MORPHOLOGICAL ADAPTATIONS TO BURROWING IN *CHIRIDOTEA COECA* (CRUSTACEA, ISOPODA)

HUGH GRIFFITH AND MALCOLM TELFORD

Department of Zoology, University of Toronto, Ontario, Canada M5S 1A1

ABSTRACT

The burrowing isopod *Chiridotea coeca* lives in medium to coarse sand. It preferentially burrows into sands of particle size ranges which most closely resemble its native substrate (particles sizes 250–1000 μm), and burrowing is fastest in these substrates. Pereiopods and pleopods are fouled in substrates with particles smaller than 100 μm.

Locomotory rhythms above and below the substrate are similar. Phase differences between adjacent legs are 30% with metachronal waves moving forward. Power stroke for all pereiopods is by extension at the coxo-basal and basi-ischial articulations. Directions of leg thrust vary from almost perpendicular to the longitudinal body axis for gnathopods, to directly posterior for the last ambulatory leg.

The body is dorso-ventrally flattened. Power and recovery stroke occur in very nearly the same plane and limb planes approach vertical posteriorly. Pereiopods lack the ventrally directed carpo-propodal flexure found in most free living isopods. Setae provide a conspicuous morphological adaptation to burrowing. Stout, posteriorly directed serrulate setae on the pereiopods increase the area of contact with sand grains, and provide an expanded tip around the dactyl. On the second and third gnathopods and all locomotory legs, a fringe of posteriorly directed plumose setae provides a shelter into which the leg behind can swing during recovery stroke. These setae increase in length and number with body size but the intersetal distance remains sufficiently close to exclude virtually all of the native sand grains from the spaces between the legs. Other morphological adaptations are discussed and the species is compared with other burrowing Peracarida.

INTRODUCTION

Isopods are a common faunal constituent of marine sand beaches. Dahl (1952) proposed a scheme of beach faunal zonation in which members of the family Cirolanidae comprise a distinct and regular horizontal zone in many regions of the world. This phenomenon does not seem to apply to the east coast of North America, where there is little or no evidence of a "cirolanid belt." One intertidal species which frequently occurs, however, is *Chiridotea coeca* (Valvifera: Idoteidae). This species ranges from Nova Scotia to Florida (Richardson, 1905), and is typically intertidal (Tait, 1927; Wigley, 1960), but may extend into the subtidal zone (Shealy *et al.*, 1975).

The distributions of many infaunal Peracaridia are limited by substrate particle size (Crawford, 1937; Meadows, 1964; Jones, 1970; Morgan, 1970; Rees, 1975; Oakden, 1984, and others). This also appears to be the case with *C. coeca,* which occurs in coarse sand (Tait, 1927). Few attempts have been made to relate morphology of burrowing peracaridans to substrate particle size preference. The functional morphologies of interstitial forms have been described (Pearse *et al.*,

1942; Swedmark, 1964), but larger crustaceans have been, for the most part, neglected. These forms often bear extensive setal armature, but very rarely has setation in beach-dwellers been described functionally. An understanding of setal functions greatly increases the understanding of the habits and general lifestyle of a species. The work of Manton (1952; 1977) and Hessler (1981; 1982) dealt with surface walking forms bearing few, inconspicuous setae. Species descriptions commonly do not include any details on setation. Menzies (1957) and Fish (1972) described in detail the setation of *Limnoria* sp. and *Eurydice pulchra* respectively, but did not provide a functional explanation for them. Few isopodan species are as setose as *C. coeca,* so workers on other forms have not felt obliged to examine setal function. in *Chiridotea,* a study of burrowing would not be complete without consideration of the role of setal armature.

Locomotory mechanisms for surface-walking arthropods have been thoroughly studied (Manton, 1952; Lochhead, 1961; Hessler, 1982), as have burrowing mechanisms for true burrowers such as *Leptocheirus* (Goodhard, 1939). The locomotory mechanisms of forms such as *Chiridotea,* which plow forward beneath the substrate, are known only vaguely (Lochhead, 1961).

Chiridotea and other members of the subfamily Glyptonotinae show marked morphological divergence from the more primitive Idoteidae. In this study, the morphology of *C. coeca* will be discussed in terms of functional adaptation to the burrowing habit.

Materials and Methods

Specimens of *C. coeca* were collected from among sand ripples in shallow puddles in the intertidal zone of New River Beach, Bay of Fundy, New Brunswick in August, 1982 and 1984. They were kept in lots of 100 animals in shallow plastic trays (inside dimensions 24 by 36 cm) with 2 cm of native beach sand and 4 cm of sea water, at 10°C, and were fed scraps of earthworms and fish. The water was changed every two days.

Five large sand samples were gathered at New River Beach from the top 1 cm in areas where *Chiridotea* trails were found. The sand was oven dried at 80°C and passed through a series of mechanically shaken, graded sieves and weighed. Mineral particle size fractions were expressed as percent of total weight. A further sample of several kilograms was similarly fractioned for substrate preference tests.

To determine the organic content of the native substrate of *C. coeca,* five 0.5 l samples of surface sand from areas of the beach where isopods were found were oven dried and weighed before and after ashing in a muffle furnace at 550°C for 1 hour. *C. coeca* does not occur on muddy substrates. Five substrate samples from a mudflat close to New River Beach were dried and ashed for comparison with the habitat of *C. coeca.*

A substrate choice experiment was set up in order to determine if *C. coeca* preferentially burrows into substrates of certain particle size ranges. A plastic tray with inside dimensions 24 by 36 cm was subdivided into 5 equal areas using 2 cm deep plastic dividers. Each area was filled to the level of the dividers with a fraction of New River Beach sand of one of the following particle size ranges: <250 μm, 251–500 μm, 501–1000 μm, 1001–2000 μm, 2001–4000 μm. The tray was then filled with sea water, care being taken to prevent mixing of the substrates. Fifty isopods were placed in the tray, 10 in each area. After six hours, the five substrate areas were removed, one at a time, and the number of individuals per substrate was recorded. Five trials were performed, with random rotation of substrate positions between trials.

The ability of *Chiridotea* to burrow in different substrates was tested. Surface sand gathered randomly at New River Beach was passed through the same set of sieves. Six particle size ranges were obtained (from 126–500 μm up to 4001–8000 μm). Five cm of each sand substrate were placed in a 10 cm diameter finger bowl. An additional bowl was filled 5 cm deep with mud. The finger bowls were topped with sea water. Groups of five isopods, 9 to 10 mm in length, were allowed to burrow in each substrate. Mean time taken for each individual to disappear completely beneath the substrate was recorded from 5 to 10 separate trials. In the two coarsest substrates, *Chiridotea* could not burrow, so behavior was noted.

To examine the effects of lowered water content of substrate, as at low tide, surface water was removed from each substrate. Isopods were reintroduced to the finger bowls and burrowing time was recorded as before. Buried animals were gently prodded with a glass rod to determine ability to move.

Specimens were fixed in 10% formalin or in 2% glutaraldehyde for 24 hours for light microscopy and SEM respectively. Storage was in 3% formalin. Gross morphology and pereiopod orientation were examined using a stereoscopic dissecting microscope. For SEM, dissected appendages were cleaned and rinsed in distilled water, freeze-dried, and sputter-coated with gold. In each leg segment, setae were counted and classified according to the scheme of Pohle and Telford (1981). Because this study is concerned with functional morphology related to burrowing, only the larger types of macrosetae (*sensu* Fish, 1972) will be dealt with in detail. Ten individuals ranging from 4.0 to 14.2 mm were used. Detailed setal descriptions are based on an individual 8.9 mm in length but many more individuals were used to confirm the observations and to determine the extent of variation. Intersetal spacing of plumose setae on the posterior margins of the pereiopods was determined from SEM micrographs and by direct measurement under a compound microscope with an eyepiece micrometer.

Preliminary observations of burrowing indicates that burrowing motions seem to be a continuation of the walking mechanism during and after submergence in the sand. Films of walking individuals were used to determine leg movements and locomotory rhythms. Walking animals were filmed from above and below, in a five gallon aquarium containing about 5 cm of sea water. A JVC video camera fitted with a macro lens was used. Animals were allowed to roam freely, and were cooled by frequent changes of water. Walking was analyzed frame by frame by tracing images from the video monitor directly onto acetate sheets. The sequences, gait patterns, and phase differences were determined for all pereiopods. This was done by recording the displacement of each leg over time, by measuring the change in angle at the midline between the tip of the dactyl and a transverse line through the body at the level of the coxae.

Burrowing was also filmed, from above and below the substrate surface, using a 16 mm motion picture camera at 36 frames per second. To permit viewing of burrowing from underneath, less than 1 cm of sand was placed in a glass-bottomed aquarium, covered with approximately 3 cm of sea water. In sand this deep, animals could bury themselves entirely, but became visible from below. Contact with the glass surface of the aquarium did not significantly affect locomotory behavior so far as we could see. These films were viewed frame by frame and in slow motion. Leg movements were charted frame by frame on to paper from the projected image.

RESULTS

Substrate and behavior

The percentages of the different size classes of substrate particles in New River Beach sand are summarized in Table I. More than 90% of the substrate (by weight)

TABLE I

Percentages of size classes of particles in New River Beach sand

Particle size class (µm)	Percentage in substrate (by weight)	Standard deviation
<250	2.4	0.57
251–500	61.3	9.18
501–1000	29.4	9.98
1001–2000	5.1	2.05
2001–4000	1.4	0.53
>4000	0.4	0.32

was made up of particles between 251 and 1000 µm in diameter, with the greatest portion (61.3%) between 251 and 500 µm.

New River Beach sand has a low percentage of organic content. In five samples, the mean organic content was 1.2% ± 0.3 S.D. The extreme values were 0.8% and 1.6%. Mud samples from an adjacent beach contained 6.7% ± 1.4 S.D. organic content.

In five substrate selection tests, most animals (mean 44.7%) chose the particle size range 251–500 µm, which was found by sieving to be the dominant fraction of sand (Table I). The next most frequently chosen particle size range was 501–1000 µm (18.2%). These fractions together comprise about 90% of the natural sand by weight. A chi-square test (Sokal and Rolf, 1981) showed that this distribution differed significantly from random ($P < 0.005$) which would be expected if no selection occurred.

Analysis of variance (Sokal and Rohlf, 1981) showed that burrowing times (Fig. 1) differ significantly ($P < 0.0001$) among different substrates. An *a posteriori* test,
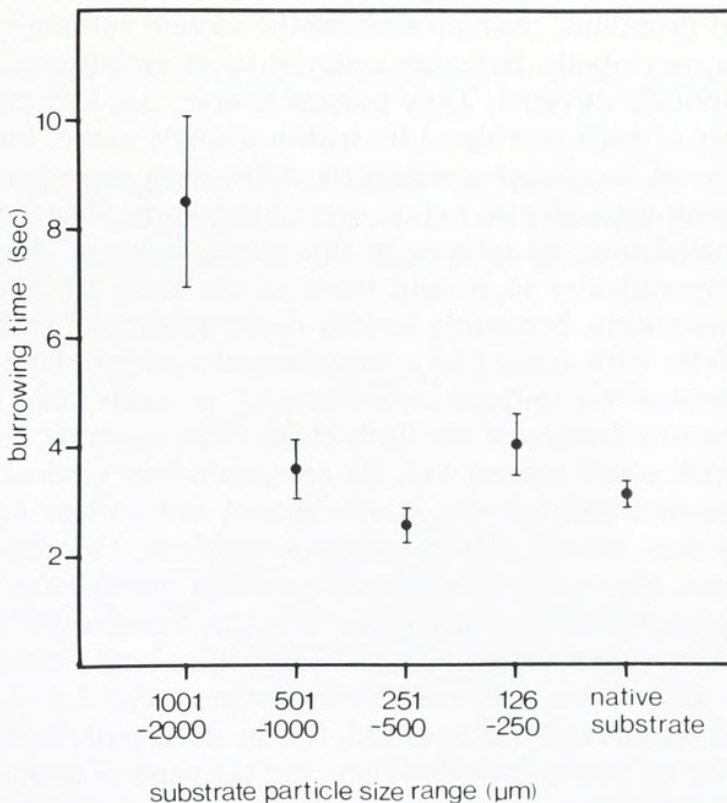

FIGURE 1. Time required for complete burial in various substrates. Vertical bars represent 95% confidence intervals.

the Newman-Keuls procedure (Snedecor and Cochran, 1967), at the 0.05 level separated the mean values into three homogeneous subsets. The first contained the value for the 1001–2000 μm size range. In this substrate burrowing was slowest. The second group contained burrowing times from substrate particle size ranges 126–250 μm, 501–1000 μm, and the native substrate. The third group contained the lowest burrowing time which was found in the substrate of particle sizes 251–500 μm, the dominant fraction of New River Beach sand (Table I). No burrowing time was recorded for the two coarsest substrates because the isopods could only rarely manage to bury themselves. In most instances they merely wedged themselves between pebbles. Burrowing in mud was as fast as, or faster than in the sand particle size range with the lowest burrowing time (251–500 μm).

Reduced water content, achieved by pouring off all free water, hampered locomotory abilities to some degree in all substrates. Burrowing time increased, and once buried, little horizontal movement was found in any substrate. In coarser substrates, most individuals worked their way down deeper into the sediment to a level of greater interstitial water content. After six hours, the experimental animals were recovered from the substrate samples. Those in sand were readily responsive to stimuli and capable of burrowing. Those in mud were unresponsive, and required 1–2 hours in fresh sea water before recovering. The pereiopods and pleopods of individuals which had been in mud for even a short period of time were befouled, but this did not occur in the coarser substrates.

General morphology

In *Chiridotea,* the middle pereonites (3rd and 4th) are the widest (Fig. 2). The body is flattened and the head is depressed and shield-like (Fig. 3). The abdomen is elongate and tapers unevenly to a point. The first three pairs of pereiopods (Fig. 4A, C), hereafter referred to as gnathopods, are stout and subchelate with a compact merus, carpus, and propodus, characteristic of the idoteid subfamily Glyptonotinae. The posterior four pereiopods, hereafter referred to as ambulatory legs, are robust, elongate, and posteriorly directed. They possess simple, peg-like dactyls. The major axes of all segments of each pereiopod lie within a single plane, known as the limb plane. Limb planes of successive pereiopods differ with respect to a hypothetical vertical plane passing through the major axis of the body. The limb planes of the gnathopods are angled forward relative to this plane, those of the first ambulatory legs are almost perpendicular to it, and those of the third to seventh ambulatory legs are directed posteriorly, becoming serially closer to parallel with it. Limb planes also differ successively with respect to a hypothetical vertical plane passing through the points of insertion (coxo-basal articulations) of each pair of legs. For all pereiopods, the anterior surface of the limb plane faces upwards, towards the body. The angle each limb plane makes with its corresponding vertical plane decreases gradually from the first gnathopods, whose planes are almost horizontal, to the fourth ambulatory legs, whose planes approach vertical. The regions of the limb planes which contain locomotory motions are stacked one on top of another, each lying beneath its adjacent anterior neighbor (Fig. 5). Because the bases of the last pair of legs have the greatest degree of vertical direction, and bases of all legs are of similar length, the animal has a forward-leaning stance (Fig. 3.)

The abdominal appendages are arranged, for the most part, in the typical idoteid fashion, as described by Naylor (1955). There are six pairs of abdominal limbs, five pairs of pleopods and one pair of uropods. Each pleopod is a biramous lamellar structure which projects posteriorly beneath the abdomen. The uropods are large,
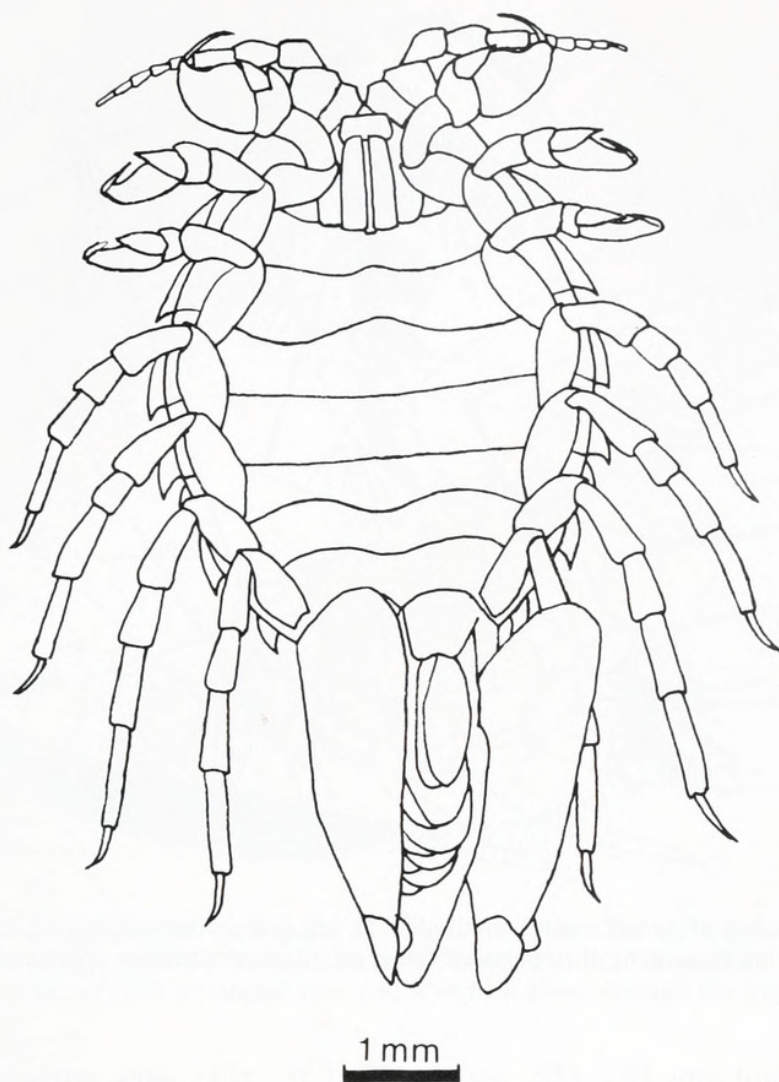
FIGURE 2. Ventral view of *C. coeca* showing arrangement of thoracic and abdominal appendages. Setae omitted.

flattened, and laterally hinged to the abdomen so that they are able to fold under the abdomen and cover the pleopods. They bear small endopods which are attached to the postero-lateral margin and lie ventral to the apex of the telson when the uropods are closed (Fig. 2).
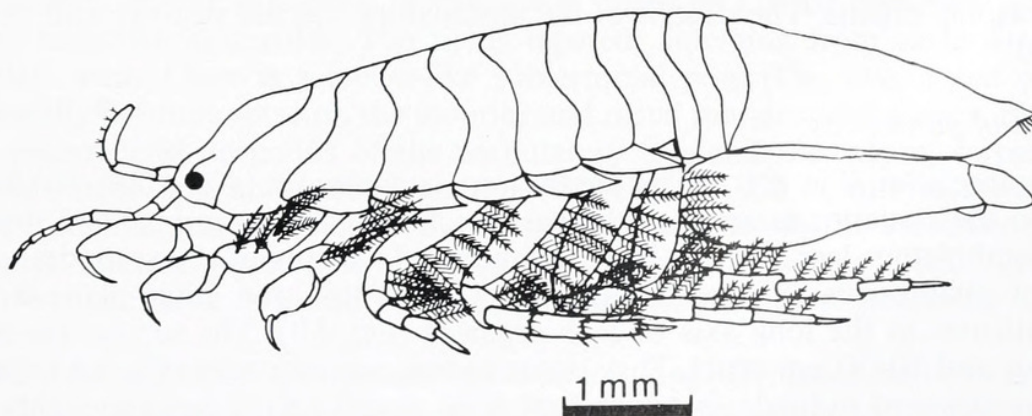

FIGURE 3. Lateral view of *C. coeca* showing pereiopod orientation and distribution of plumose setae.
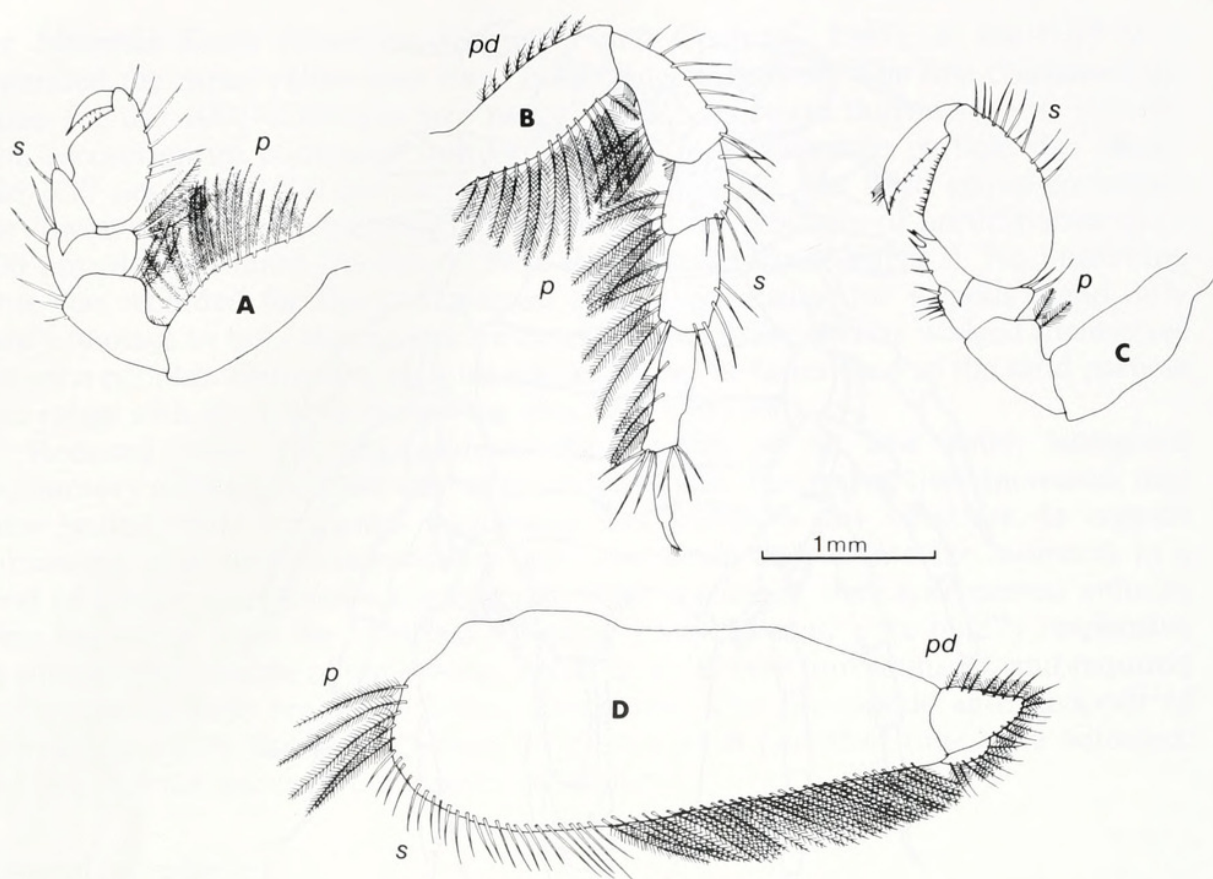
FIGURE 4.   Setation of A, left second gnathopod; B, left first ambulatory leg; C, left first gnathopod; D, left uropod, showing placement of p, plumose setae; pd, plumodenticulate setae; and s, serrulate setae.

Leg articulation

There are two major flexures of the pereiopods in resting *Chiridotea* (Fig. 4). The first is between the coxa and basis: the basis projects ventro-medially in the gnathopods and ventro-laterally in the ambulatory legs. The second articulation is between the basis and ischium: from this articulation, the leg extends as a relatively straight limb, antero-laterally in the gnathopods, almost laterally in the first ambulatories, and posterolaterally in the remaining pairs (Fig. 2). There is no ventral flexure between carpus and propodus (Fig. 4A–C). A third major flexure is found in the gnathopods; the dactyls are articulated against the propodi to form food grasping organs. The dactyls of the ambulatory legs are peg-like and ventrally directed.

Setation of pereiopods

Plumose setae (Fig. 6A). These are the very conspicuous (400–1000 μm) feathery setae on the posterior margins of the basis, ischium, merus, carpus, and propodus of the ambulatory legs and the basis, ischium, and merus of the second and third pairs of gnathopods (Figs. 4A, 4B). They lie within the limb plane and are perpendicular to the long axis of each segment (Fig. 6B). The setules are 50–150 μm long, and 10–30 μm apart. They occur in two opposite rows (Fig. 6A). Plumose setae are arranged in single, evenly spaced rows, except on the basal segments where they occur in two adjacent rows. The first gnathopods may bear a few plumose setae (Fig. 4C), but often have none.
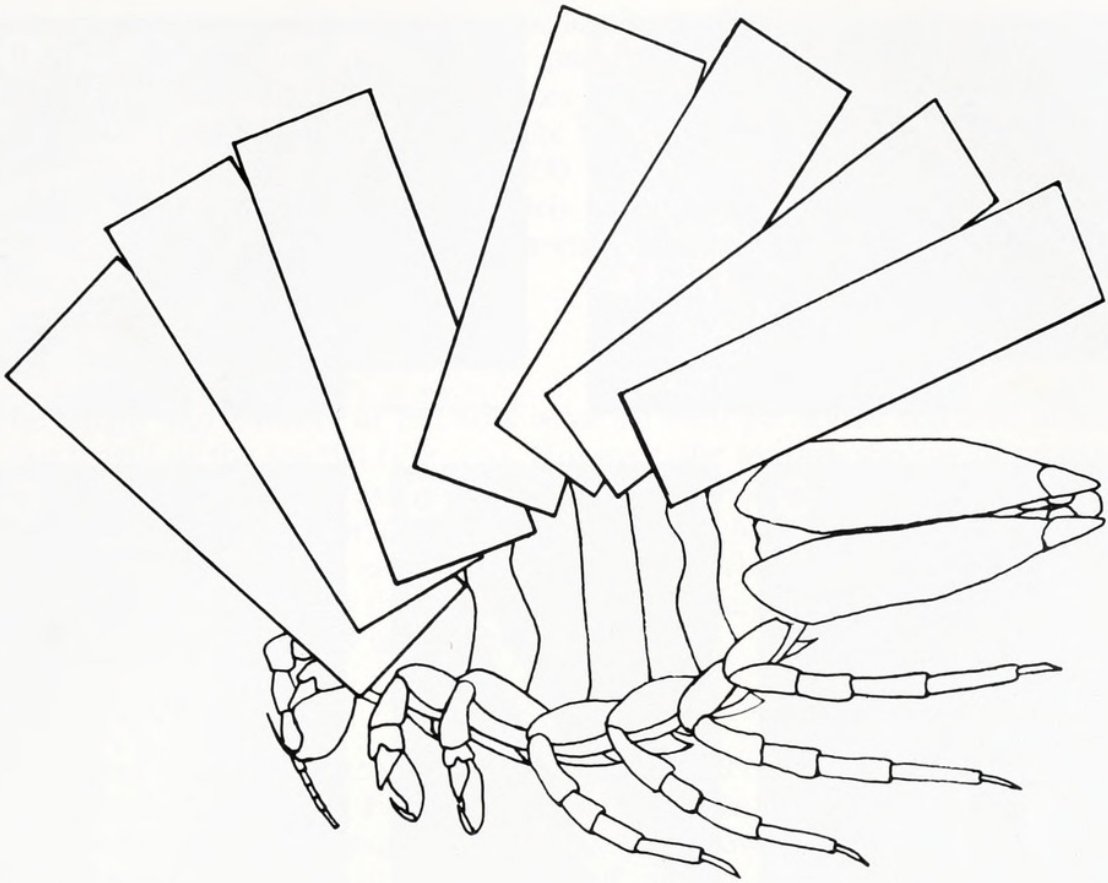
FIGURE 5. Limb planes of pereiopods of *C. coeca*. Quadrilaterals represent planes of equal dimensions oriented within the limb plane of each pereiopod, identical in position relative to a vertical plane through the coxae of each pereiopod pair, and a vertical plane through the major axis of the body.

Plumodenticulate setae (Fig. 6C). These are 200–250 μm long, with a basal diameter of 10 μm. The setules are 80–120 μm long, with pointed, tooth-like setulettes. Two opposite rows of pointed denticules, 1–4 μm long, occur post-annularly. These become narrower and more closely applied to the shaft near the pointed tip. There is no terminal pore (Fig. 6D). Plumodenticulate setae occur in a single row of 5–10 on the anterior margin of the basis of each ambulatory leg (Fig. 4B).

Serrulate setae (Fig. 6E). These setae, 200–400 μm long, have a basal diameter of 10–15 μm. The shaft is smooth until approximately one-tenth the length from the tip, where, on one side only, the surface is raised in a dense concentration of 3 μm-long fingerlike denticules. The tip is tapered, emerging from underneath the denticulate area. There is a crease-like subterminal pore (Fig. 6E). These are the stout, distally pointing setae on the anterior and distal margins of the basis, ischium, merus, carpus, and propodus of the ambulatory legs and the merus, carpus, and propodus of the first and second gnathopods (Fig. 4A–C). A tuft of these setae emerges from the posterior side of the tip of the propodus on the ambulatory legs. The dactyl emerges adjacent to the setal tuft, forming a "splayed foot." A single row of serrulate setae is found on the posterior margin of the propodus of each gnathopod.

Serrate setae (Fig. 6F). These are 400–500 μm long. The basal diameter is about 15 μm. There are two rows of large, V-shaped denticules which end approximately 10 μm from the roughened, expanded tip. There is a cup-like terminal depression, but no pore. One or two setae of this type may occur on the distal margin of the
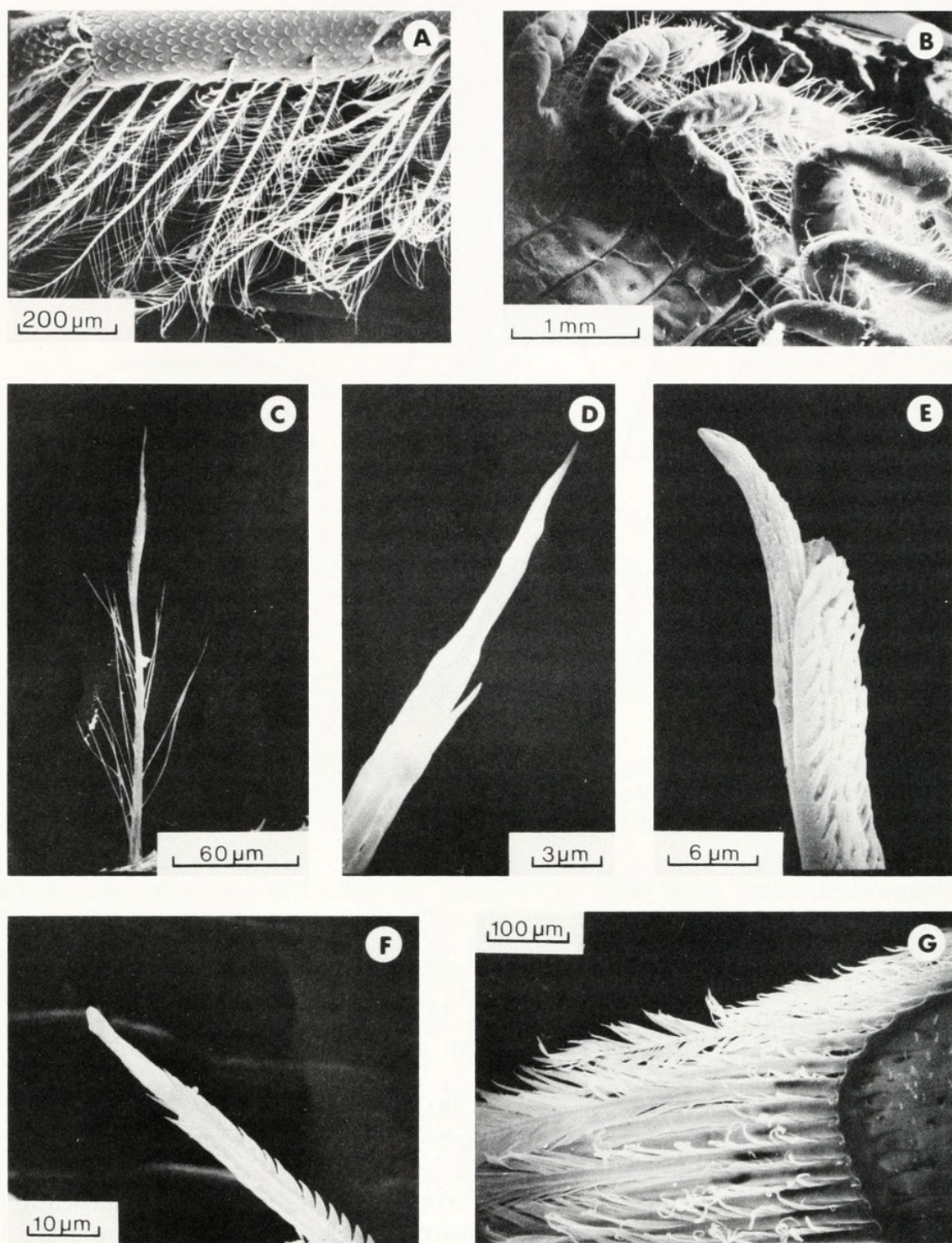
FIGURE 6.   SEM of *C. coeca* setae. A, pallisade of plumose setae from basis of first ambulatory leg; B, ventral view of several consecutive pereiopods, showing continuous overlap of setae between legs; C, plumodenticulate seta; D, tip of plumodenticulate seta; E, tip of serrulate seta; F, tip of serrate seta; G, plumose setae on first pleopod.

merus on the ventral faces of the ambulatory legs, and the second and third gnathopods (not shown in Fig. 4).

Setation of abdominal appendages

There is a single dense row of plumose setae on the margins of both rami of the first two pleopods. The third pleopod bears plumose setae only on the margin of

the outer ramus. Pleopodal plumose setae are longer (800–1200 μm), thicker (basal diameter 20–30 μm), and more densely packed than pereiopod setae. The setules are 40–50 μm long, and intersetal spaces are approximately 5–8 μm (Fig. 6G). Plumose setae (500–950 μm) occur on the anterior margin of the exopodite of the uropods. Shorter plumose setae (300–500 μm), line most of the lateral margin, except for the antero-lateral region, which bears a row of widely spaced serrulate setae (Fig. 4D). The endopods bear plumodenticulate setae of the sort found on the bases of ambulatory legs (Fig. 4D).

Setation and growth

The length and number of plumose setae on each pereiopod segment increases with the length of the animal (Fig. 7A). However, the average spacing of setae on a given segment does not increase with size (Fig. 7B). For animals of all size classes, plumose setae on each thoracic leg are sufficiently long to overlap the anterior margins of the two or three most proximal segments (basis, ischium, merus) of the adjacent posterior legs. Thus there is a continuous layer of plumose setae which lies dorsal to the pereiopods and lateral to the body.

Locomotory rhythms

Chiridotea coeca has three main locomotory patterns. It swims, usually venter up, at or below the surface of the water using only the pleopods. It does this in the pools of water left on the beach at low tide. It burrows into and tunnels through submerged sandy substrate using thoracic and pleonal appendages. It walks on the surface of the substrate and may assist the walking motions of the thoracic appendages with swimming motions of the pleopods. The term "walking" will be used here to connote action of the pereiopods only.

Videotapes of walking individuals show that the first pair of gnathopods are not locomotory. They are held immobile beneath the head, while the second and third pairs are employed in the same fashion as the ambulatory legs. For all pereiopods, the power stroke involves almost simultaneous extension of the coxo-basal and baso-ischial articulations. In the recovery stroke, the reverse process takes place, with baso-ischial flexion occurring slightly before coxo-basal flexion. There is a slight rotation of limb plane at the coxo-basal articulation in the gnathopods but it appears that in the ambulatory legs, all locomotory movements are in the same plane. The point of contact with the substrate for all pereiopods is the dactyl, which is extended in the gnathopods during locomotion. Legs thrust outward, within the limb plane. They do not push in a direction parallel to the body axis. Thus, a force combining both forward and lateral components is delivered to the body by each leg.

In walking and burrowing, metachronal waves pass from posterior to anterior, with each leg about 0.3 cycles ahead of the next anterior to it. Therefore when leg "n + 1" is undergoing a recovery stroke, it swings forward beneath the palisade of plumose setae on leg "n," which is in a more posteriorly directed posture, in an earlier stage of recovery stroke.

Opposite appendages of each pair are 0.5 cycle out of phase. The leg on one side serves as a pivot for the opposite leg to work against so that there is a slight wobble in the gait. Unaided by thrust from the pleopods, *Chiridotea* walks on sandy substrates at speeds usually between 0.3 and 1.0 cm per second. In this sort of locomotion, the ratio of the durations of the forestroke and backstroke is approximately 1:1, Manton's "middle gear" (Manton, 1952). An individual traveling in a
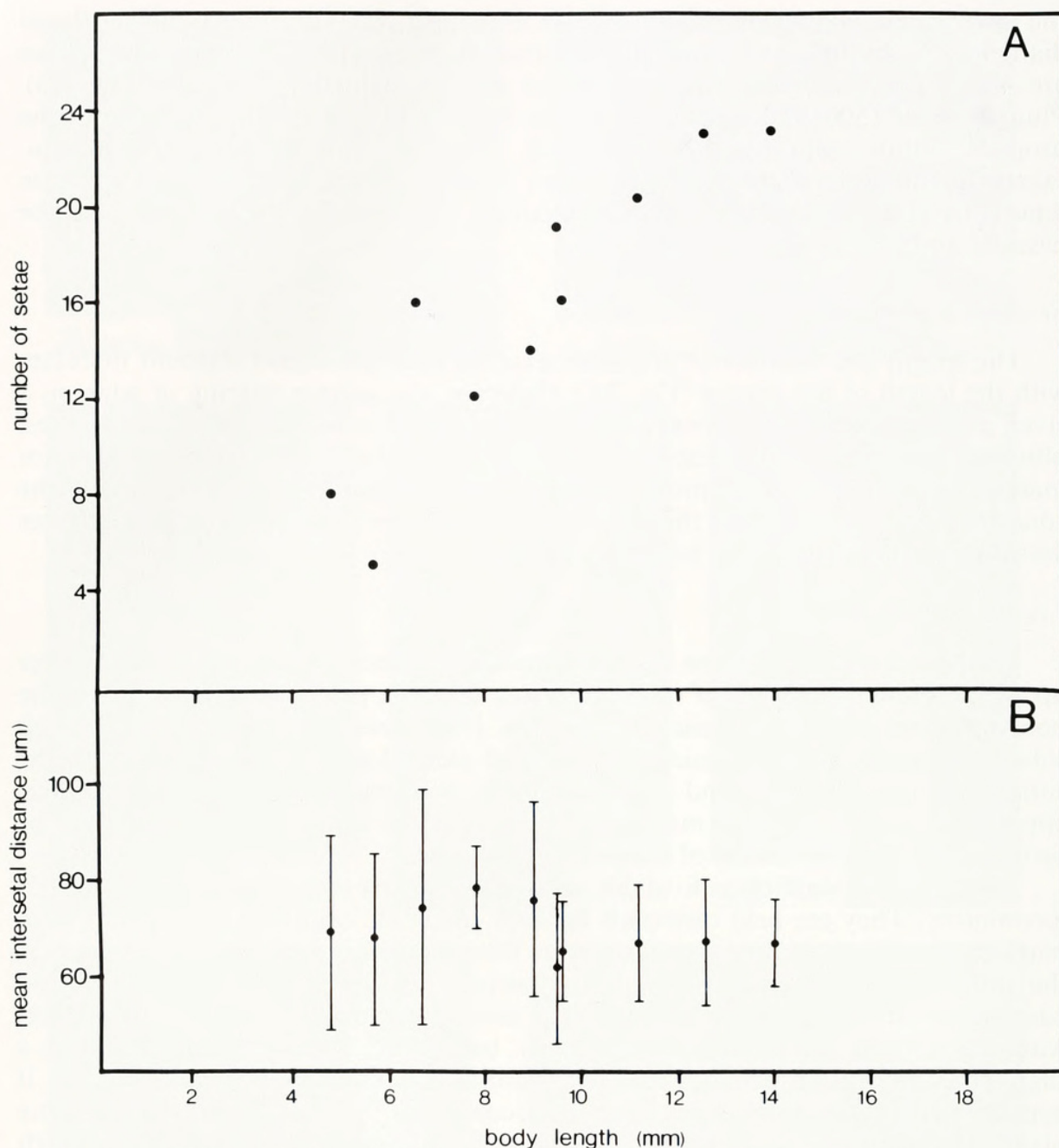
FIGURE 7. A, number of setae on a single leg segment (basis of first ambulatory leg) plotted against body length (anterior margin of head to tip of telson). B, average intersetal distance for a single leg segment (basis of first ambulatory leg) plotted against body length. Vertical bars represent one standard deviation.

straight line changes speed by alterating the period of the leg cycle. A medium-sized individual traveling at a speed of 0.5 cm per second undergoes between 2 and 3 leg cycles per second. The length of stride and angle of swing of the legs do not change with speed in animals walking in straight lines, but do change during turning. Turning may be enhanced by usage of legs on one side of the body only for one or more metachronal cycles.

Burrowing may be initiated from either reptant locomotion or resting posture. As burrowing commences, the abdomen is tilted upwards and the head is lowered against the substrate. The pleopods beat rapidly, which forces a current of water downwards and backwards and further adds to the forward tilt of the body by

forcing the pleon upwards and forward. The gnathopods thrust into the sand, and force particles to the side. The current created by the pleopods draws sand out from under the body, and adds forward thrust during the early stages of burrowing, forcing the body down into the substrate. The animal works its way down into the substrate, moving the pereiopods in the usual metachronal rhythm. Little interruption occurs between walking and burrowing, especially if the animal burrows into the side of a sand ripple or other substrate irregularity. After the head and forward half of the thorax are submerged, the uropods close under the abdomen and the animal continues to tunnel forward horizontally using the pereiopods alone. The pleopods continue to beat, but only enough to maintain a respiratory current. After total submergence, the animal commences to tunnel forward, usually less than 1 cm below the sand surface. In *Chiridotea,* the locomotory mechanism used in tunneling is only slightly altered from that of walking: forward speed during tunneling is slower than that of walking and the forestroke:backstroke ratio decreases to approximately 1:2, Manton's "low gear."

The sand-water mixture through which *Chiridotea* tunnels is a very unstable medium. Each foothold slips backward as force is applied. As a result, there is horizontal displacement of sand particles. Sand is also displaced vertically, being forced up and over the convex surface of the body as the animal moves forward. These movements have been mapped by tracing the paths of individual sand grains in video and film sequences, from above and beneath the animals. *Chiridotea* is considered a tunneler rather than a true burrower because an open burrow is not left behind as it moves forward. The surrounding sand settles, loosely packed, at the posterior of the animal as it passes, and that which is carried over the dorsal surface of the body settles on top of this sand, forming a raised trail in the substrate.

DISCUSSION

The surface sand at New River Beach is moderately coarse (36% of particles by weight greater than 500 μm in diameter) and contains a certain amount of pebbles and shell fragments (represented as particles greater than 4000 μm in diameter). This substrate is similar to, or perhaps somewhat finer than that described by Tait (1927) who said that this species occurs in sand with occasional fragments of shell and stone, the diameters of particles being between 500 and 1500 μm. Ashing showed that New River Beach sand has an organic content of less than 1.2%. This is much lower than that of the nearby mudflat (6.7%). The physical effects of substrate on psammobionts at New River Beach are almost entirely due to the movement of sand particles within a water matrix and are not complicated by the presence of interstitial organic material.

When offered a choice, *C. coeca* preferentially burrowed into substrates which comprise a large portion of its native substrate. Individuals were unable to burrow in particles greater than 2000 μm. Burrowing speed increased inversely with substrate coarseness between substrates 1001–2000 μm and 251–500 μm. This, no doubt, is due to the ease with which the smaller particles can be moved by the combined action of pereiopods and pleopods. The porosity of packed particles of uniform shape is independent of particle size (Allen, 1982; Leeder, 1982; Beard and Weyl, 1973). However, the permeability decreases as the particles become smaller (Beard and Weyl, 1973). In the finest sand substrate (<250 μm), burrowing was slower than in the native substrate, or in the two substrates which comprise more than 90% of it (Fig. 1). The finest substrate comprises very little of the native substrate (<3% by weight). *C. coeca* apparently has difficulty penetrating sands which are significantly finer than its native substrate.

Maintenance of a fresh respiratory flow probably becomes increasingly difficult as the mean sediment particle size decreases. Very fine particles in clays and organically rich muds are held together by cohesive electrostatic forces (Allen, 1982) and by adhesiveness of organic molecules. *Chiridotea coeca* became mired very rapidly in mud. The porosity of well sorted natural sands is 40–45% (Beard and Weyl, 1973). In poorly sorted sediments, porosity can be as low as 5–10% (Allen, 1982). *Chiridotea* species have only been reported in well-sorted substrates consisting principally of medium-coarse sand grains (Tait, 1927; Wigley, 1960; Harper, 1974). This marked preference is probably due to ease of locomotion and maintenance of respiratory flow.

Burrowing is a behavior common to beach macrofauna of widely divergent taxa. It provides protection against desiccation and reduces the occurrence of dislocation due to wave action. At high water, burrowing provides protection from predation by fish, which may be an important biotic pressure on intertidal isopods (Wallerstein and Brusca, 1982). At low water, predation from terrestrial animals such as shorebirds (Myers *et al.*, 1980) is counteracted by burrowing.

The walking mechanism of *Chiridotea* is different from that of the primitive asellotan, oniscoidean, valviferan, and phreaticoidean forms as described by Hessler (1982). In those forms, the dactyl of an anterior pereiopod (*e.g.*, pereiopod II) "is lifted from the substrate, stretched forward, primarily through extension at co.-ba., ba.-i. and c.-p., but also at i.-m. and p.-d., and set down again so that the dactyl again makes contact. The limb is then flexed, primarily at the same articulations, and this pulls the animal forward. Flexion is the propulsive mechanism, and extension is used in recovery. With posteriorly directed appendages, such as pereiopod VII, flexion and extension are also the dominant motions, but their roles are reversed" (Hessler, 1982: p. 259). In contrast, frame by frame analysis of video and motion picture film of *C. coeca* shows that the power stroke for all pereiopods (except gnathopod I, which does not participate in locomotion) involves extension at the coxo-basal and basi-ischial articulations, and the recovery stroke involves flexion at these articulations. There is a substantial amount of lateral thrust in the power stroke of each leg, which varies over the pereiopodal series. The movement of the gnathopods provides very little forward propulsion. These legs push laterally and sweep through a small angle, so that the greatest direction of thrust is almost perpendicular to the direction of body motion. The gnathopods thus push sand aside, allowing the widest part of the body to move forward unimpeded. Isopods which utilize "extensible strut" (Hessler, 1982) or the swinging of legs beneath the body as in *Ligia* (Manton, 1952) involve vertical displacement of legs. These sorts of mechanisms would be inefficient and impractical for moving beneath an unstable substrate, where vertical motions encounter resistance, and a small anterior surface area is desirable. *Chiridotea* does not lift pereiopods, and the anteriorly tilted stance and flattened body provide a small anterior surface area.

For many crustaceans which plow through mud or sand, locomotory rhythms in the substrate are the same as those used in walking (Lochhead, 1961). This is mostly true in *Chiridotea*, where leg motions above and below the substrate surface are identical, except for a decreased forestroke:backstroke ratio. This decrease is probably due to the greater resistance to backward thrust encountered by legs during tunneling. The metachronal rhythm remains the same, as does the 0.5 cycle phase difference between opposite legs. This difference in phase cycle is not unique to *Chiridotea*, but in combination with the lateral component of pereiopod movement may be an asset to tunneling, for it produces the wobble of the body which may exert a shearing force on the surrounding substrate, reducing resistance to forward motion.

Chiridotea is morphologically very different from the Idoteinae (*sensu* Tait, 1927). Dorso-ventral flattening of the head is extreme, and lateral expansion of the middle pereonites is much greater than in most idoteine species. The pereiopods of *Chiridotea* are robust. There is a marked dimorphism between the strongly subchelate gnathopods and the elongate ambulatory legs, reflecting the importance of the feeding role and different locomotory role of the former. In *Idotea* and related species, pereiopods are weakly subchelate, adapted for grasping onto fronds of marine grasses (Hessler, 1982). The pereiopods of *Chiridotea* lack the carpo-propodal flexure found in *Idotea* and the other groups described by Hessler (1982). The presence of this flexure causes the body to have a half-hanging stance (Lochhead, 1961), which is adaptive for clinging. The absence of this flexure in *Chiridotea* reflects the function of these pereiopods, which act as poles which push against the substrate. Any flexure below the basi-ischial articulation would reduce the rigidity of the leg, and reduce the force delivered to the dactyl.

In the primitive isopodan configuration, the angle of the limb plane with vertical shifts for successive limbs (Hessler, 1982). In anterior pereiopods, the anterior surface of the plane is tilted upwards. In posterior pereiopods it is tilted downwards. The plane of the fourth pereiopod is almost vertical. In *Chiridotea*, the anterior surfaces of all limb planes are tilted upwards. The regions of the limb planes within which the legs move are stacked one on top of another, each lying beneath its anterior neighbor (Fig. 5). The anterior slope of all limb planes ensures a flattened form. A more extreme case of anterior slope of all limb planes is found in *Serolis* (Flabellifera: Serolidae). This is an extremely flattened form which also plows beneath the substrate (Moreira, 1974).

Setae are a very conspicuous element of the morphology of *Chiridotea*. Tait (1927) and Pearse *et al.* (1942) discussed morphological adaptations of *Chiridotea* to burrowing, but did not describe the function of the pereiopod plumose setae. Because pereiopods extend laterally, they are not sheltered by the body. In the absence of setae, there would be a tendency for sand to fall between the legs and beneath the body, which would hinder or block the anterior swing of pereiopods during recovery stroke. Metachronal waves move anteriorly, therefore during recovery stroke, each pereiopod swings forward beneath the palisade of setae on the adjacent anterior leg, which is in a posterior position, in an earlier stage of recovery stroke.

The spacing of plumose setae suggests that they are very effective in screening out the sand grains of the native substrate. The vast majority of the substrate particles were too large to pass through the intersetal spaces. During growth, intersetal spacing does not change significantly (Fig. 7B). Number of setae per segment increases (Fig. 7A), as does setal length, but intersetal distance does not. The spacing is therefore thought to be important to the animal, most likely for the screening mechanism described.

The possession of palisades of plumose setae is relatively rare in sand-dwelling Peracarida. Members of the dominant sand-dwelling isopod family, the Cirolanidae, may bear short plumose setae on the posterior margin of the telson (Richardson, 1905; Menzies and Frankenberg, 1966; Jones, 1974; 1976; Fish, 1972) but the pereiopods typically bear stout spine-like setae. Beach-dwelling cirolanids are usually smaller than *Chiridotea* species, and have relatively smaller limbs which are ventrally directed beneath the body in a more typical isopodan fashion. Haustoriid amphipods are commonly found on exposed sand beaches (Dahl, 1952; Bousfield, 1973) and typically have a lot of plumose setae. Watkin (1940) described the burrowing method of the haustoriid *Urothöe marina*. Burrowing locomotion in this species is dependent on the maintenance of a water current which is drawn through a trough

beneath the body. The walls of the trough are formed by coxal plates and the plumose setae on the pereiopods. These setae form a screen which prevents sand from falling into the ventral trough. The plumose setae of *Chiridotea* are analagous to those of haustoriid amphipods. The coxal plates of *Chiridotea* are moderately setose and probably also perform a sand-blocking role. In the flabelliferan isopod *Serolis* the coxal epimeres are expanded to such a degree that the legs are entirely covered. The pereiopods of *Serolis* bear no plumose setae, the coxal epimeres performing the same function as the plumose setae in *Chiridotea.*

The plumose setae on the pleopods of *Chiridotea* (Fig. 6G) differ from those on the pereiopods and gnathopods. They are longer, thicker, more closely packed, and much more densely setulose. They increase the propulsive area of the swimming appendages without increasing their inertia.

Serrulate setae increase the area of contact between pereiopods and substrate during the power stroke. The direction of thrust of each pereiopod is described by the motion of the tip of the leg. These setae are located on the lateral surfaces of the ischium, merus, carpus, and the lateral and medial surface of the propodus of the pereiopods. Because they are distally directed, each exerts a force on the substrate through its tip, parallel to the force exerted by the dactyl. They therefore increase the thrust delivered to the unstable surrounding substrate.

Chiridotea and its glyptonotine allies have diverged significantly from the primitive idoteid stock. The typical members of the family (*Idotea* and similar forms) have retained a stance, general morphology, and locomotory pattern which are shared with members of other suborders. *Chiridotea* and closely related species are seen as highly modified, having a unique posture, general morphology, setal complement and locomotory mechanism, which are seen as adaptations to a fossorial existence in a sandy substrate.

LITERATURE CITED

ALLEN, J. R. L. 1982. *Sedimentary Structures: Their Character and Physical Basis.* Elsevier Scientific Co., New York. 594 pp.

BEARD, D. C., AND P. K. WEYL. 1973. Influence of texture on porosity and permeability of unconsolidated sand. *Bull. Am. Petrol. Geol.* **51**: 349–369.

BOUSFIELD, E. L. 1973. *Shallow Water Gammaridean Amphipoda of New England.* Comstock Publishing Co., Ithaca, New york. 312 pp.

CRAWFORD, G. I. 1937. Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *J. Mar. Biol. Assoc. U. K.* **21**: 631–646.

DAHL, E. 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos* **4**: 1–27.

FISH, S. 1972. The setae of *Eurydice pulchra* (Crustacea: Isopoda). *J. Zool. Lond.* **166**: 163–177.

GOODHARD, C. B. 1939. Notes on the bionomics of the tube-dwelling amphipod, *Leptocheirus pilosus* Zaddach. *J. Mar. Biol. Assoc. U. K.* **23**: 311–324.

HARPER, D. E., JR. 1974. *Chiridotea excavata* n.sp. (Crustacea, Isopoda) from marine waters of Texas. *Contrib. Mar. Sci.* **18**: 229–239.

HESSLER, R. R. 1981. Evolution of arthropod locomotion: a crustacean model. Pp. 9–30 in *Locomotion and Energetics in Arthropods,* C. F. Herreid and C. R. Fourtner, eds. Plenum Press, New York. viii + 546 pp.

HESSLER, R. R. 1982. The structure morphology of walking mechanisms in eumalacostracan crustaceans. *Phil. Trans. R. Soc. Lond.* **B296**: 245–298.

JONES, D. A. 1970. Factors influencing the distribution of the intertidal isopods *Eurydice pulchra* Leach and *E. affinis* Hansen in Britain. *J. Anim. Ecol.* **39**: 455–472.

JONES, D. A. 1974. The systematics and ecology of some sand beach isopods (Family Cirolanidae) from the coasts of Saudi Arabia. *Crustaceana* **26**: 201–211.

JONES, D. A. 1976. The systematics and ecology of some isopods of the genus *Cirolana* (Cirolanidae) from the Indian Ocean region. *J. Zool.* **178**: 209–222.

LEEDER, M. R. 1982. *Sedimentology Process and Product.* George Allen and Unwin, London. 344 pp.

LOCHHEAD, J. H. 1961. Locomotion. Pp. 313–364 in *The Physiology of Crustacea,* Vol. II, T. W. Waterman, ed. Academic Press, London.

MANTON, S. M. 1952. The evolution of arthropodan locomotary mechanisms. Part 2. A general introduction tothe locomotory mechanisms of the Arthropoda. *J. Linn. Soc. Lond. Zool.* **42**: 93–117.

MANTON, S. M. 1977. *The Arthopoda: Habits, Functional Morphology, and Evolution.* Clarendon, Oxford. 527 pp.

MEADOWS, P. S. 1964. Substrate selection by *Corophium* species: the particle size of substrates. *J. Anim. Ecol.* **33**: 387–394.

MENZIES, R. J. 1956. A study of the microscopic structure of isopod setae. *Ann. Mag. Nat. Hist. Ser. 12* **9**: 698–700.

MENZIES, R. J., AND D. FRANKENBERG. 1966. *Handbook of the Common Marine Isopod Crustacea of Georgia.* University of Georgia Press. 93 pp.

MOREIRA, P. S. 1974. Cryptic coloration in *Serolis laevis* and *Serolis polaris* (Isopoda, Flabellifera). *Crustaceana* **27**: 1–5.

MORGAN, E. 1970. The effects of environmental factors on the distribution of the amphipod, *Pecteno-gammarus planicrurus,* with particular reference to grain size. *J. Mar. Biol. Assoc. U. K.* **50**: 769–785.

MYERS, J. P., S. L. WILLIAMS, AND F. A. PITELKA. 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. *Can. J. Zool.* **58**: 1564–1574.

NAYLOR, E. 1955. The comparative external morphology and revised taxonomy of the British species of *Idotea. J. Mar. Biol. Assoc. U. K.* **34**: 467–493.

OAKDEN, D. M. 1984. Feeding and substrate preference in five species of phoxocephalid amphipods from central California. *J. Crust. Biol.* **4**: 233–247.

PEARSE, A. J., H. J. HUMM, AND G. W. WHARTON. 1942. Ecology of sand beaches at Beaufort, North Carolina. *Ecol. Monogr.* **12**: 136–190.

POHLE, G., AND M. TELFORD. 1981. Morphology and classification of decapod crustacean larval setae: A scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae). *Bull. Mar. Sci.* **31**: 736–752.

REES, C. P. 1975. Competitive interactions and substratum preferences of two intertidal isopods. *Mar. Biol.* **30**: 212–25.

RICHARDSON, H. 1905. A monograph of the isopods of North America. *Bull. U. S. Nat. Mus.* **54**: 1–717.

SHEALY, M. H., JR., B. B. BOOTHE, JR., AND C. M. BEARDEN. 1975. A survey of the benthic macrofauna of Fripp Inlet and Hunting Island, South Carolina, prior to beach nourishment. *South Carolina Marine Resources Center Technical Report Series Number 7.* 30 pp.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. *Statistical Methods,* 6th. ed. Iowa State University Press. 593 pp.

SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry,* 2nd. ed. W. H. Freeman and Co., San Francisco. 859 pp.

SWEDMARK, B. 1964. The interstitial fauna of marine sand. *Biol. Rev.* **39**: 1–42.

TAIT, J. 1927. Experiments and observations on Crustacea. Part VII. Some structural and physiological features of the valviferous isopod *Chiridotea. Proc. R. Soc. Edinburgh* **46**: 334–348.

WALLERSTEIN, B. R., AND R. BRUSCA. 1982. Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). *J. Biogeog.* **9**: 135–150.

WATKIN, E. E. 1940. The swimming and burrowing habits of the amphipod *Urothöe marina* (Bate). *Proc. R. Soc. Edinburgh* **60**: 271–280.

WIGLEY, R. L. 1960. A new species of *Chiridotea* (Crustacea, Isopoda) from New England waters. *Biol. Bull.* **119**: 153–160.