological Laboratory, Faculty of Fisheries, KU, helped in installing the aquarium set-up and other experimental work. We are also indebted to Ak-

ihiko Shinomiya for technical assistance with microphotography and Sumeth Pongchinrit with illustration.

LITERATURE CITED

- Astall, C. A., S. J. Anderson, and A. C. Taylor. 1997. Comparative studies of the branchial chamber, gill area and gill ultrastructure of some thalassinid mud-shrimps (Crustacea: Decapoda: Thalassinidea).—*Journal of Zoology* 241: 665–688.
- Bate, S. C. 1888. Report on the Crustacea Macrura collected by HMS Challenger during the years 1873–1876.—*Challenger Report, Zoology* 24: 1–942.
- Bauer, R. T. 1975. Grooming behaviour and morphology of the caridean shrimp *Pandalus danae* Stimpson (Decapoda: Natantia: Pandalidae).—*Zoological Journal of the Linnean Society* 56: 45–71.
- . 1977. Antifouling adaptation of marine shrimps (Decapoda: Caridea): functional morphology and adaptive significance of antennular preening by the third maxillipeds.—*Marine Biology* 40: 260–276.
- . 1978. Antifouling adaptations of caridean shrimp: cleaning of the antennal flagellum and general body grooming.—*Marine Biology* 49: 69–82.
- . 1979. Antifouling adaptations of caridean shrimp (Decapoda: Caridea): gill-cleaning mechanisms and grooming of brooded embryos.—*Zoological Journal of the Linnean Society* 65: 281–303.
- . 1981. Grooming behavior and morphology in the decapod Crustacea.—*Journal of Crustacean Biology* 1: 153–173.
- . 1989. Decapod crustacean grooming: functional morphology, adaptive value, and phylogenetic significance.—*In*: B. E. Felgenhauer *et al.*, eds., *Functional morphology of feeding and grooming in Crustacea*. Crustacean Issues 6: 49–73. A. A. Balkema, Rotterdam, The Netherlands.
- . 1998. Gill-cleaning mechanisms of the crayfish *Procambarus clarkii* (Astacidea: Cambaridae): experimental testing of setobranch function.—*Invertebrate Biology* 117: 129–143.
- Borradaile, L. A. 1907. On the classification of decapod crustaceans.—*Annals and Magazine of Natural History, Series 7*, 19: 457–486.
- Felgenhauer, B. E. 1992. External anatomy and integumentary structures.—*In*: F. W. Harrison, treatise ed., *Microscopic anatomy of invertebrates*. Vol. 10, F. W. Harrison and A. G. Humes, eds., *Decapod Crustacea*. Pp. 19–43. Wiley-Liss, New York, New York.
- Fleischer, J., M. Grell, J. T. Høeg, and J. Olesen. 1992. Morphology of grooming limbs in species of *Petrolisthes* and *Pachycheles* (Crustacea: Decapoda; Anomura: Porcellanidae): a scanning electron microscopy study.—*Marine Biology* 113: 425–435.
- Hindley, J. P. R., and C. G. Alexander. 1978. Structure of the chelate pereopods of the banana prawn *Penaeus merguensis*.—*Marine Biology* 48: 153–160.
- Huxley, T. H. 1880. *The crayfish*.—C. Kegan Paul and Co., London, England. Pp. 1–371.
- Jacques, F. 1989. The setal system of crustaceans: types of setae, groupings, and functional morphology.—*In*: B. E. Felgenhauer *et al.*, eds., *Functional morphology of feeding and grooming in Crustacea*. Crustacean Issues 6: 1–13. A. A. Balkema, Rotterdam, The Netherlands.
- Kensley, B. 1996. New thalassinidean shrimp from the Pacific Ocean (Crustacea: Decapoda: Axiidae and Calocarididae).—*Bulletin of Marine Science* 59: 469–489.

- Konishi, K. 1989. Larval development of the mud shrimp *Upogebia (Upogebia) major* (de Haan) under laboratory conditions, with comment on larval characters of thalassinid families.—*Bulletin of National Research Institute of Aquaculture* 15: 1–17.
- Labadie, L. V., and A. R. Palmer. 1996. Pronounced heterochely in the ghost shrimp, *Neotrypa californiensis* (Decapoda: Thalassinidea: Callinassidae): allometry, inferred function and development.—*Journal of Zoology* 240: 659–675.
- McMahon, B. R., and J. L. Wilkins. 1983. Ventilation, perfusion and oxygen uptake.—*In*: D. E. Bliss, ed.-in-chief. *The biology of Crustacea*. Vol. 5, L. H. Mantel, ed., *Internal anatomy and physiological regulation*. Pp. 289–372. Academic Press, New York, New York.
- Maitland, D. P. 1992. Carapace movement associated with ventilation and irrigation of the branchial chambers in the semaphore crab, *Heloecius cordiformis* (Decapoda: Brachyura: Ocypodidae).—*Journal of Comparative Physiology* 162: 365–374.
- Martin, J. W., and L. G. Abele. 1986. Phylogenetic relationship of the genus *Aegla* (Decapoda: Anomura: Aeglididae), with comments on anomuran phylogeny.—*Journal of Crustacean Biology* 6: 576–616.
- , and B. E. Felgenhauer. 1986. Grooming behaviour and the morphology of grooming appendages in the endemic South American genus *Aegla* (Decapoda, Anomura, Aeglididae).—*Journal of Zoology* 209: 213–224.
- Nash, R. D. M., C. J. Chapman, R. J. A. Atkinson, and P. J. Morgan. 1984. Observation on the burrows and burrowing behaviour of *Calocaris macandreae* (Crustacea: Decapoda: Thalassinidea).—*Journal of Zoology* 202: 425–439.
- Nickell, L. A., R. J. A. Atkinson, and E. H. Pinn. 1998. Morphology of thalassinid (Crustacea: Decapoda) mouthparts and pereopods in relation to feeding, ecology and grooming.—*Journal of Natural History* 32: 733–761.
- Pillai, G. 1990. Notes on the chelae of the mangrove lobster *Thalassina anomala* (Decapoda, Thalassinidae).—*Crustaceana* 59: 89–95.
- . 1992. *Thalassina anomala* fishery in Fiji.—*Technical Report on Marine Studies Program of the University of South Pacific*, no. 1, 5 pp.
- Pohle, G. 1989a. Structure, function, and development of setae on gill-cleaning appendages and associated mouthparts of pinnotherid crabs (Decapoda: Brachyura).—*Canadian Journal of Zoology* 67: 1690–1701.
- Pohle, G. 1989b. Gill and embryo grooming in lithodid crabs: comparative functional morphology based on *Lithodes maja*.—*In*: B.E. Felgenhauer *et al.*, eds., *Functional morphology of feeding and grooming in Crustacea*. *Crustacean Issues* 6: 75–94. A. A. Balkema, Rotterdam, The Netherlands.
- Scholtz, G., and S. Richter. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea: Malacostraca).—*Zoological Journal of the Linnean Society* 113: 289–328.
- Suzuki, H., and C. L. McLay. 1998. Gill-cleaning mechanisms of *Paratya curvirostris* (Caridea: Atyidae) and comparison with seven species of Japanese atyid shrimps.—*Journal of Crustacean Biology* 18: 253–270.
- Taylor, H. H., and E. W. Taylor. 1992. Gills and lungs: the exchange of gases and ions.—*In*: F. W. Harrison, treatise ed., *Microscopic anatomy of invertebrates*. Vol. 10. F. W. Harrison and A. G. Humes, eds. *Decapod Crustacea*. Pp. 203–293. Wiley-Liss, New York, New York.
- Watling, L. 1989. A classification system for crustacean setae based on the homology concept.—*In*: B. E. Felgenhauer *et al.*, eds., *Functional morphology of feeding and grooming in Crustacea*. *Crustacean Issues* 6: 15–26. A. A. Balkema, Rotterdam, The Netherlands.
- Whitehead, N. E., J. de Vaugelas, P. Parsi, and M. C. Navarro. 1988. Preliminary study of uranium and thorium redistribution in *Calichirus laurae* burrows, Gulf of Aqaba (Red Sea).—*Oceanologica Acta* 11: 259–266.
- Wilkins, J. L., and B. R. McMahon. 1972. Aspects of branchial irrigation in the lobster *Homarus americanus*. I. Functional analysis of scaphognathite beat, water pressures and currents.—*Journal of Experimental Biology* 56: 469–480.
- Yunker, M. P., and E. D. Scura. 1985. An improved strategy for building brackish water culture ponds with iron pyrite soil in mangrove swamps.—*In*: Y. Taki *et al.*, eds., *Proceedings of the International Conference on the Culture of Penaeid Prawns/Shrimps*. Southeast Asian Fisheries Development Center—Aquaculture Department, Iloilo City, Philippines.
- Ziebis, W., S. Forster, N. Huettel, and B. Jorgensen. 1996. Complex burrows of the mud shrimp *Callinassa truncata* and their geochemical impact in the sea bed.—*Nature* 382: 619–622.

RECEIVED: 17 September 1998.

ACCEPTED: 11 December 1998.

Addresses: (ZBB) Institute of Marine Fisheries and Oceanology, College of Fisheries, University of the Philippines in the Visayas, Miagao, Iloilo 5023, Philippines; (HS) Marine Biological Laboratory, Faculty of Fisheries, Kagoshima University, 4-50-20 Shimoarata, Kagoshima 890-0056, Japan.