

Fig. 6. *Thalassina anomala* Herbst, 1804. A, setiferous epipod (E) on coxa of first pereopod. 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-scaphognathite. Scale bars: A = 750  $\mu\text{m}$ ; B = 30  $\mu\text{m}$ ; C = 10  $\mu\text{m}$ ; D = 150  $\mu\text{m}$ ; E = 717  $\mu\text{m}$ ; F = 299  $\mu\text{m}$ .

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)

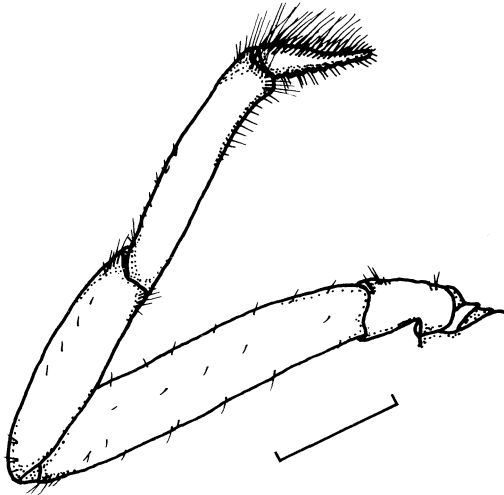


Fig. 7. Left fifth pereopod of *Thalassina anomala* Herbst, 1804. Scale: 5 mm.

(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 (phyllid type) or cylindrical (filamentous type) (Astell *et al.*, 1997). Both phyllid 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 phyllid 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 (Astell *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 phyllid 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 phyllid gill forms were structurally trichobranchiolate, although cuticular differences were recognized. The thinner cuticular membrane of phyllid

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 (Astell *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 multidenticate and serrate setae on the scaphognathite, coxal surfaces, and epipods. Multidenticate, serrate, pappose, and plumose setal types are all considered typical grooming and antifouling structures in decapods (Bauer, 1989; Pohle, 1989b; Fleischer *et al.*, 1992).

Astell *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.

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