THE FLORIDA STATE UNIVERSITY

COLLEGE OF ARTS AND SCIENCES

TWO NEW DIOSACCIDS (COPEPODA, HARPACTICOIDA) FROM THE NORTHERN GULF OF MEXICO AND THEIR RESPONSES TO WINTER STORMS

By

LORI BOUCK

A Dissertation submitted to the
Department of Oceanography
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Degree Awarded:
Fall Semester, 2003

The members of the Committee approve the dissertation of Lori Bouck defended on September 3, 2003.

David Thistle
Professor Directing Dissertation

William Herrnkind
Outside Committee Member

Richard Iverson
Committee Member

William Landing
Committee Member

Nancy Marcus
Committee Member

Approved:

Nancy Marcus, Chairperson, Department of Oceanography

The Office of Graduate Studies has verified and approved the above named committee members.

ACKNOWLEDGEMENTS

The work detailed in chapters 1 and 2 was supported by ONR grant N00014-95-1-0750 to D. Thistle. The encouragement of M. Schratzberger, discussions with A. Ahnert, D. Danielopol, and G. Paterson, and the comments of A. Ahnert, P. Leitman, K. Suderman, A. Thistle, D. Thistle, and R. Wetzer improved chapter 1. The comments of R. Huys, D. Thistle, and an anonymous reviewer improved chapter 2. The comments of D. Thistle improved chapter 3. M. Bouck assisted with the figures in chapter 3. Chapters 1 and 2 are reprinted by permission of their respective publishers.

TABLE OF CONTENTS

LIST OF FIGURES

ABSTRACT

The traditional method for producing taxonomic illustrations requires the preparation of inked copies of pencil originals. These individual figures are then grouped into plates for publication. I describe an alternative, computer-based approach. In a preliminary step, a pencil drawing is digitized and imported into an illustration program. The program's tools are then used to trace the image. Each figure is stored as a separate computer file. To make a plate for publication or a slide for presentation, several figures can be combined. The approach has several advantages. (1) It is easier to master than the pen-and-ink method. (2) Figures can be manipulated electronically, so the size and orientation of a figure is infinitely adjustable, providing great flexibility in the preparation of plates. (3) Multiple "originals" can be printed. (4) Mistakes can be corrected easily.

I describe two new species of Diosaccidae (Harpacticoida, Copepoda) from an unvegetated sand at 18 m depth in the northern Gulf of Mexico. One is assigned to the genus *Protopsammotopa*; the other is assigned to *Actopsyllus*, and traits in common with *Eoschizopera* Wells & Rao (1976) are noted. I used the computer-based techniques to produce the figures for these descriptions.

The effects of winter storms on the two new diosaccids described here were studied through a reanalysis of data from Thistle *et al*. (1995a). I found that *Actopsyllus* sp. nov. did not migrate downward in response to erosive flow. *Protopsammotopa* sp. nov. males, but not females, did. *Protopsammotopa* sp. nov. is found at shallower depths in the sediment than *Actopsyllus* sp. nov., which may explain the difference in response to erosion by two morphologically similar and phylogenetically related species.

INTRODUCTION

Despite the unique role that taxonomy plays as a foundation for biological research, a decline in the number of taxonomic specialists has been recognized since the 1950’s (Hedgepeth *et al*., 1953), and funding for taxonomic research has decreased (Gaston & May, 1992). Alpha taxonomy, the detection and description of species, is key in supporting the biodiversity research that has recaptured interest in recent years in both scientific circles and the environmentally-aware public. In some habitats, the biodiversity is vastly underdescribed. The deep sea is an obvious example (Lambshead, 1993), but even in shallow-water coastal systems, researchers have found that 33-99 percent of the organisms have not been described (Butman & Carlton, 1995). Alpha taxonomy has also been recognized as the largest problem in systematic biology research, yet little has been done to revive the field (Disney, 1998). Butman & Carlton (1995) describe the situation as a crisis so severe that recovery may not be possible without immediate action to recruit new systematists. In addition, interpretation of ecological studies has been hindered by a lack of taxonomic understanding of the species involved (Knowton & Jackson, 1994).

A partial solution to the predicament of declining numbers of taxonomists would be the training of new scientists in basic taxonomic skills to supplement their research interests. The research described in this dissertation was funded by an Office-of-Naval-Research grant for this purpose. The dissertation has a three-part structure that promotes the goals of the funding grant. The first chapter is a methodological paper that outlines a means of speeding the production of new taxonomic descriptions. The second chapter is a taxonomic paper that describes two new species of harpacticoid copepod. (It should be noted that to avoid confusion in the literature the full names will not be given here but will be published in the journal *Crustaceana*.) The third chapter is an ecological paper that reanalyzes previous work in light of the discovery of the two new harpacticoids described in the second chapter.

CHAPTER 1

A COMPUTER-ASSISTED METHOD FOR PRODUCING ILLUSTRATIONS FOR TAXONOMIC DESCRIPTION

Introduction

The traditional method of preparing species descriptions requires the preparation of figures for publication (Mayr and Ashlock, 1991) by arranging original drawings into plates and tracing them onto velum with pen and ink. I found inking the figures to be the limiting step in my taxonomic work. I turned to illustration software as a possible solution and found that I could produce figures of a quality equivalent to that of the pen-and-ink method. Below, I outline the methods I use, discuss their advantages, and report potential pitfalls.

Methods

Scanning the Original

My approach requires that the original pencil drawings (“drawing” always refers to the pencil rendering) first be digitized. I use a Hewlett-Packard ScanJetIIcx scanner and Adobe Photoshop® 3.0 for this step, but any scanner and software can be used that have previewing features that allow the image (“image” always refers to the computer rendering) to be resized and permit optimizing the contrast and brightness of the image. After some preliminary experimentation, I select settings that provide sufficient detail but allow the digitized image to be stored on a 1.4 MB floppy disk so it can be transferred from a central scanning station to the working computer. In particular, I select black-and-white (1 bit) scanning, set the resolution to match that of my laser printer, set crop marks to include the drawing but exclude as much bordering white space as possible, and reduce the image size to 80% or less. I then save the image in a format (TIFF) recognizable by my illustration software. If the original drawing is larger than the scanner can accomodate, I make separate scans of different sections of the drawing, with care to be consistent in the reduction of the image (*e.g.* all scans reduced to 60%), and piece them together in the illustration software.

Creating an Illustration File

A tracing of the image can begin once the image file is imported into the drawing software. Two types of drawing software are available, vector-based programs (*i.e.* illustration software), which represent lines by means of equations, and bitmap-based programs (*i.e.* painting software), which represent lines as groups of pixels (Adobe Systems Incorporated, 1997). The use of vectors, rather than a bitmapped computer representation, creates smooth curves that can be adjusted in several desirable ways. For example, line widths can be altered, and the size of a figure (both on screen and printed) can be changed without creating the jagged edges characteristic of bitmapped images (Alspach, 1997). I use Adobe Illustrator® 7.0, but any vector-based software with the capabilities discussed below could be used (*e.g.* Corel Draw® and Freehand®).

Illustration software allows different elements of an illustration to be placed on separate “layers” within the file. The final image prints as a single unit, but the manipulation of multiple parts of the image is greatly facilitated by the layering feature. I create a file in my illustration software such that one layer contains only the scanned TIFF image and serves as a template. To facilitate tracing, I set the options of the template layer such that the scanned image (1) is dimmed, (2) will not be printed, and (3) cannot be changed. I create a tracing of the template on as many additional layers as necessary.

Tracing the Template

I trace the template by creating curves with the illustration software, in turn by setting anchor points and manipulating the lengths and angles of accompanying handle bars (Fig. 1.1). The portion of the image on the screen is enlarged or reduced as needed before a curve is drawn. I select options in the software that produce curves with rounded ends and corners that resemble those made with a pen. If dashed lines are needed (*i*.*e*. to show underlying structure), the dashing option in the software can turn a solid line into a series of dashes. The technique can take a novice 5-10 hours to master.

Several conventions used in taxonomic illustration can be implemented easily in vector software, often with results superior to those possible with pen and ink. For example, different line widths are used traditionally to convey structural information (*e*.*g*., in harpacticoid copepod drawings, the outside of the cuticle is represented by the thickest lines and the inside edge of the cuticle by thinner ones; e.*g*. Huys, 1987, Fig. 3A.) Illustration software includes a larger selection of line widths than is available in pens. Also, if all the curves of a given thickness are made on a single layer, their width can be changed quickly (Ahmed Ahnert, pers. comm.). For example, if the thinnest curves are too thin, the layer with those curves can be selected while other layers are locked, all thin curves can be selected with two keystrokes, and the width can be increased.

By convention in taxonomic illustration, when one feature lies above another, the lines representing the lower feature are broken in the vicinity of the upper feature (*e*.*g*. Huys, 1987, Fig. 2C). These line breaks can be produced by creating a white halo around the top feature (Ahmed Ahnert, pers. comm.). When this top feature is placed onto another feature, the white halo acts to create gaps at the intersections of the two features (Fig. 1.2, step 4). When several copies of the same feature are added to an existing structure, this technique is faster than drawing the underlying structure with many short lines (*e*.*g*. Fig. 1.2, steps 4-8).

Taxonomic illustrations frequently require the addition of visual texture, which is traditionally represented by stippling (*e*.*g*. Huys, 1987, Fig. 3D). Illustration software can produce a great variety of textures, which can be added to images easily. When a region to be shaded is enclosed by a curve, I select the curve and fill it with the appropriate shading. If a region to be shaded is not defined by a closed curve, I enclose it by drawing a curve with the line color set to “none” and fill it with the appropriate shading. As the size of the area to be shaded increases, shading with illustration software becomes increasingly more efficient than stippling.

Illustration software can speed drawing in additional ways. When several of the same type of object occur, I draw one object and then copy and paste it several times, rotating the copies and adjusting the anchor points and handle bars as needed. When several of the same object are in a row, I draw one at each end of the row (Fig. 1.2, steps 3-5), and use a “blending” tool to fill in a specified number of copies (Fig. 1.2, step 6). When mirror-image rows of objects are needed, I create one row as described above and add the second by copying and reflecting the first row (Fig. 1.2, steps 7-8). Also, an experienced operator can use keyboard commands rather than choosing menu options with the mouse. Although menus may be easier for a novice, working with keyboard commands speeds the overall process.

After a figure is completed, I save an archive file with the tracing and the template layers in case they are needed for later reference. I then make a working copy of the file and delete the template layer, which is no longer necessary. This smaller “tracing-only” file is used when I create a plate. See Figure 1.3 for an example of a completed figure. For a comparison of pen-and-ink and computer-illustrated figures, see Bouck *et al*. (1999); in that paper the illustrations of the first three species descriptions were pen-and-ink rendered; the illustrations of the last two descriptions were produced with Adobe Illustrator® 7.0.

Creating a Plate

Although desktop-publishing software could be used to produce plates, I have found that the illustration software I use suffices. To produce a plate for publication, I create a “plate” file that is distinct from the many individual “figure” files on which I have been working. I import the required figures from their respective figure files into the plate file. Within the plate file, I place each figure on its own layer so that individual figures can be easily selected and moved without affecting the others. On an additional layer of the plate file, I draw a rectangular border to represent the outer edge of the plate in the proportions of the page of the journal to which the paper will be submitted. I adjust the options for the border layer so that the outline will not print; it simply serves as a guide. The individual figures can be moved, rotated, and resized as necessary to produce the desired layout of a plate. I add letters to label each figure. I rotate the scale bars to a vertical or horizontal orientation and move them so that they are associated with their respective figures. If desired, text can be added to each scale bar (both horizontally and vertically), indicating the scale within the figure itself rather than in the figure caption. If cropmarks are desired, the bordering rectangle can be changed to print as cropmarks.

Results and Discussion

Perhaps the most important benefit of illustration software is that it speeds the production of figures and plates. If all goes well with both the computer-aided method and the pen-and-ink method, the two approaches are about equally time consuming. Computer illustration speeds production because almost anyone can master the technique. That is, my experience has been that even after days of practice, three artistically talented novices were unable to produce figures of sufficient quality with pen and ink. In contrast, with 10 hours of training, two undergraduate lab assistants could produce publishable figures, and even the work they produced during their training period could be used after minor corrections.

The ability to develop an electronic library of images also speeds production. After a period of creating illustrations, the illustrator develops an archive of images that can be used in other situations. Producing plates for keys, reviews, or broad systematic papers will be speeded when figures are already available and need only to be arranged. Figures can be combined and key points highlighted for teaching slides. For example, sexual dimorphism could be illustrated with a slide showing both male and female appendages with differences shown by colored rather than black lines. I created such a plate for harpacticoid copepods in approximately 15 minutes, including planning and several changes to the layout, with images saved from a species description.

The computer-aided approach allows much faster correction of mistakes and recovery from accidents. A mistake that, on a traditional plate, might destroy hours of effort can be “undone” with a few keystrokes on the computer. If an accident occurs (*e.g*. coffee is spilled on a plate or the plates are lost in the mail on the way to the publisher), the illustrator with computer-generated plates can print another set of “originals,” but the traditional illustrator must begin again.

Ironically, the very capabilities that make computer-aided drawing ideal for producing species descriptions warrant several cautions. Objects are easily copied and reflected, but the reflecting feature must be used only when justifiable. For very small repeated objects (*e.g*. ornamentation on harpacticoid copepod setae), I use the “reflect” tool to speed illustration as described in the methods (Fig. 1.2). I perform the operation at a very high magnification, check the results against the template, and adjust objects as necessary. It is my experience that figures with reflected elements can, with these precautions, be as accurate as those created with pen and ink at a smaller scale.

An additional potential source of difficulty is resizing figures. For example, a figure can be accidentally resized independently of its scale bar. Also, resizing is not automatically proportional; specific procedures must be followed to make it so. I recommend care in use of the “scale” tool, as several small errors may accumulate, escaping the attention of the user. Despite the care required, the ability to resize figures easily is an advantage over the traditional pen-and-ink method.

Because failures of power and computer system must be guarded against, work should be saved often during a session and backed up on removable media at the conclusion of a session. Because, a floppy disk is generally too small to hold a work in progress that contains both the template and the overlying curves (sometimes as large as 4.6 MB), a large-capacity, removable media device (*e.g*. a Zip™ drive) is an important component of a computer system to be used for taxonomic illustration.

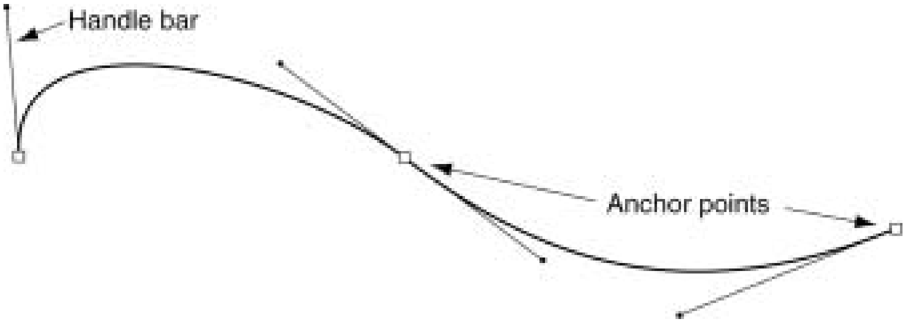
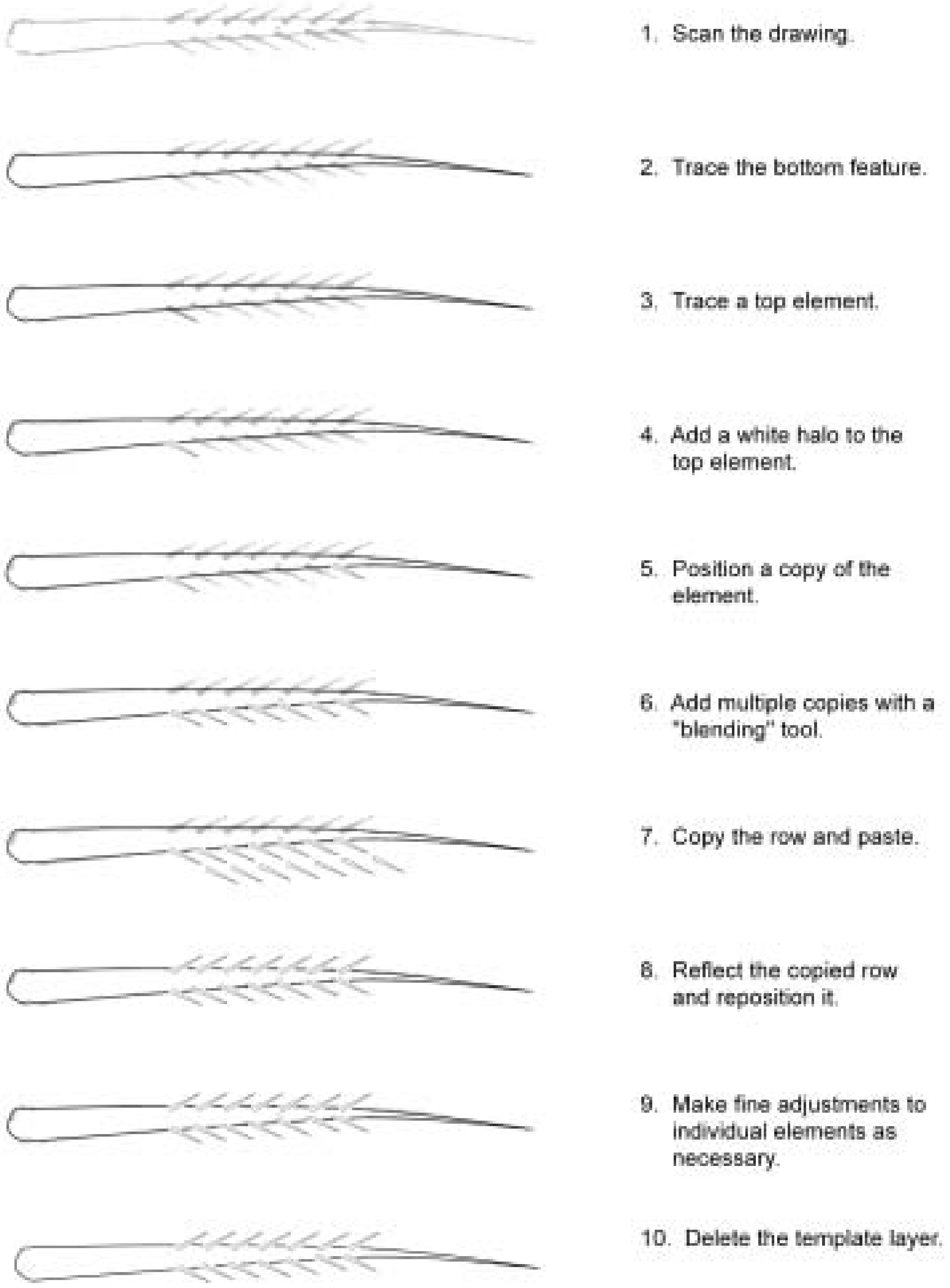


Fig. 1.1. Vector Curve with the Anchor Points and Handle Bars Used to Manipulate its Shape



1. Scan the drawing.
2. Trace the bottom feature.
3. Trace a top element.
4. Add a white halo to the top element.
5. Position a copy of the element.
6. Add multiple copies with a "blending" tool.
7. Copy the row and paste.
8. Reflect the copied row and reposition it.
9. Make fine adjustments to individual elements as necessary.
10. Delete the template layer.

Fig. 1.2. Steps Used in Tracing a Template with Several Time-saving Techniques Demonstrated

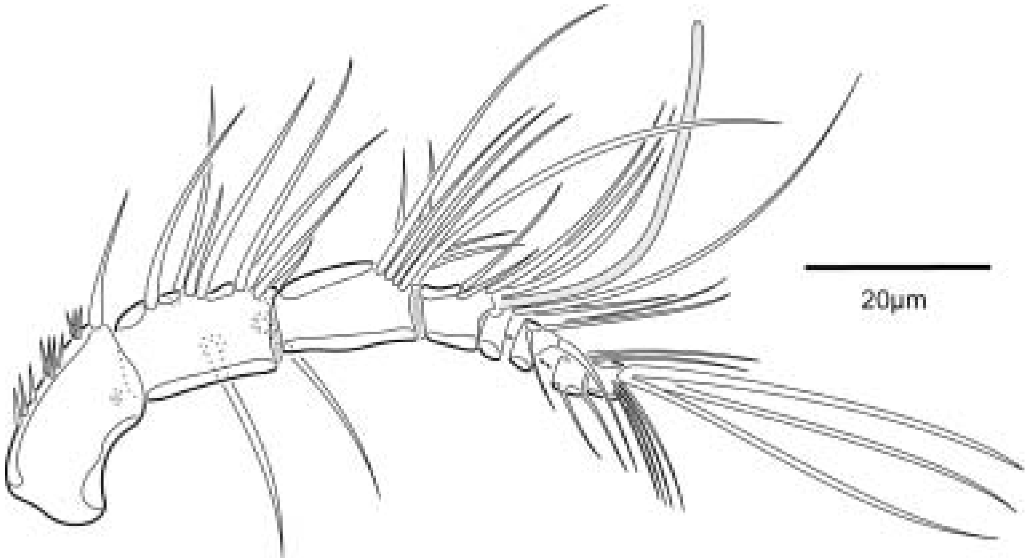


Fig. 1.3. Antennule from a Female Harpacticoid Copepod Illustrated with Adobe Illustrator® 7.0

CHAPTER 2

TWO NEW DIOSACCIDS (COPEPODA, HARPACTICOIDA) FROM THE NORTHERN GULF OF MEXICO

Introduction

In the course of an ecological experiment in the northern Gulf of Mexico (Thistle *et al*., 1995), many of the harpacticoid copepod species studied could be identified only to genus level. Here we describe two of these species from the related Diosaccidae genera *Protopsammotopa* and *Actopsyllus*. Neither genus is well known taxonomically. *Protopsammotopa* is composed of one completely described (Geddes, 1968) and one partially described (Wells, 1977) species; *Actopsyllus* is monotypic. The descriptions of two additional species will provide further understanding of both the variability within each genus and the phylogenetic relationships in this branch (*sensu* Wells & Rao, 1976) of the Diosaccidae.

Materials and Methods

Specimens were obtained from sediment samples that had been preserved in sodium-borate-buffered seawater formaldehyde (9 : 1, v : v). Harpacticoids were dissected in lactophenol, and the parts were mounted on H-S slides (Shirayama *et al*., 1993) in Hoyer’s mounting medium (Pfannkuche & Thiel, 1988). Pencil drawings were made with a *camera lucida* on a Zeis Optiplex compound microscope equipped with differential interference contrast. Habitus views were drawn at 1024 x; other views were drawn at 2560 x. Plates were produced with Adobe Illustrator® (Bouck & Thistle, 1999). Terminology follows Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1-P6, first to sixth thoracopods; exp(enp)-1(2,3), to denote an exopod's (endopod's) first or proximal (second, third) segment.

Systematics

Family Diosaccidae G. O. Sars, 1906

Protopsammotopa Geddes, 1968

Diagnosis (amended). — Diosaccidae. Body cylindrical, without clear demarcation between prosome and urosome. Genital double somite with spherical epicopulatory bulb. Rostrum elongate, defined at base. Antennule 8-segmented; second segment longest; with aesthetascs on fourth and eighth segments. Antenna with incomplete division of basis and first endopodal segment; exopod 1-segmented with 2 terminal setae; second endopodal segment with lateral armature of 2 large spines and 2 smaller elements, with distal armature of 4 geniculate spines plus 2 other free elements. Mandible with biramous palp; basis with 2 terminal setae; endopod length less than 1.5 times width, with 5 setae. Maxillule praecoxa with 7 spines along distal margin; coxa with 1 seta; endopod represented by single seta subdistal to terminal setae on basis; exopod 1-segmented with 2 setae. Maxilla syncoxa with 3 endites, proximal and middle endites each with single seta. Maxilliped syncoxa with seta at distal corner; endopod with 1 claw and 1 seta extending approximately half the length of the claw.

P1 endopod prehensile, 2-segmented, first segment approximately equal in length to exopod; exopod 3-segmented. P2-P4 with 3-segmented endopods and exopods; bases with an outer spine or seta; rami segments elongate; exp-3 of each leg with 2 outer spines. P5 with distinct rami; baseoendopod with 4 setae on endopodal lobe; exopod longer than wide, with 5 prominent setae.

Sexual dimorphisms in male include haplocer antennule; P2 endopod 2-segmented, enp-2 distinctly modified, with large outer spine; P5 endopodal lobe with 2 setae; exopod shorter than in female, with 4 prominent setae.

Type species: *Protopsammotopa norvegica* Geddes, 1968.

Other species: *Protopsammotopa wilsoni* Wells, 1977; *Protopsammotopa* sp. nov.

Protopsammotopa **sp. nov. (Figs. 2.1-2.4)**

Material examined. — National Museum of Natural History (Smithsonian Institution, Washington, D. C.): holotype female in alcohol; allotype male in alcohol; additional paratypes in alcohol (11 females, 24 males) or dissected on slides (5 females, 3 males).

Type locality. — Northern Gulf of Mexico: 29°40.63' N 84°22.80' W, 18 m depth, unvegetated medium sand; see Thistle *et al*. (1995) for additional description.

Description. — All illustrations are from paratypes except Fig. 2.1C, which is from the holotype.

Female holotype body length measured from anterior margin of rostrum to posterior margin of caudal rami (not including caudal setae) 365 μm. Body (Fig. 2.1A-C) slender, cylindrical. Sensillae present dorsally and ventrally on genital double somite and fourth urosomite and dorsally on sixth urosomite (Fig. 2.1A-B). Genital double somite with fused P6's, each side bearing 3 setae (Fig. 2.1B), and spherical epicopulatory bulb. Serrated hyaline fringe present dorsally on genital double somite, urosomites 4-5, and ventrally on urosomite 5 (Fig. 2.1A-B). Posterior, dorsal margin of urosomite 5 drawn out into pseudoperculum (Fig. 2.1A). Anal somite partially divided with spinules along dorsal and ventral posterior margin (Fig. 2.1A-B); anus triradiate, bordered by incised frill (not illustrated). Caudal rami (Fig. 2.1A-B) slightly longer than wide, with 7 setae: seta I thick with blunt tip, setae II-VI bare, dorsal seta (VII) carried on a biarticulate socle.

Rostrum (Fig. 2.1D) slender, defined at base, with subapical sensilla on each side.

Antennule (Fig. 2.1E) 8-segmented; second segment longest; third and sixth segments with blunt setae; fourth segment with an aesthetasc; eighth segment with an acrothek of 2 setae and an aesthetasc; with armature formula 1-[1], 2-[10], 3-[6 + 1 blunt], 4-[2 + (1 + ae)], 5-[2], 6-[2 + 1 blunt], 7-[4], 8-[4 + acrothek].

Antenna (Fig. 2.2A) coxa short and unornamented; basis and first endopodal segment incompletely subdivided; basis with proximal spinular row; second endopodal segment with spinules and hyaline fringe as indicated in Fig. 2A; lateral armature consisting of 1 pinnate and 1 bare spine and 2 slender setae; distal armature consisting of a pinnate spine, 1 slender seta, and 4 geniculate spines, the posterior one bears spinules and is fused at base to a seta; exopod 1-segmented with 1 bare and 1 pinnate distal setae.

Mandible (Fig. 2.2E) cutting edge with many slender teeth, spinular row near insertion of basis; palp biramous, comprising basis and 1-segmented exopod and endopod; basis with several spinular rows, 1 pinnate and 1 bare setae; endopod with 2 subdistal and 3 distal setae; exopod with 2 distal setae.

Maxillule (Fig. 2.2F) praecoxa with 7 spines along distal margin and 1 seta; coxa with 1 seta; basis with subdistal spinular row and 3 distal setae; endopod represented by single seta subdistal to basis setae; exopod with 2 setae.

Maxilla (Fig. 2.2D) syncoxa with 3 endites; proximal endite with unipinnate seta, middle endite with single seta; distal endite with 1 unipinnate and 2 bare setae; allobasis with 1 short, slender seta, 1 bare and 1 unipinnate setae; endopod 2-segmented, proximal segment with 1 bare and 1 pinnate setae, distal segment with 1 pinnate and 3 bare setae.

Maxilliped (Fig. 2.2C) syncoxa with 1 slender subdistal seta, 1 longer distal seta and spinules as indicated in figure; basis with several inner spinules, 2 subdistal setae along palmar margin, and a row of spinules along outer margin; endopod with 1 strong, pinnate seta drawn into a claw, 1 slender, pinnate seta, and 2 minute bare setae.

P1 (Fig. 2.2B) coxa with many spinular rows; basis with inner spinules and spinules at insertion of endopod and exopod, with 1 inner and 1 outer spine; exopod 3-segmented, with outer margins and inner margin of exp-2 spinulose, exp-3 with 1 geniculate and 3 shorter spines; endopod 2-segmented, prehensile, and longer than exopod; enp-1 roughly equal in length to exopod, with inner, outer, and distal spinular rows; enp-2 with spinules, 1 slightly curved, pinnate and 1 geniculate, pinnate spines and 1 slender seta distally.

P2-P4 (Fig. 2.3A-C) with 3-segmented exopods and endopods. Coxae with several anterior spinular rows and a posterior spinular row. Bases with outer short, bipinnate spine (P2) or bipinnate (P3) or bare (P4) seta. Endopods roughly equal to (P2) or slightly longer than (P3-P4) exopods. Seta and spine formula as follows:

	Exopod	Endopod
P2	0.0.022	0.1.021
P3	0.0.022	1.1.121
P4	0.0.022	1.1.121

P5 (Fig. 2.3D) Baseoendopod with 1 short, bare and 3 bipinnate inner setae; outer basal seta long and arising from conical process. Exopod 2.6 times as long as wide (excluding distal setae) with inner spinules, 1 inner, 1 long, pinnate, apical, and 3 prominent, outer setae, outer margin also with 2 very short tube-like elements.

Male allotype body length equal to that of female (365 µm). P6 asymmetrical, each side with 3 setae (Fig. 2.4B; the P6 illustration is a composite: the far left seta was drawn based on a second specimen). Caudal rami without seta III (Fig. 2.4A-B).

Antennule (Fig. 2.4D) haplocer, 9-segmented; third and fifth segments with blunt setae; fourth segment with an aesthetasc; ninth segment with an acrothek of 2 setae and an aesthetasc; with armature formula 1-[1], 2-[10], 3-[6 + 1 blunt], 4-[4 + (1 + ae)], 5-[1 blunt], 6-[1], 7-[1], 8-[4], 9-[4 + acrothek].

P1 (Fig. 2.3E) basis with modified shape, inner seta more slender than in female, inner spinules thicker than in female.

P2 (Fig. 2.3F) endopod 2-segmented; enp-2 distinctly modified with 1 inner, bare and 1 apical, distally pinnate setae and with outer subdistal elements modified into 1 bifurcate seta and 1 thick spine.

P3 (Fig. 2.3G) exp-3 with anterior hyaline spine.

P5 (Fig. 2.3H) baseoendopods fused medially; endopodal lobe with 2 bipinnate spines; outer basal seta long and arising from conical process; exopod with 4 setae and 1 short, tube-like element.

Etymology. — The species is named for Ronald C. Tipper. The full name will be published in *Crustaceana*.

Remarks. — *Protopsammotopa* sp. nov. shares several traits with the two currently described *Protopsammotopa* species (Geddes, 1968; Wells, 1977). Based on the male P2 endopod of *P. norvegica* Geddes, 1968, Geddes assigned his newly created genus, *Protopsammotopa*, and moved the obviously related *Psammotopa*, to the Diosaccidae. He suggested that both *Protopsammotopa* and *Psammotopa* be placed near the genus *Schizopera*, with which they share a reduced limb armature. Wells & Rao (1976) split *Schizopera*, creating the genus *Eoschizopera* (note Mielke, 1992, rejected this genus), and suggested a close relationship between *Eoschizopera* and *Protopsammotopa*-*Psammotopa*. *Protopsammotopa* sp. nov. has the reduced limb armature of the species in this group of genera. The structure of the male P2 endopod of *Protopsammotopa* sp. nov. is similar to that found in species of

Protopsammotopa and *Eoschizopera*. We assigned *Protopsammotopa* sp. nov. to *Protopsammotopa*, rather than *Eoschizopera*, based on the mandibular endopod, which has a distinct squarish shape that can be contrasted with the typical, rectangular shape found in genera that are more distantly related, as defined by Wells & Rao's (1976) phylogeny. The lack of an inner seta on the P1 enp-1 and an antenna with a 1-segmented exopod also support placing the species within *Protopsammotopa*.

Protopsammotopa sp. nov. differs from other *Protopsammotopa* in the following aspects. Geddes' (1968) description of the *P. norvegica* male antennule notes that the fourth segment is "partially sub-divided by an indistinct suture line". In *Protopsammotopa* sp. nov., this division is complete, resulting in two distinct segments. The male P3 exp-3 in *Protopsammotopa* sp. nov. has a membranous projection not found in other *Protopsammotopa*. The membranous projection is more similar in structure to the hyaline spines reported for species of the genera *Schizopera* and *Eoschizopera* (*e.g*., Lang, 1965; Wells & Rao, 1976; Apostolov, 1982; Mielke, 1992, 1995) than to the tube pores described by Gee & Fleeger (1990) in other diosaccids. The structure does not appear to have the opening at the tip found in Gee & Fleeger's (1990) tube pores. The presence of a hyaline spine would seem to support the assignment of the species to *Eoschizopera*. Considering the close relationship between *Eoschizopera* and *Protopsammotopa* and the ubiquity of a sexually dimorphic structure on the male P3 exp-3 within the Diosaccidae, we feel it is reasonable to allow species with hyaline spines to be assigned to *Protopsammotopa*.

***Actopsyllus* Wells, 1967**

Diagnosis (amended). — Diosaccidae. Body cylindrical, without clear demarcation between prosome and urosome. Rostrum elongate, defined at base. Genital double somite with dorso-lateral strip of chitin and mildly produced epicopulatory bulb; P6's fused with 3 setae on each side. Pseudoperculum present.

Antennule 8-segmented; first through fourth segments elongate; fourth segment with aesthetasc. Antenna with distinct or incompletely divided basis; exopod 2- or 3-segmented. Mandible with biramous palp; basis with 3 setae; endopod 1-segmented with 4 terminal and 2 lateral setae; exopod 1- or 2-segmented with 5 setae. Maxilla syncoxa with 3 endites; allobasis with claw; endopod 1-

segmented with 3 setae. Maxilliped syncoxa with slender seta at distal corner; basis with 2 setae along palmar margin; endopod with claw, 1 long, strong seta, and 2 minute setae.

P1 endopod prehensile, first segment distinctly longer than exopod, with inner seta; exopod 3-segmented, third segment with 4 spines. P2-P4 with 3-segmented endopods and exopods; bases with an outer spine or seta; rami segments elongate; enp-2 of each leg with outer distal corner acutely produced; exp-3 of each leg with 2 outer spines. P5 with distinct rami; exopod longer than wide.

Sexual dimorphisms in male include haplocer antennule; P1 basis with inner projection; P2 endopod 2-segmented, enp-2 distinctly modified, with large outer spine; P5 baseoendopods fused medially, with 2 setae.

Type species: *Actopsyllus longipes* Wells, 1967.

Other species: *Actopsyllus* sp. nov.

***Actopsyllus* sp. nov. (Figs. 2.5-2.8)**

Material examined. — National Museum of Natural History (Smithsonian Institution, Washington, D. C.): holotype female in alcohol; allotype male in alcohol; additional paratypes in alcohol (11 females, 11 males) or dissected on slides (5 females, 5 males).

Type locality. — Northern Gulf of Mexico: 29°40.63' N 84°22.80' W, 18 m depth, unvegetated medium sand; see Thistle *et al*. (1995) for additional description.

Description. — All illustrations are from paratypes except Fig. 2.5A, which is from the holotype.

Female holotype body length measured from anterior margin of rostrum to posterior margin of caudal rami (not including caudal setae) 335 μm. Body (Fig. 2.5A,C-D) slender, cylindrical. Sensillae present dorsally on genital double somite, fourth and sixth urosomites, and ventrally on fourth urosomite (Fig. 2.5C-D). Genital double somite with dorso-lateral strip of chitin, fused P6’s, each side bearing 3 setae (Fig. 2.5C), and mildly produced epicopulatory bulb. Serrated hyaline fringe present dorsally and ventrally on urosomite 5 (Fig. 2.5C-D). Posterior, dorsal margin of urosomite 5 drawn out into slight pseudoperculum (Fig. 2.5D). Anal somite mildly indented at posterior margin with spinules along posterior margin; with minute spinular ornamentation dorsally (Fig. 2.5C-D); anus triradiate, bordered by incised frill (not illustrated). Caudal rami (Fig. 2.5C-D) slightly longer than wide, with 6 setae: setae I-II bare, seta III absent, setae IV-VI bare, dorsal seta (VII) carried on a biarticulate socle.

Rostrum (Fig. 2.5E) slender, defined at base; with subapical sensilla on each side.

Antennule (Fig. 2.5B) 8-segmented; second segment longest; fourth segment with an aesthetasc; an acrothek was not obvious on the eighth segment; with armature formula 1-[1], 2-[8], 3-[6], 4-[3 + (1 + ae)], 5-[2], 6-[3], 7-[3], 8-[7].

Antenna (Fig. 2.6B) coxa short and unornamented; basis and first endopodal segment incompletely subdivided; second endopodal segment with spinules and hyaline fringe as indicated in Fig. 2.6B; lateral armature consisting of 2 bare spines and 2 slender setae; distal armature consisting of 1 pinnate spine, 1 slender seta and 4 geniculate spines, the posterior one bearing spinules and fused at base to a seta; exopod 2-segmented, exp-1 with bipinnate seta, exp-2 with distal seta.

Mandible (Fig. 6C) cutting edge with many slender teeth, spinular row near insertion of basis; palp biramous, comprising basis and 1-segmented exopod and endopod; basis with spinular row and 3 pinnate setae; endopod with 2 lateral and 4 distal setae; exopod with 2 lateral, pinnate setae and 3 distal, bare setae. No complete mandible was obtained, so the drawing is a composite; the 3 basis setae are based on a second specimen.

Maxillule (Fig. 2.6D) praecoxa with 7 pinnate spines along distal margin and 2 setae; coxa with 1 bipinnate seta; basis with spinular rows and 1 pinnate and 1 bare setae; endopod represented by single seta (indicated by arrow in illustration) adjacent to basis setae; exopod with 2 pinnate setae and lateral spinules.

Maxilla (Fig. 2.6E) syncoxa with 3 endites; proximal endite with pinnate seta, middle endite with 2 pinnate setae; distal endite with 2 pinnate and 1 bare setae; allobasis with claw, 1 bare and 1 pinnate setae; endopod 1-segmented with 2 bare and 1 pinnate setae.

Maxilliped (Fig. 2.6F) syncoxa with slender seta at distal corner and spinules as indicated in figure; basis with several inner spinules and 2 subdistal setae along palmar margin; endopod with 1 pinnate claw, 1 pinnate, long seta, and 2 minute setae.

P1 (Fig. 2.6A) coxa with several spinular rows; basis with spinules along inner margin and at insertions of endopod and inner bipinnate and outer pinnate spines; exopod 3-segmented, with outer margins and inner margin of exp-2 spinulose, exp-3 with 2 curved and 2 geniculate spines; endopod 2-segmented, prehensile, and distinctly longer than exopod; enp-1 distinctly longer than exopod, with inner spinular row and subdistal bipinnate seta; enp-2 with spinules, 1 curved and 1 geniculate spines and 1 slender seta distally.

P2-P4 (Fig. 2.7A-C) with 3-segmented exopods and endopods. Coxae with anterior and posterior spinular rows. Bases with short outer, bipinnate spine (P2) or bare setae (P3-P4). Endopods slightly longer than (P2-P3) or roughly equal to (P4) exopods. Seta and spine formula as follows:

	Exopod	Endopod
P2	0.1.022	1.1.121
P3	0.1.022	1.1.121
P4	0.1.122	1.1.121

P5 (Fig. 2.7D) Baseoendopod with 1 long, bare and 2 bipinnate inner setae; outer basal seta long and arising from conical process. Exopod 1.9 times as long as wide (excluding distal setae) with 1 inner, 1 long, apical, and 1 long and 3 shorter outer setae.

Male allotype body length roughly equal to that of female (330 µm). P6 asymmetrical, each side with 3 setae (Fig. 2.8C). Caudal rami setae III and VI absent (Fig. 2.8C-D).

Antennule (Fig. 2.8A) haplocer, 9-segmented; fourth segment with an aesthetasc; with armature formula 1-[1], 2-[8], 3-[6], 4-[3 + (1 + ae)], 5-[1], 6-[1], 7-[1], 8-[3], 9-[7].

P1 (Fig. 2.7F) basis with slender, bare seta rather than bipinnate spine found in female, inner margin spinules thicker than in female, inner seta and spinules on projection.

P2 (Fig. 2.7G) endopod 2-segmented; enp-1 with bare inner seta and no spinules; enp-2 distinctly modified with 2 inner, bare and 1 apical, bipinnate setae and with outer subdistal elements modified into 1 bifurcate seta and 1 thick spine.

P5 (Fig. 2.7E) baseoendopods fused medially; each side with 2 bipinnate inner setae and long, outer seta arising from conical process; exopod 1.7 times as long as wide (excluding distal setae) with 1 inner, 1 apical, and 1 long and 2 shorter outer setae.

Etymology. — The species is named for Matthew Bouck, the first author’s husband. The full name will be published in *Crustaceana*.

Remarks. — Wells (1967) established the monotypic genus *Actopsyllus* based on specimens from Ilha dos Portuguesos, Mozambique. Kunz (1971) added a second species that was later removed by Wells & Rao(1976) because the species lacked a strong claw on the male P2 endopod. We have placed *Actopsyllus* sp. nov. in *Actopsyllus* based on the male P2 endopod, which is very similar to that of the *Actopsyllus* type-species, and the two strong spines on the maxilliped endopod, found in no other related genus. It also has the much greater length of the P1 enp-1 in comparison with the P1 exp and the presence of an inner seta on the male P2 enp-1 as in the type-species.

Actopsyllus sp. nov. differs from the type-species in the position of the P1 enp-1 seta and the setation of the P2-P5. In the male, the second segment of the endopod has an additional strong seta not found in *A. longipes*. *Actopsyllus* also has two rather than three segments in the A2 exopod.

As an aside, Gee & Fleeger (1990) identified the presence of a tube pore on the male P3 exp-3 as a common sexual dimorphism within the Diosaccidae. They were able to find tube pores in several species for which the structure had not been previously reported. Although they considered it pertinent, they were unable to examine any *Actopsyllus* specimens. After careful examination, we could find no tube pore, other pore, nor hyaline spine present on the male P3 exp-3 of *Actopsyllus* sp. nov.

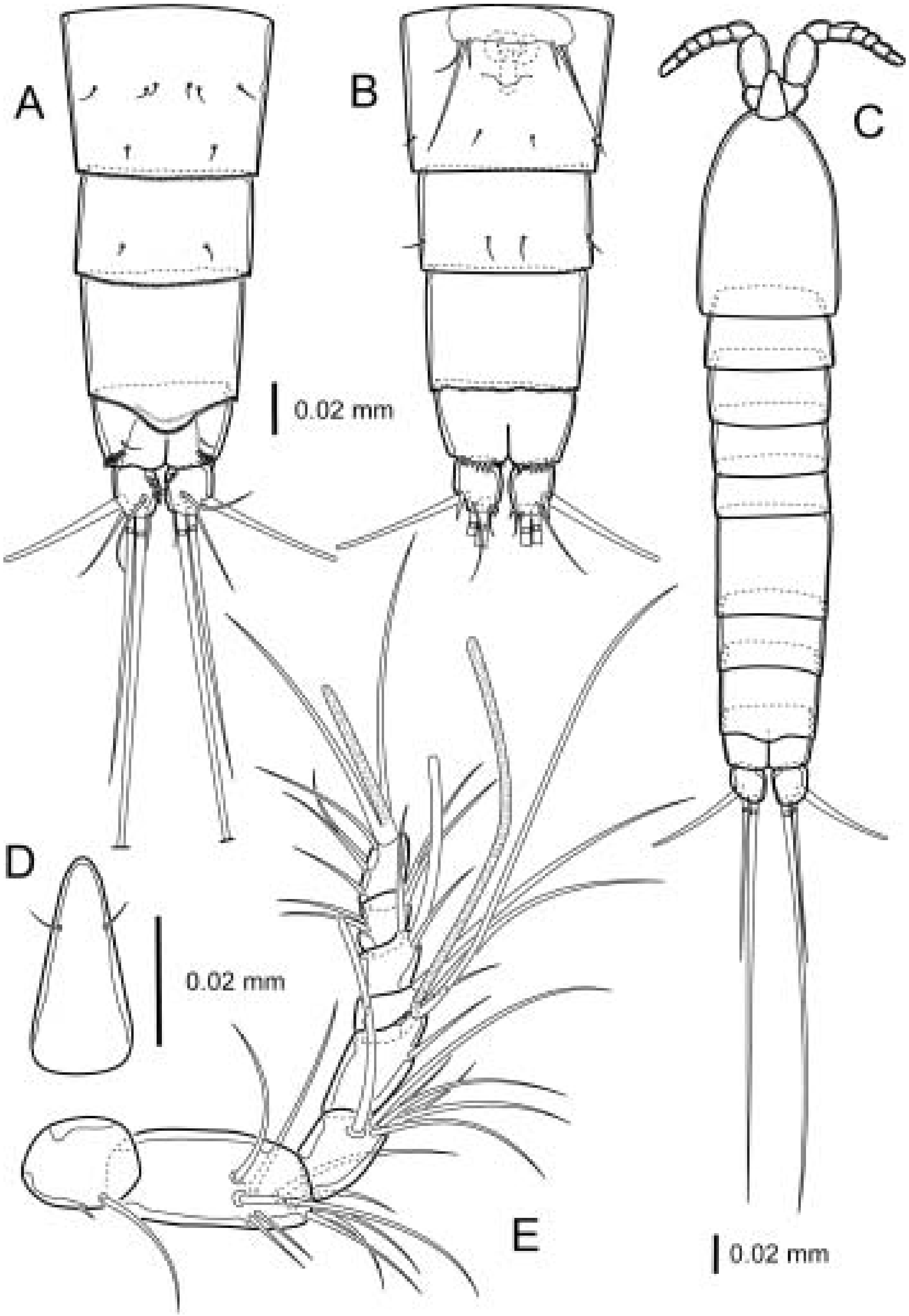


Fig. 2.1. *Protopsammotopa* sp. nov. Female: A. Urosome, Dorsal; B. Urosome, Ventral; C. Habitus; D. Rostrum; E. Antennule

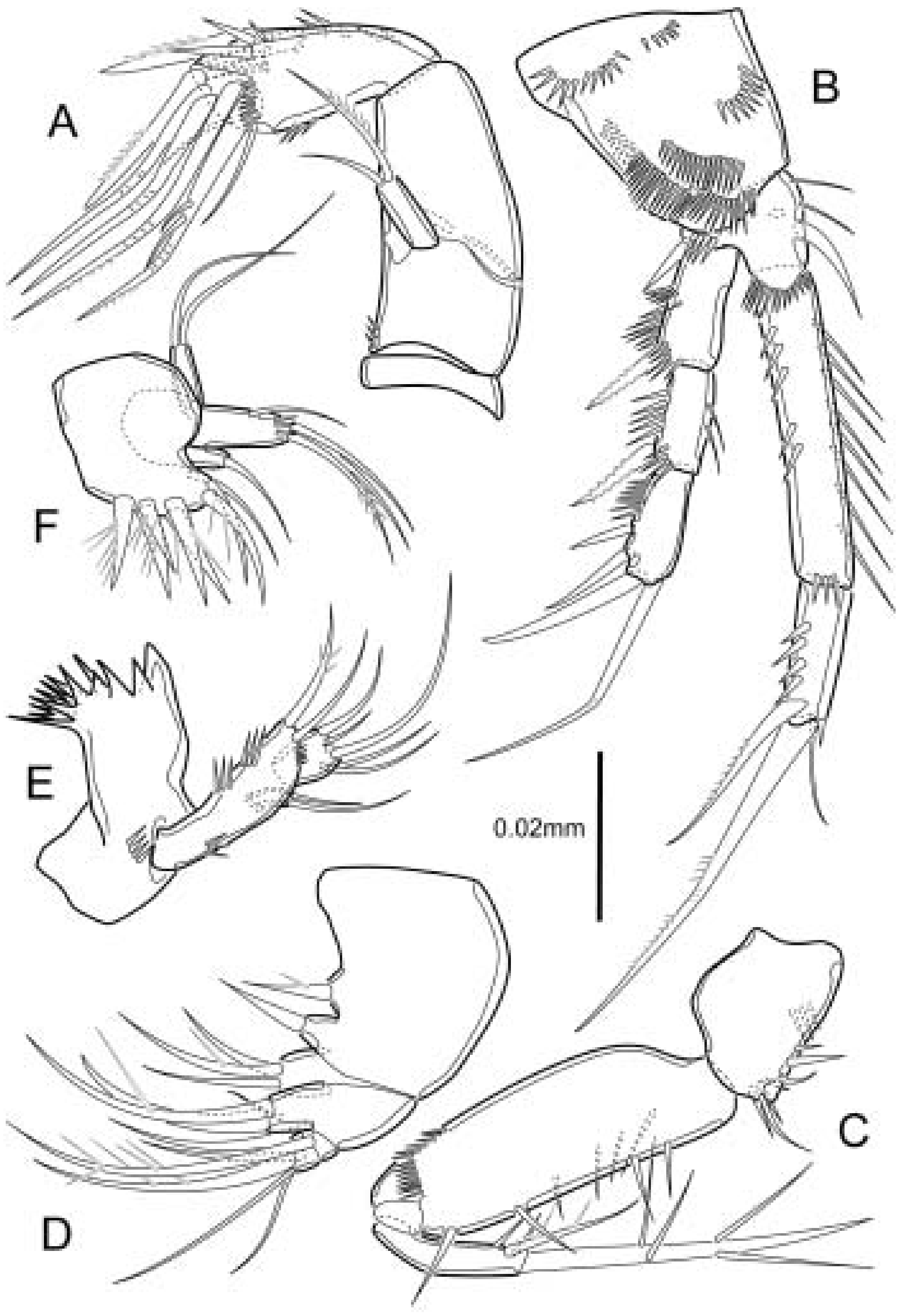


Fig. 2.2. Protopsammotopa sp. nov. Female: A. Antenna; B. P1; C. Maxilliped; D. Maxilla; E. Mandible; F. Maxillule

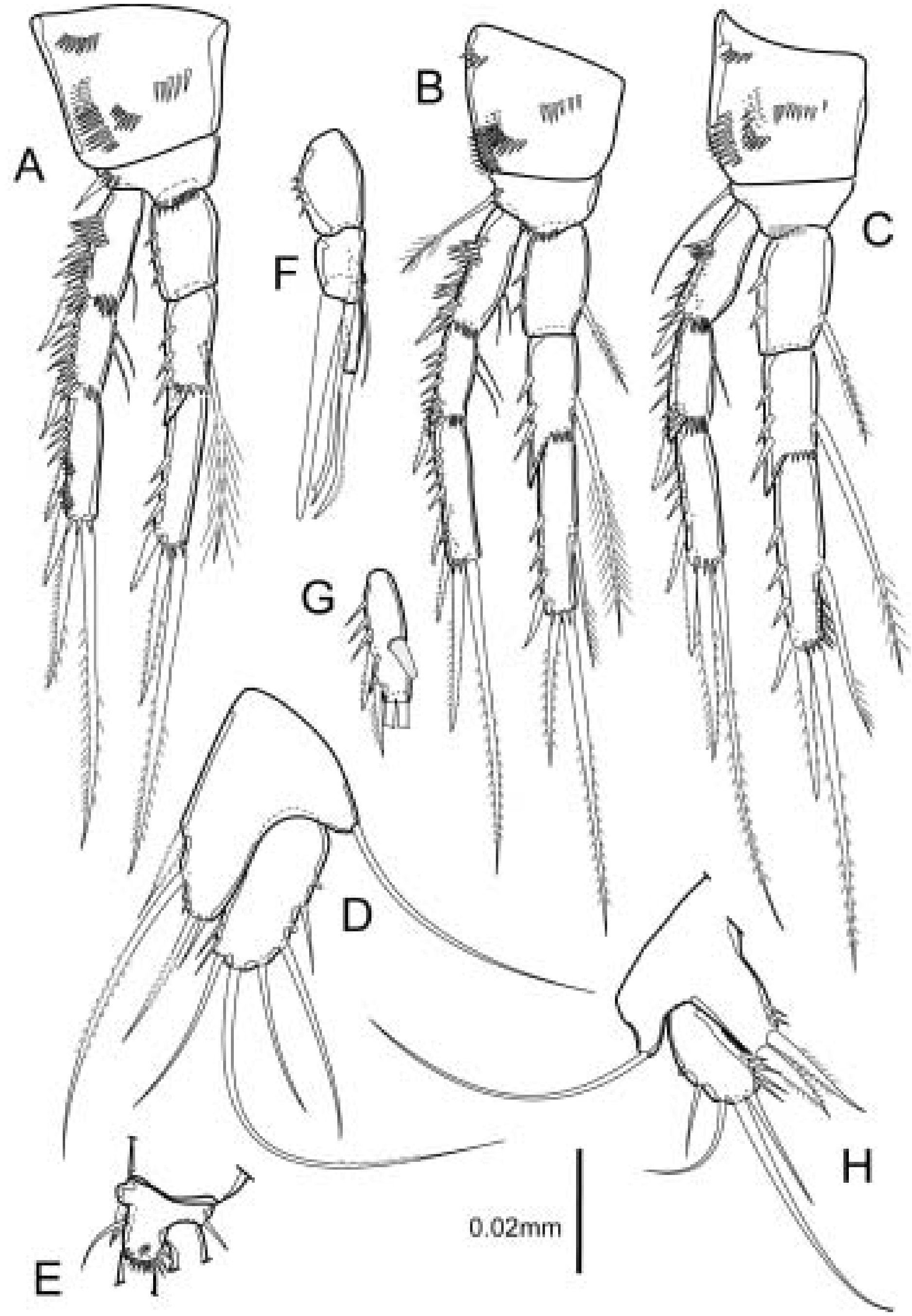


Fig. 2.3. *Protopsammotopa* sp. nov. Female: A. P2; B. P3; C. P4; D. P5. Male: E. P1 Basis; F. P2 Endopod; G. P3 Exp-3; H. P5

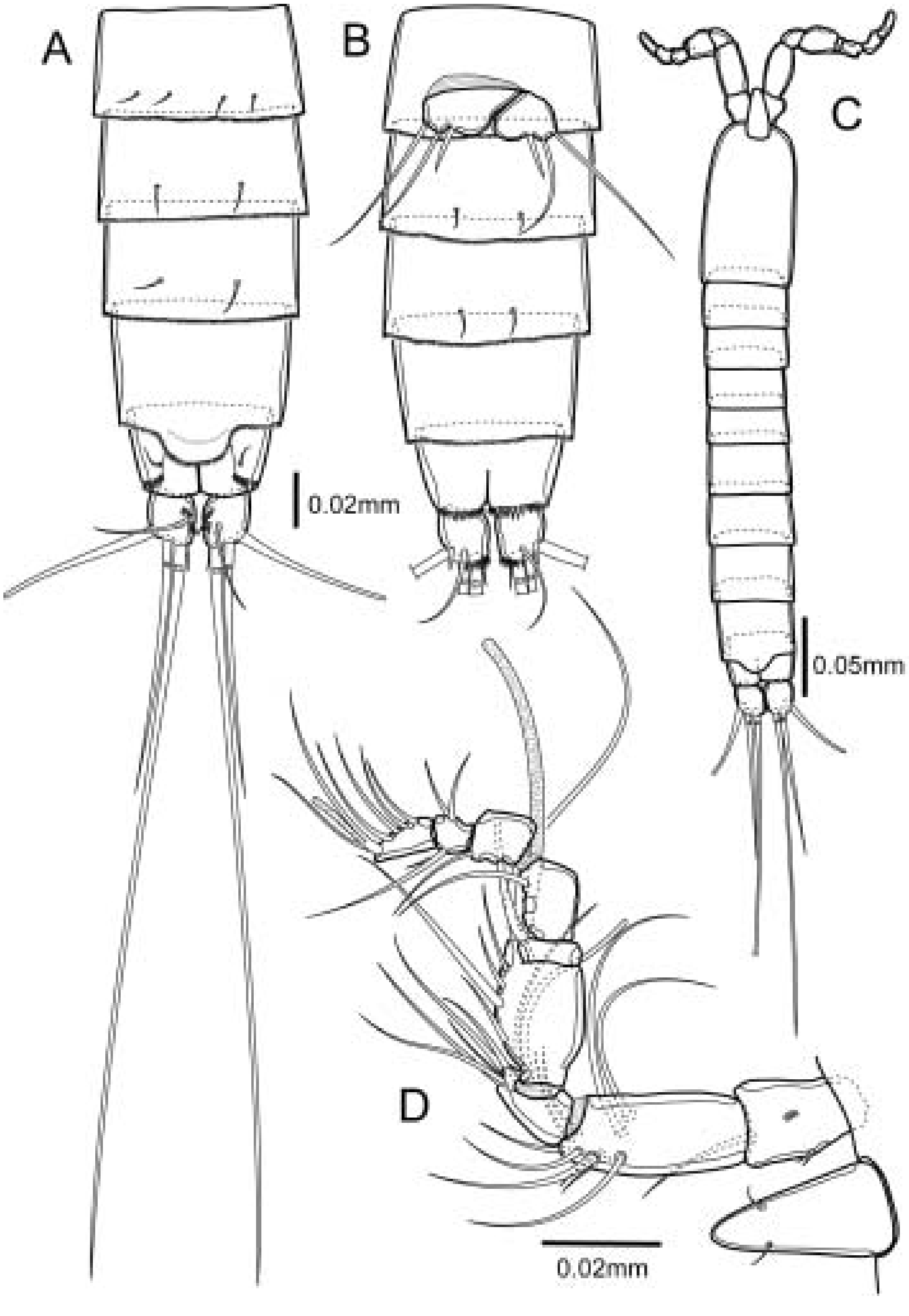


Fig. 2.4. *Protopsammotopa* sp. nov. Male: A. Urosome, Dorsal; B. Urosome, Ventral; C. Habitus; D. Rostrum and Antennule

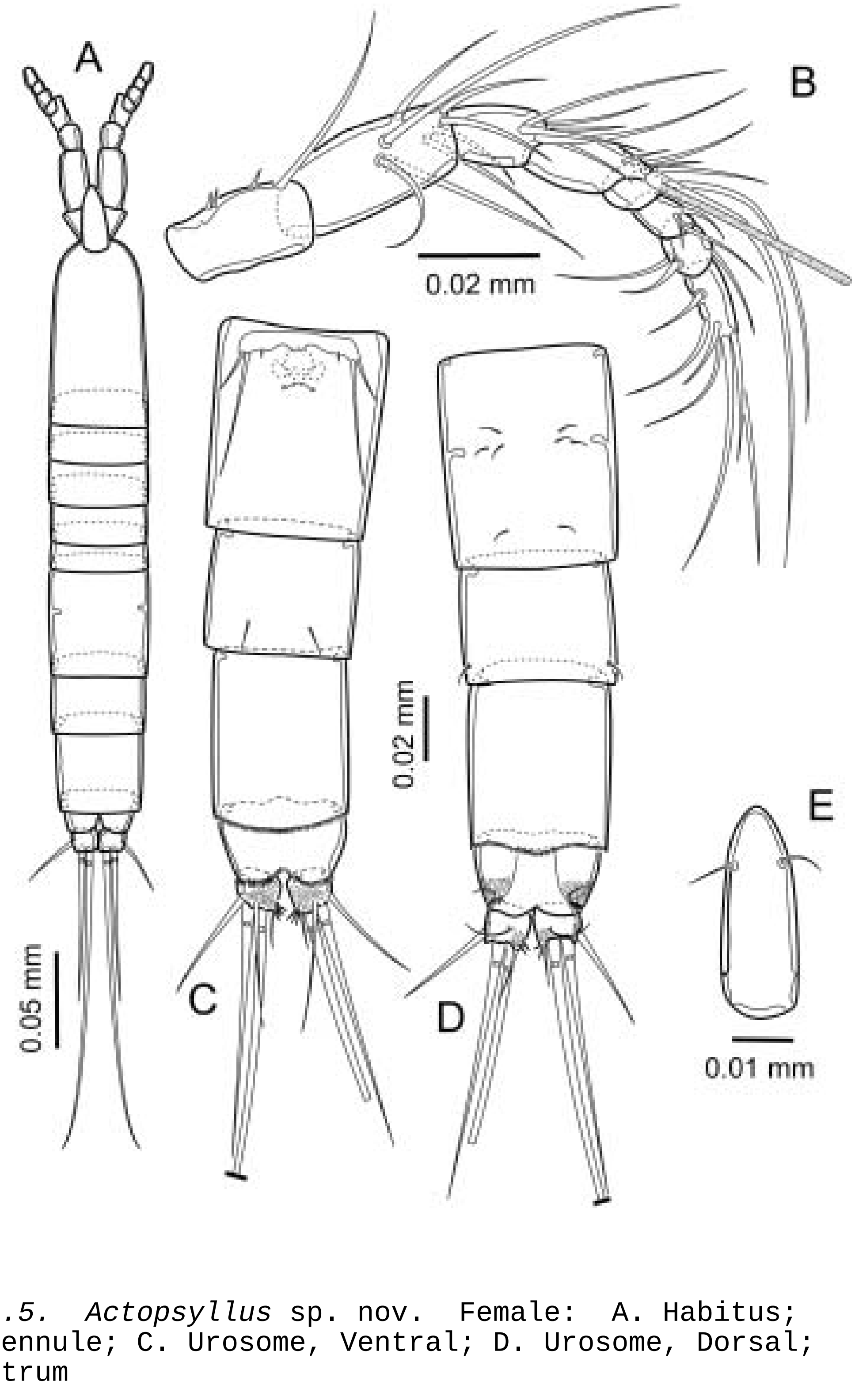


Fig. 2.5. *Actopsyllus* sp. nov. Female: A. Habitus; B. Antennule; C. Urosome, Ventral; D. Urosome, Dorsal; E. Rostrum

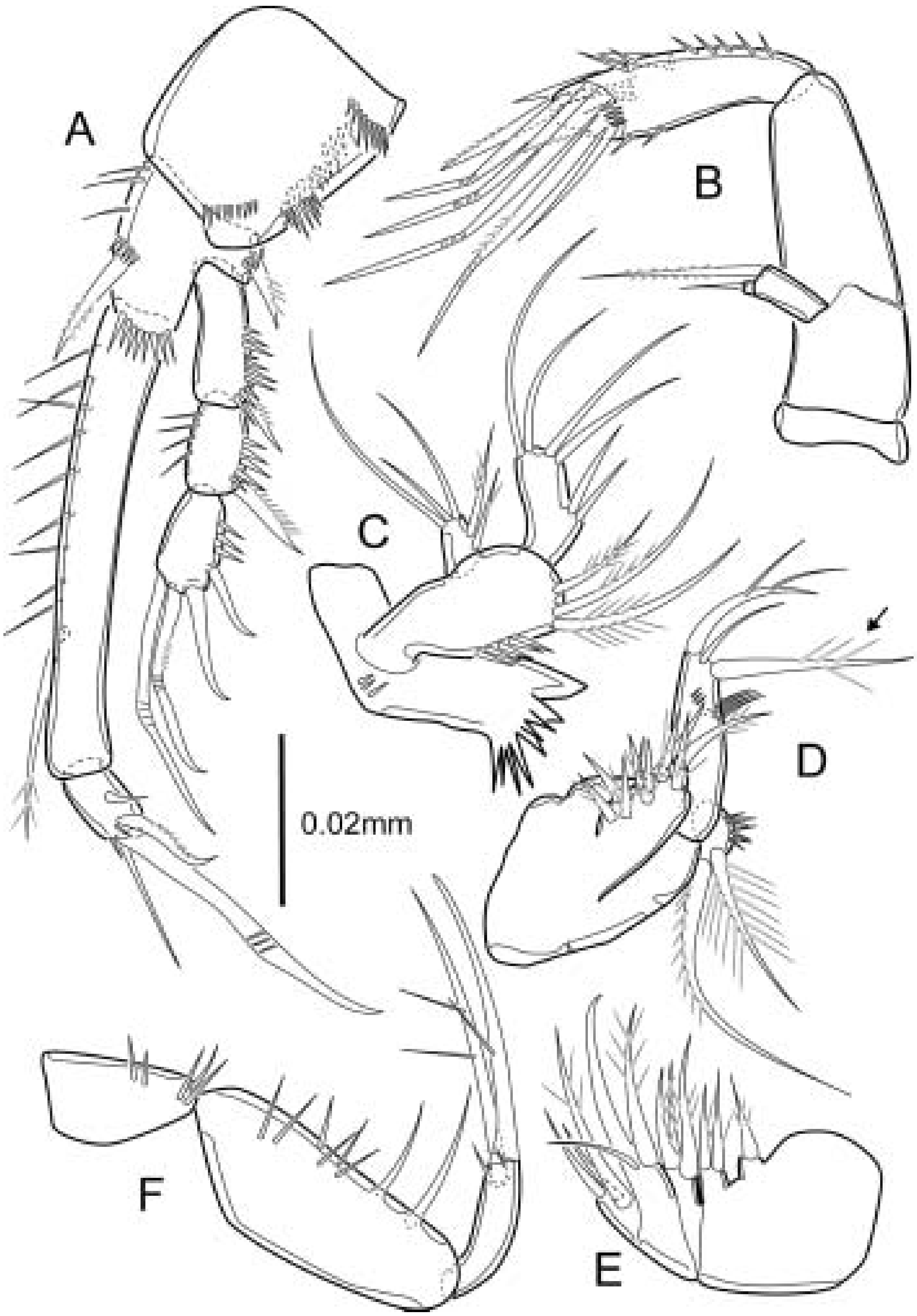


Fig. 2.6. *Actopsyllus* sp. nov. Female: A. P1; B. Antenna; C. Mandible; D. Maxillule (arrow indicates endopod represented by single seta); E. Maxilla; F. Maxilliped.

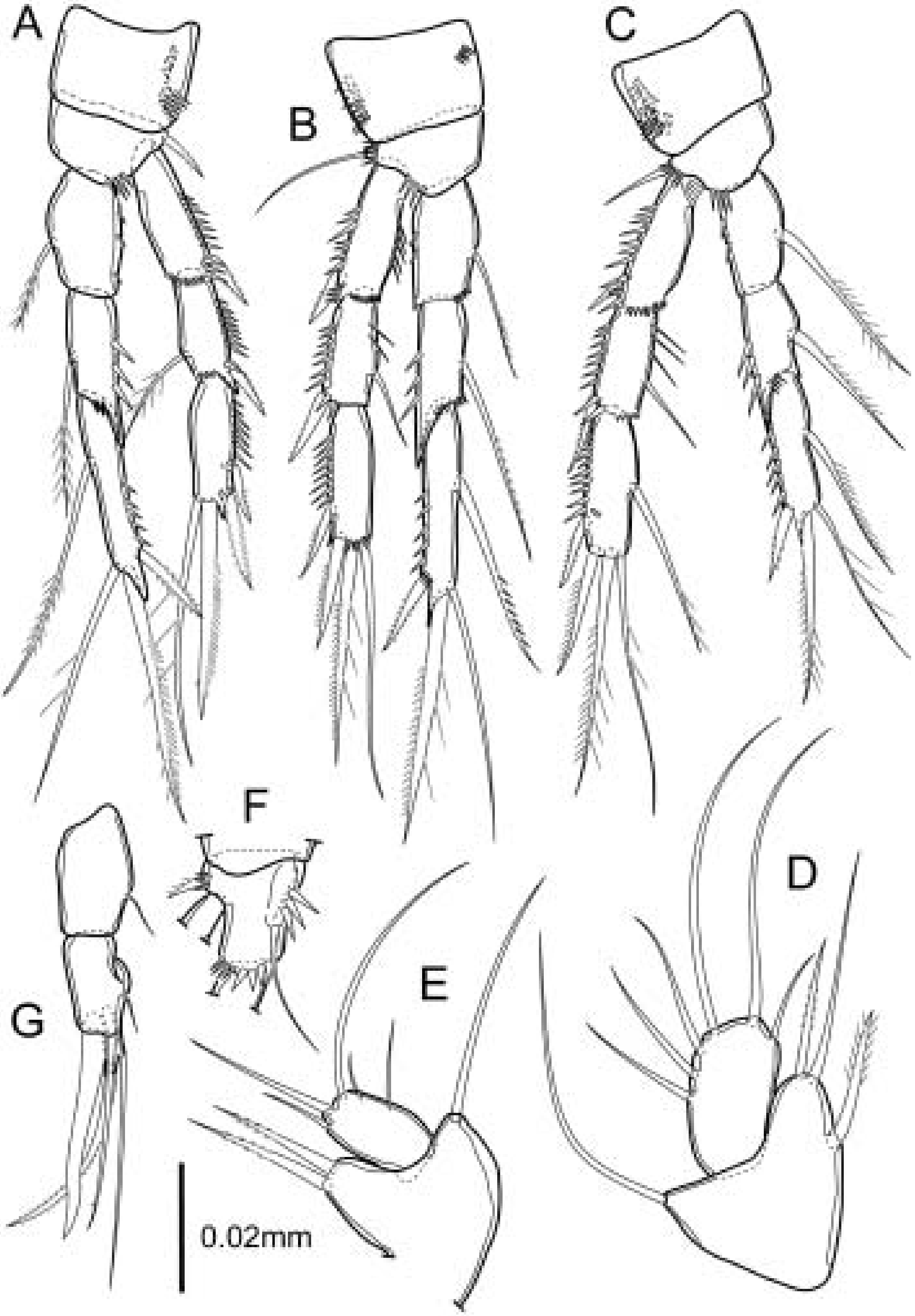


Fig. 2.7. *Actopsyllus* sp. nov. Female: A. P2; B. P3; C. P4; D. P5. Male: E. P5; F. P1 Basis; G. P2 Endopod

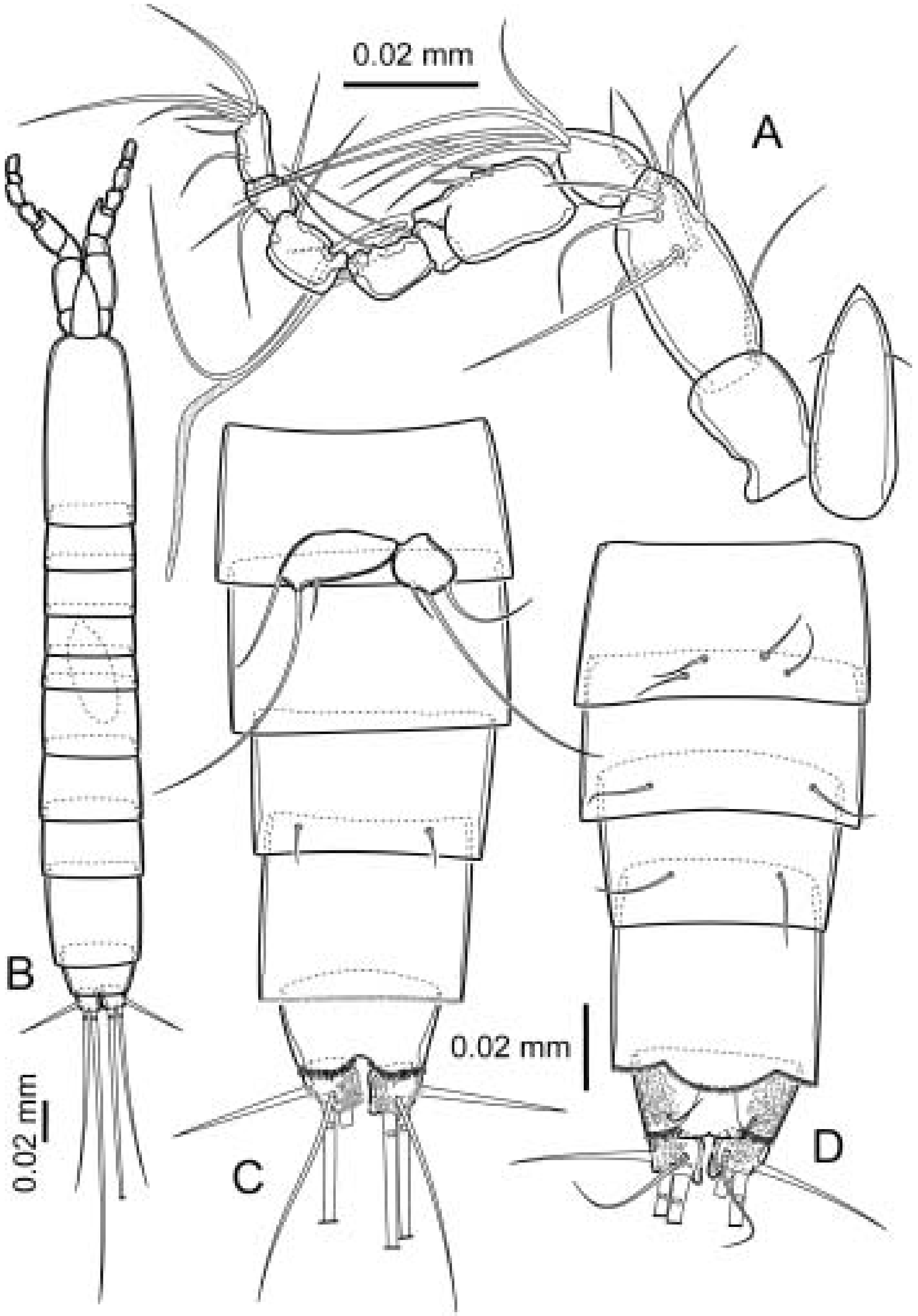


Fig. 2.8. *Actopsyllus* sp. nov. Male: A. Rostrum and Antennule; B. Habitus; C. Urosome, Ventral; D. Urosome, Dorsal

CHAPTER 3

RESPONSE OF TWO HARPACTICOID COPEPODS (FAMILY DIOSACCIDAE) TO A SIMULATED WINTER STORM

Introduction

The traditional concept of the meiobenthos as obligate residents of the seabed has given way to the discovery that it consists of dynamic communities that also can comprise part of the water-column fauna. This change in view has led to the examination of the mechanisms by which meiofauna enter the water column. Several studies have focused on the ability of meiofauna to actively emerge from the sediment (*e.g.*, Armonies, 1988a) and the factors that influence emergence behavior (*e.g.*, Armonies, 1988b, 1988c; Walters, 1991). Other studies have examined the passive erosion of meiofauna through physical processes (Palmer & Molloy, 1986; Palmer, 1992; Guidi-Guivard & Buscail, 1995). Passive entrainment may be voluntary and thus akin to active emergence with both processes allowing meiofauna to escape unfavorable habitats (Kern, 1990). Potential benefits of entering the water column include relief from crowded habitats (Service & Bell, 1987), maximized dispersal (Dobbs & Vozarik, 1983; Chandler & Fleeger, 1983; Palmer, 1988), greater access to mates (Bell *et al*., 1988; Bell *et al*., 1989), and access to planktonic food (Decho, 1986; Pace & Carman, 1996; Suderman & Thistle, 1998). Suspended meiofauna are passively deposited into depressions (Savidge & Taghon, 1988; Sun & Fleeger, 1994; Fleeger *et al*., 1995) as are particles similar in size to their food (Huettel *et al*., 1996), so meiofauna that enter the water column would receive the additional benefit of increased food once they reenter the seabed. Possible risks of entering the water column include expatriation (Palmer & Gust, 1985), mortality due to predation (McCall & Fleeger, 1995), and energy usage outweighing energy acquisition (Thistle *et al*., 1995b).

Although active emergence behavior has received much attention, the study of passive erosion and particularly meiofauna response to flow (*i.e.*, avoidance of erosion by burrowing or voluntary entrainment) has been limited, with contradictory results (Palmer, 1984; Palmer & Molloy, 1986; Foy & Thistle, 1991). Most work on the passive erosion of meiofauna has focused on tidal (*e.g.*, Palmer & Brandt, 1981) or stream effects (*e.g.*, Palmer & Gust, 1985). Prior to Thistle *et al.*'s (1995a) paper, no experimental response of meiofauna to storms had been reported, although storms represent a potentially important mechanism of passive erosion (see also Hall, 1994). Winter storms on continental shelves in temperate regions have large spatial scales and occur several times per month (Sherwood *et al.*, 1994). The flow created by these storms reworks the layer of sediment in which meiofauna predominantly live (Sherwood *et al.*, 1994; Huys *et al.*, 1986), leading potentially to the erosion of the indwelling meiofauna (Barnett, 1968; Palmer, 1992). Meiofauna that allow themselves to be passively eroded would enjoy the benefits of entering the water column outlined above. Animals that instead burrow deeper into the seabed to avoid entrainment would not reap these benefits, but they would avoid the risks of entering the water column. Moving deeper within the sediments, however, potentially brings its own risks such as reduced food (Joint *et al.*, 1982) and adversely low oxygen levels (Hicks & Coull, 1983).

Thistle *et al.* (1995a) experimentally examined the response of harpacticoid copepods, a major component of the meiobenthos (Hicks & Coull, 1983), to storm conditions. Their results suggested that, although most harpacticoid copepods do not appear to burrow deeper into sediments in order to avoid erosion, the males of a few species might in fact move deeper into the seabed in an attempt to escape erosive flow. Later work (Bouck & Thistle, in press) revealed that a “species” that appeared to avoid erosion in this study actually consisted of two separate species. The two species are from the same family and look quite similar, although they are not congeners. Storms are potentially such large influences on meiofaunal community structure and information on species’ responses is so limited, it seemed worthwhile to reanalyze Thistle *et al.*'s (1995a) data in light of this taxonomic discovery.

Methods

In the original study, Thistle *et al*. (1995a) chose a field site in the northern Gulf of Mexico, off the Florida panhandle (29° 40.63’N, 84° 22.80’W), at 18 m depth (Fig. 3.1). They defined a 3-m by 10-m plot for study that had sediment comprised of unvegetated, moderately sorted, medium sand with <1% silt-clay by weight. This region is exposed to winds strong enough to ripple the sediment several times per month during the winter (December - March), and reworking occurred to depths greater than 3 cm. Thistle *et al*. (1995a) sampled the sediment with hand-held corers and found that the bulk of the harpacticoids were located in the reworked layer, the great majority inhabiting depths less than 1 cm. They determined the rate of sediment erosion during storms at this site (> 2 mm per 5 minutes) by converting a field-measured, near-bottom-pressure time series into a peak horizontal speed (found to be 35 cm s^{-1} during a storm) and observing erosion at representative speeds in an oscillatory water tunnel.

After confirming and quantifying storm-induced erosive flow at their field site, Thistle *et al*. subjected harpacticoid copepods from the site to either non-storm or storm flows simulated in a laboratory flume to test for a burrowing response to erosive flow. They conducted both a low-speed (non-storm) and a high-speed (storm) run on 6 dates. For each run, two randomly collected, 15.5-cm^2 cores were mounted in a laboratory flume with the tops of the corers and the sediment in them flush with the bottom of the flume. All water flowing out of the flume passed through a 50-μm sieve, which collected the harpacticoids that had left the cores.

For the low-speed runs, the cores were subjected to an average friction velocity (U_*) of 0.6 cm s^{-1}. Five minutes after establishing the flow regime, the downstream portion of the flume was brushed into the 50-μm sieve, which was then replaced with a fresh sieve. This first sieve contained harpacticoids that may have eroded during the establishment of the flow regime. After an additional 75 minutes, the flume was brushed again, and the sieve was removed. This second sieve contained harpacticoids that either had eroded or had actively emerged from the sediment. The cores were removed from the flume and sectioned in 2-mm increments to 4 cm.

For the high-speed runs, the cores were subjected to the low speed for 5 minutes (after which the flume was brushed and harpacticoids collected as above), then the high-speed flow regime (average $U_* = 1.9$ cm s^{-1}) was established and run for 75 minutes. During this time, sediment eroded at a rate of 2 mm per 5 minutes. Every 5 minutes, the flume was brushed, the sieve was replaced, and the cores were extruded 2 mm to bring the sediment flush again with the flume’s bottom. Over the course of the run, 3 cm of sediment were collected in 2-mm increments. After the run was complete, an additional 1 cm of sediment was sliced from the cores in 2-mm increments.

The samples from both runs, either 2-mm sediment sections or sieve contents, were sorted for harpacticoids. Adults were then identified to working species and archived. For this paper, I examined the archived harpacticoids previously identified as working species 240, *Pholenota* cf. *spatulifera*. I identified them as either *Actopsyllus* sp. nov. or *Protopsammotopa* sp. nov., and constructed depth profiles for each sex and run. As in Thistle *et al*. (1995a), I used parametric *t*-tests for hypothesis testing for each species and sex.

Results

To test for migration deeper into the sediment, I compared the median depths of harpacticoids in both treatments separately for each sex. I also applied the Bonferroni procedure for multiple testing (total number of tests = 22, including the comparisons made in Thistle *et al*., 1995a) to ensure an overall significance level of 5% (*i.e*., individual tests had an alpha • 0.002 to judge significance). For the *Actopsyllus* sp. nov. males, there was no significant increase in depth in response to the high flow treatment (paired, 1-tailed *t*-test, p=0.141; Fig. 3.2). *Actopsyllus* sp. nov. females showed no significant downward movement during the high-speed treatment (paired, 1-tailed *t*-test, p=0.202; Fig. 3.2). For *Protopsammotopa* sp. nov. males, there was a significant increase in depth in response to the high flow treatment (paired, 1-tailed *t*-test, p=0.001; Fig. 3.2). This result remained significant under the Bonferroni procedure. The average movement of *Protopsammotopa* sp. nov. males downward was 11 mm. *Protopsammotopa* sp. nov. females showed no significant downward movement during the high-speed treatment (paired, 1-tailed *t*-test, p=0.191;

Fig. 3.2). The median depths used in the statistical analysis are given as layers in Table 3.1.

During the data analysis, *Actopsyllus* sp. nov. appeared to occur deeper within the sediment than *Protopsammotopa* sp. nov. To test this suspicion, I compared median depths for each species from 4 monthly samples taken from the field site during the winter. Although, for each sample, the *Actopsyllus* sp. nov. median depth was greater than that for *Protopsammotopa* sp. nov., the low number of samples produced a suggestive but not significant result (paired, 2-tailed *t*-test, p=0.072). (See Fig. 3.3 for depth profile). The median depths for the low-speed treatment can be considered equivalent to field samples (Thistle, *et al*., 1995). When the median depths for each species are compared with the results for the low-speed treatment, *Actopsyllus* sp. nov. occurs at a significantly greater depth than *Protopsammotopa* sp. nov. (paired, 2-tailed *t*-test, p<0.02). The average median depth of *Actopsyllus* sp. nov. was 9 mm greater than that for *Protopsammotopa* sp. nov. in the low-flow treatment. (See Fig. 3.4 for depth profile).

Discussion

Reanalyzing Thistle *et al*.'s (1995a) experiment yielded two interesting results. Firstly, two morphologically similar and phylogenetically related species were found to have different responses to storm conditions. The relatively shallower occuring *Protopsammotopa* sp. nov. males burrowed deeper into the sediment in response to higher flow levels, but the relatively deeper *Actopsyllus* sp. nov. males made no significant similar movement downward. This difference implies that for *Protopsammotopa* sp. nov. males, the costs of suspension outweigh the benefits whereas for *Actopsyllus* sp. nov. males, suspension is a neutral or beneficial event.

One hypothesis for the difference in response between the two species follows from the discovery of their relative stratification within the sediment. Harpacticoid vertical segregation has been suggested as a method of avoiding interspecific competition (Hicks & Coull, 1983). *Protopsammotopa* sp. nov. may be the better competitor, dominating a shallower, more desirable habitat (*i.e.* containing more, higher quality food; Joint *et al*., 1982) with *Actopsyllus* sp. nov. forced to a greater depth. When a storm presents the opportunity to escape a relatively poor habitat and exploit a better habitat (*i.e*. recently enriched with food; Huettel, 1996) for a brief time until competition is re-established, *Actopsyllus* sp. nov. may allow itself to be eroded. The costs of suspension may be minimal in comparison with the benefits of resettling in a higher quality habitat. *Protopsammotopa* sp. nov., however, already occupies a higher-quality habitat and thus avoiding suspension may be its best choice.

Another explanation for the difference in response may be that *Actopsyllus* sp. nov. males reside at a limiting border with downward migration prohibited by food and oxygen levels. *Actopsyllus* sp. nov. was present, however, in deeper sediment layers (4-7 cm) that were not included in the experiment’s analysis (Thistle, *et al*., unpublished), so a refuge appears to be available to burrowing harpacticoids.

Finally, experimental artifact may be responsible for the lack of a significant result in the movement of *Actopsyllus* sp. nov. The experiment compared harpacticoids from only the first 4cm of depth. Any downward movement beyond 4cm would not affect the calculation of the median depth for that run. For a deeper occuring species, such as *Actopsyllus* sp. nov., when most individuals move below the experimentally imposed 4cm limit, a few shallow outliers will have an undue influence on the calculation of the median and skew it upwards.

A second interesting result of the reanalysis of Thistle *et al*.’s (1995a) experiment is the difference in response to erosive flow shown by *Protopsammotopa* sp. nov. males and females. *Protopsammotopa* sp. nov. males moved deeper into the sediment in response to increased flow, but the females did not. Thus males and females of this species must experience different costs and/or benefits associated with suspension and escaping erosion. Thistle *et al*. (1995b) found that suspension had an energetic cost (indicated by reduced neutral lipids) for harpacticoid males as a class but not for females. They hypothesized that females may either reduce their metabolic rate or feed while suspended, whereas males do neither because they are occupied with looking for mates. I identified the *Protopsammotopa* sp. nov. individuals from Thistle *et al*.’s (1995b) experiment, matched them with their corresponding neutral lipid scores, and found no significant reduction in neutral lipids when either males or females were suspended. It must be noted, however, that many of the runs had no *Protopsammotopa* sp. nov.

individuals, so the potential of a Type-II error is substantial. Thus the possibility remains that *Protopsammotopa* sp. nov. follows the general trend found by Thistle *et al*. (1995b) with suspension extracting costs from males but not females, and the different responses of *Protopsammotopa* sp. nov. males and females to erosive flow may be due to these differing costs.

The reanalysis of Thistle *et al*. (1995a) demonstrates the importance of good taxonomy in marine ecological studies. Several researchers have concluded that high taxonomic resolution is not important in certain areas of study, such as pollution impacts and biological monitoring (*e.g*., Somerfield & Clarke, 1995; Rumohr & Karakassis, 1999). The use of lower taxonomic resolution when identifying individuals, particularly identification to family level, has been proposed as a means of reducing the costs of bioassessment (Hewlett, 2000; Karakassis & Hatziyanni, 2000; Mistri & Rossi, 2000) although the resulting loss of information concerning species richness reduces the sensitivity of bioassessment methods (Cao, *et al*., 1998). In the present study, analysis at the family level masked differing responses between two species. In the original study, where the two species were unknowingly pooled at the family level, a significant burrowing response to erosion was merely implied. In the reanalyis, the response was shown to be highly significant for one of the species. High taxonomic resolution was essential for producing this result.

That species-level analyis is necessary for understanding the ecology of marine organisms is becoming clearer as more sibling species are discovered that vary in important ecological aspects. For example, niche diversification was found to be more important in maintaining diversity in coral reefs than previously thought when nominal species of coral were discovered to contain two or more separate species, each with unique depth distributions, growth forms, physiological characteristics, and/or resident zooxanthellae (Knowlton & Jackson, 1994). Good taxonomy affects not only basic research but also the applications of marine science. Reef protection and restoration is hindered by poor taxonomy or analyis at low taxonomic resolution (Knowlton, 2001), and ignorance of sibling species can result in inconsistent recovery of marine compounds for pharmaceutical research (Davidson & Haygood, 1999). Although good taxonomy can be costly and time consuming, it is necessary for productive research.

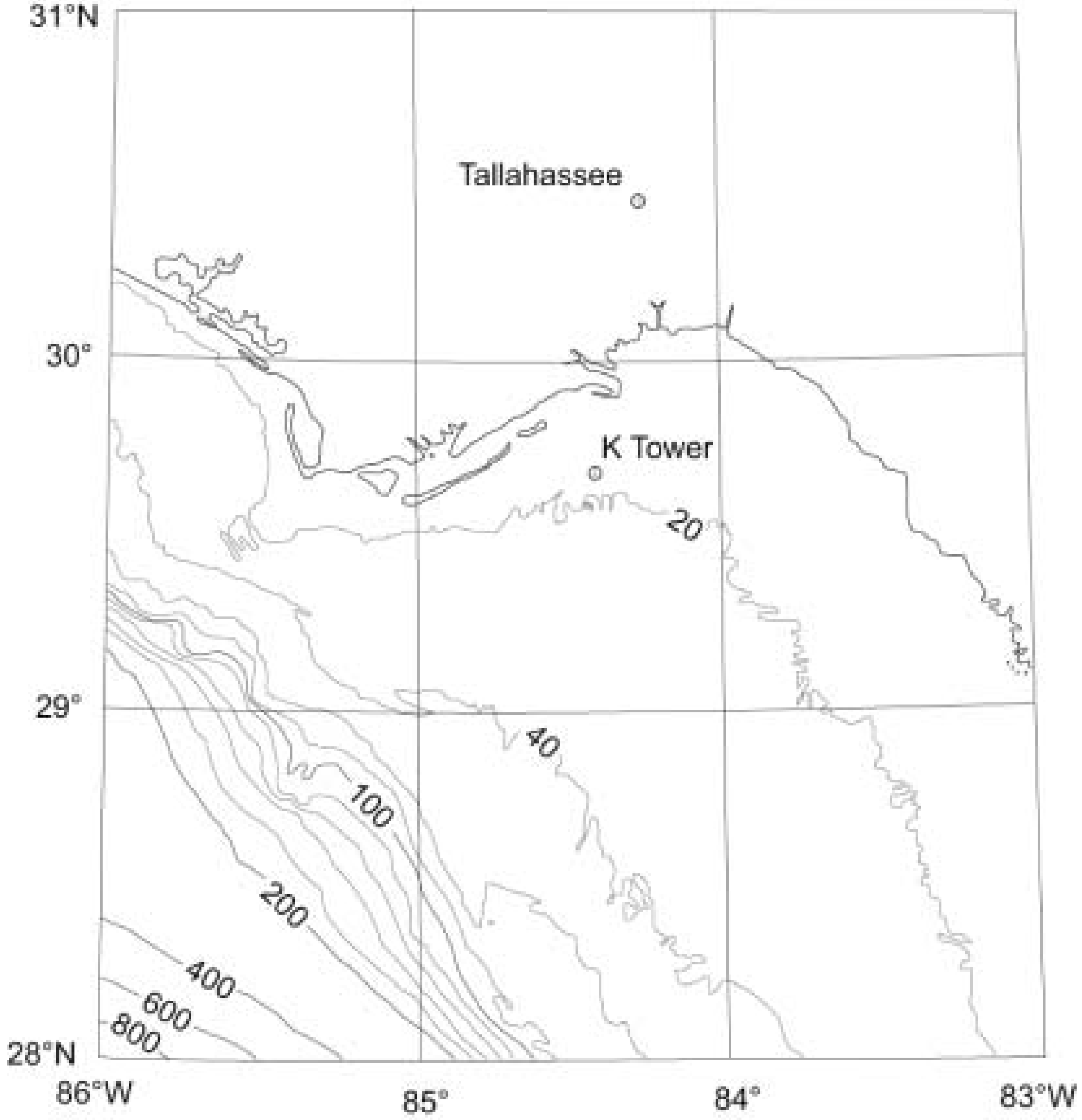


Fig. 3.1. Chart of Thistle *et al*.'s Study Area. Contours are in meters. Study site is indicated by an offshore circle labeled K Tower.

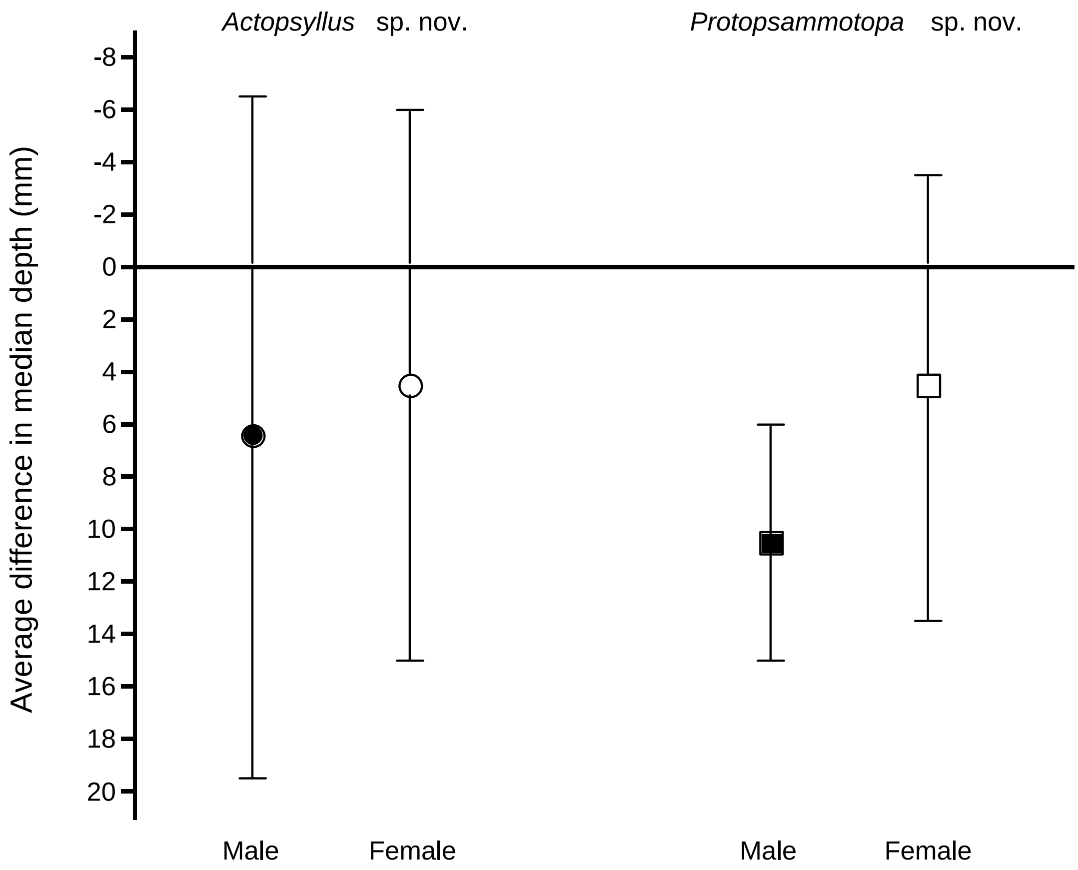


Fig. 3.2. Difference in Harpacticoid Median Depth (High Flow Median Depth Minus Low Flow Median Depth) by Species and Sex. Points indicate average median depth over 6 runs. Error bars indicate ±1 standard deviation.

Table 3.1. Median Depth and Number of Individuals for Low Flow and High Flow Treatments for Each Run. When the median depth occured between layers, a single number indicating the boundary is given. (*e.g*. “12” indicates the median depth was between the 10-12 mm and the 12-14 mm layers). When no individuals were present in one of the treatments of a run, that run was not used in the analysis for that particular sex and species.

	Actopsyllus sp. nov.				*Protopsammotopa* sp. nov.			
	Male		Female		Male		Female	
Run	Low	High	Low	High	Low	High	Low	High
1	26-28	34-36	30-34	30-34	20-22	34-36	18-20	18-20
	5	4	3	7	7	10	4	2
2	26-28	32-34	34-36	30-32	14-16	26-28	—	14-16
	5	3	1	7	8	6	0	2
3	22-24	32-34	12-14	34-36	14-16	22-24	12	24
	3	3	1	5	4	37	4	6
4	10-12	30-32	30-32	32	16-18	20-22	20-22	14-16
	3	17	5	14	15	9	9	4
5	20-22	2-4	22-24	14-16	6-8	16	10	22-24
	5	2	9	9	7	2	8	5
6	20-22	32-34	12-14	28	8-10	26	—	12-14
	5	7	5	6	1	6	0	3

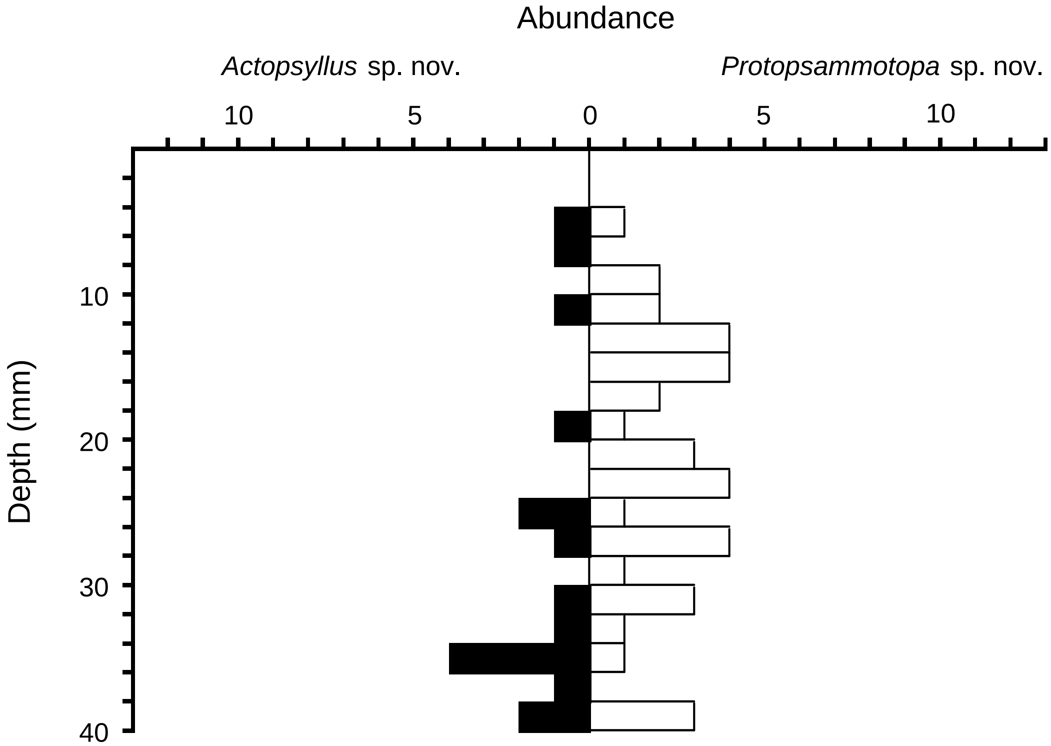


Fig. 3.3. Abundances of Adults by Depth Suggestive of a Deeper Distribution for *Actopsyllus* sp. nov. than for *Protopsammotopa* sp. nov. Data are pooled from four months (November, January, February, and March).

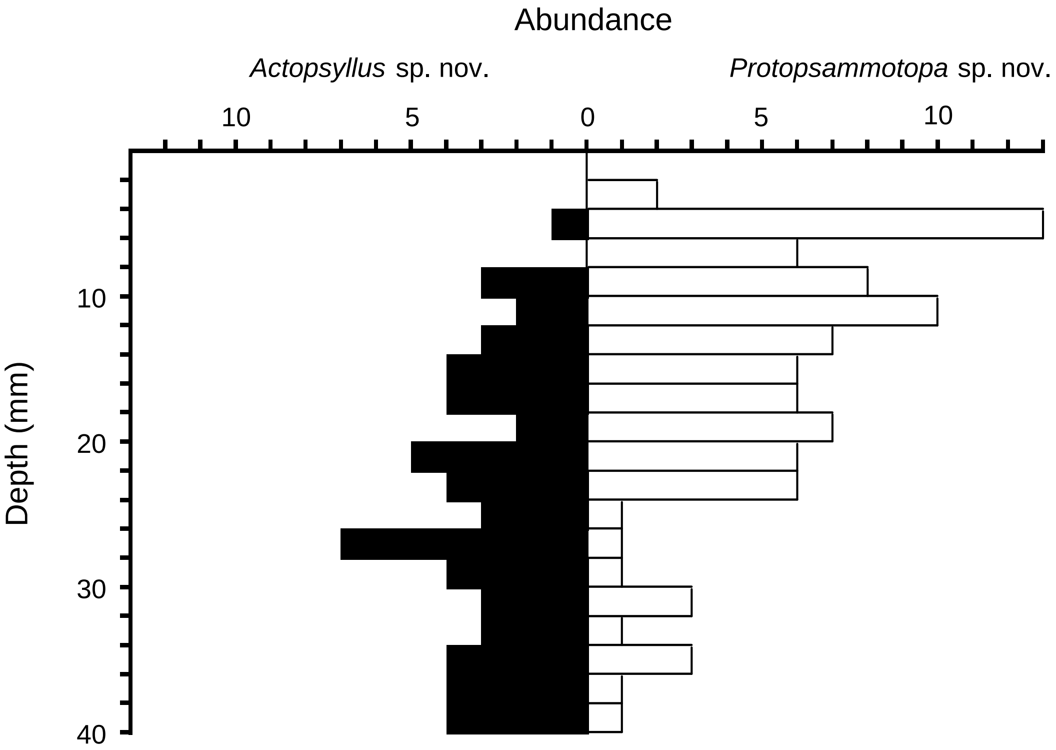


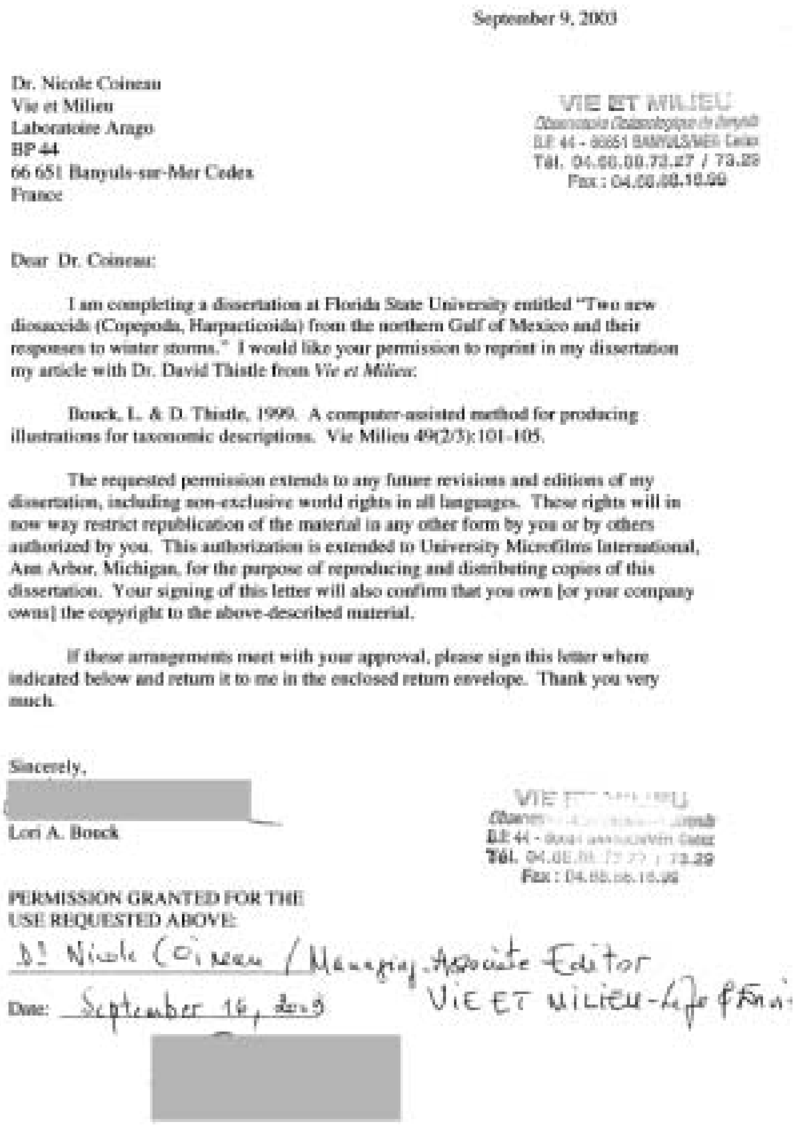
Fig. 3.4. Abundances of Adults by Depth Showing a Deeper Distribution for *Actopsyllus* sp. nov. than for *Protopsammotopa* sp. nov. Data are pooled from six runs of the low-flow treatment.

CONCLUSION

The conclusions of this dissertation follow the three-part structure of the manuscript. Firstly, the use of illustration software in species descriptions can increase the productivity of taxonomists. Secondly, two new diosaccids, *Protopsammotopa* sp. nov. and *Actopsyllus* sp. nov., were found and described. Thirdly, although phylogenetically related and morphologically similar, these two diosaccids showed differing responses to storm conditions; *Actopsyllus* sp. nov. showed no response, but *Protopsammotopa* sp. nov. males migrated deeper in the sediment when exposed to erosive flow.

APPENDIX A

COPYRIGHT PERMISSION FORM



September 9, 2003

Dr. Nicole Coineau
Vie et Milieu
Laboratoire Arago
BP 44
66 651 Banyuls-sur-Mer Cedex
France

VIE ET MILIEU
Observatoire Océanologique de Banyuls
B.P. 44 - 66651 BANYULS/MER Cedex
Tél. 04.68.88.73.27 / 73.29
Fax : 04.68.88.16.99

Dear Dr. Coineau:

I am completing a dissertation at Florida State University entitled "Two new diosaccids (Copepoda, Harpacticoida) from the northern Gulf of Mexico and their responses to winter storms." I would like your permission to reprint in my dissertation my article with Dr. David Thistle from *Vie et Milieu*:

Bouck, L. & D. Thistle, 1999. A computer-assisted method for producing illustrations for taxonomic descriptions. Vie Milieu 49(2/3):101-105.

The requested permission extends to any future revisions and editions of my dissertation, including non-exclusive world rights in all languages. These rights will in now way restrict republication of the material in any other form by you or by others authorized by you. This authorization is extended to University Microfilms International, Ann Arbor, Michigan, for the purpose of reproducing and distributing copies of this dissertation. Your signing of this letter will also confirm that you own [or your company owns] the copyright to the above-described material.

If these arrangements meet with your approval, please sign this letter where indicated below and return it to me in the enclosed return envelope. Thank you very much.

Sincerely,

[redacted]

Lori A. Bouck

VIE [illegible]
B.P. 44 - [illegible]
Tél. [illegible] / 73.29
Fax : 04.68.88.16.99

PERMISSION GRANTED FOR THE
USE REQUESTED ABOVE:

Dr Nicole Coineau / Managing Associate Editor
VIE ET MILIEU - Life & Envi

Date: September 16, 2003

[redacted]

APPENDIX B

COPYRIGHT PERMISSION FORM

CRUSTACEANA

INTERNATIONAL JOURNAL OF CRUSTACEAN RESEARCH

COPYRIGHT ASSIGNMENT

Please read the notes below and then sign and return this form.

COPYRIGHT: Notes for contributors

1. The Journal's policy is to acquire copyright in all contributions. There are two reasons for this:
   - (a) ownership of copyright by one central organization tends to ensure maximum international protection against infringement;
   - (b) it also ensures that requests by third parties to reprint a contribution, or part of it, are handled efficiently and in accordance with a general policy which is sensitive both to any relevant changes in international copyright legislation and to the general desirability of encouraging the dissemination of knowledge.
2. In assigning your copyright, you are not forfeiting your right to use your contribution elsewhere. This you may do without seeking permission and subject only to normal acknowledgement to the journal.
3. It is understood that in a few cases copyright will be held by the contributor's employer. If so, the journal requires non-exclusive permission to deal with request from third parties.

Name: Dr. D. Thistle

Address:

Dept. of Oceanography
Florida State University
TALLAHASSEE, Florida 32306-4320
U. S. A.

Assignment of Copyright

In consideration of the publication in CRUSTACEANA of my contribution entitled:

"Two new diosaccids (Copepoda, Harpacticoida) from the northern Gulf of Mexico."

I hereby assign to Koninklijke Brill full copyright in all forms and media in the said contribution. I guarantee that my article has never been published elsewhere and that the text, the illustrations and any other materials included in the article do not infringe on any existing copyright.

Proofs

I agree to refrain from introducing any changes in the proofs other than corrections of errors of fact. I recognize that if I introduce other changes or extensive changes I am liable to be charged for the costs of making them.

Signed: [redacted]

Date: 1 Aug 03

Please return to:

Dr. J.C. von Vaupel Klein / CRUSTACEANA
Editorial Board Administrative Office
Beetslaan 32
NL-3723 DX BILTHOVEN

REFERENCES

Adobe Systems Incorporated, 1997. Adobe Illustrator 7.0 User Guide. 1-362. (Adobe Systems Incorporated, San Jose, California).

Alspach, T., 1997. Illustrator 7 Bible. 1-964. (IDG Books Worldwide, Inc., Foster City, California).

Armonies, W., 1988a. Active emergence of meiofauna from intertidal sediment. Mar. Ecol. Prog. Ser., 43: 151-159.

——, 1988b. Hydrodynamic factors affecting behavior of intertidal meiobenthos. Ophelia, 28: 183-193.

——, 1988c. Physical factors influencing active emergence of meiofauna from boreal intertidal sediment. Mar. Ecol. Prog. Ser., 49: 277-286.

Barnett, P. R. O., 1968. Distribution and ecology of harpacticoid copepods of an intertidal mud flat. Int. Rev. Ges. Hydrobiol., 53: 177-209.

Bell, S. S., G. R. F. Hicks & K. Walters, 1988. Active swimming in meiobenthic copepods of seagrass beds: geographic comparisons of abundances and reproductive characteristics. Marine Biology, 98: 351-358.

——, 1989. Experimental investigations of benthic reentry by migrating meiobenthic copepods. J. Exp. Mar. Biol. Ecol., 130: 291-303.

Bouck, L. & D. Thistle, 1999. A computer-assisted method for producing illustrations for taxonomic descriptions. Vie Milieu, 49: 101-105.

——, in press. Two new diosaccids (Copepoda, Harpacticoida) from the northern Gulf of Mexico. Crustaceana.

Bouck, L., D. Thistle & R. Huys, 1999. Systematics and phylogeny of *Zausodes* C. B. Wilson, 1932 (Copepoda, Harpacticoida, Harpacticidae), including three new species from the northern Gulf of Mexico. Bull. nat. Hist. Mus. Lond. (Zool.), 65: 73-122.

Butman, C. A. & J. T. Carlton, 1995. Marine biological diversity: some important issues, opportunities and critical research needs. Rev. Geophys., Suppl., July: 1201-1209.

Cao, Y, D. D. Williams & N. E. Williams, 1998. How important are rare species in aquatic community ecology and bioassessment? Limnol. Oceanogr., 43: 1403-1409.

Chandler, G. T. & J. W. Fleeger, 1983. Meiofaunal colonization of azoic estuarine sediment in Louisiana: mechanisms of dispersal. J. Exp. Mar. Biol. Ecol., 69: 175-188.

Decho, A. W., 1986. Water-cover influences on diatom ingestion rates by meiobenthic copepods. Mar. Ecol. Prog. Ser., 33: 139-146.

Davidson, S. K. & M. G. Haygood, 1999. Identification of sibling species of the bryozoan *Bugula neritina* that produce different anticancer bryostatins and harbor distinct strains of the bacterial symbiont “*Candidatus endobugula sertula*”. Biol. Bull., 196: 273-280.

Disney, H., 1998. Rescue plan needed for taxonomy. Nature, 394: 120.

Dobbs, F. C. & J. M. Vozarik, 1983. Immediate effects of a storm on coastal infauna. Mar. Ecol. Prog. Ser., 11: 273-279.

Fleeger, J. W., P. O. Yund & B. Sun, 1995. Active and passive processes associated with initial settlement and post-settlement dispersal of suspended meiobenthic copepods. J. Mar. Res., 53: 609-645.

Foy, M. S. & D. Thistle, 1991. On the vertical distribution of a benthic harpacticoid copepod:

field, laboratory, and flume results. J. Exp. Mar. Biol. Ecol., 153: 153-163.

Gaston, K. J. & R. M. May, 1992. Taxonomy of taxonomists. Nature, 356: 281-282.

Geddes, D. C., 1968. *Protopsammotopa norvegica*, a new genus and species of interstitial harpacticoid copepod from western Norway. Sarsia, 36: 69-76.

Gee, J. M. & J. W. Fleeger, 1990. *Haloschizopera apprisea*, a new species of harpacticoid copepod from Alaska, and some observations on sexual dimorphism in the family Diosaccidae. Trans. American microsc. Soc., 109(3): 282-299.

Guidi-Guilvard, L. D. & R. Buscail, 1995. Seasonal survey of metazoan meiofauna and surface sediment organics in a non-tidal turbulent sublitorral prodelta (northwestern Mediterranean). Cont. Shelf Res., 15: 633-653.

Hall, S. J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogr. Mar. Biol. Ann. Rev., 32: 179-239.

Hedgepeth, J. W., R. J. Menzies, C. H. Hand & M. D. Burkenroad, 1953. On certain problems of taxonomists. Science, 117: 17-18.

Hewlett, R., 2000. Implications of taxonomic resolution and sample habitat for stream classification at a broad geographic scale. J. N. Amer. Benth. Soc., 19: 352-361.

Hicks, G. R. F. & B. C. Coull, 1983. The ecology of marine meiobenthic harpacticoid copepods. Oceanogr. Mar. Biol. Ann. Rev., 21: 67-175.

Huettel, M., W. Ziebis & S. Forster, 1996. Flow-induced uptake of particulate matter in permeable sediments. Limnol. Oceanogr., 41: 309-322.

Huys, R., 1987. Studies on the Cylindropsyllidae (Copepoda, Harpacticoida). 1. The status of *Leptastacus laticaudatus* Nicholls. Zool. Scr., 16: 155-166.

Huys, R. & G. A. Boxshall, 1991. Copepod evolution. Ray Soc. Publs., 159: 1-486. (Ray Society, London).

Huys, R., R. L. Herman & C. Heip, 1986. Seasonal fluctuations in vertical distribution and breeding activity of a subtidal harpacticoid community in the Southern Bight, North Sea. Neth. J. Sea Res., 20: 375-383.

Joint, I. R., J. M. Gee & R. M. Warwick, 1982. Determination of fine-scale vertical distribution of microbes and meiofauna in an intertidal sediment. Mar. Biol., 72: 157-164.

Karakassis, I. & E. Hatziyanni, 2000. Benthic disturbance due to fish farming analyzed under different levels of taxonomic resolution. Mar. Ecol. Prog. Ser., 203: 247-253.

Kern, J. C., 1990. Active and passive aspects of meiobenthic copepod dispersal at two sites near Mustang Island, Texas. Mar. Ecol. Prog. Ser., 60: 211-223.

Knowlton, N., 2001. Who are the players on coral reefs and does it matter? The importance of coral taxonomy for coral reef management. Bull. Mar. Sci., 69: 305-308.

Knowlton, N. & J. B. C. Jackson, 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? TREE 9: 7-9.

Kunz, H., 1971. Harpacticoiden (Crustacea Copepoda) von einem Sandstrand Angolas. Zool. Anz., Leipzig, 186(5/6): 348-359.

Lambshead, P. J. D., 1993. Recent developments in marine benthic biodiversity research. Oceanus, 19: 5-24.

Lang, K., 1965. Copepoda Harpacticoida from the Californian Pacific coast. Kung. Svenska Vetensk. Akad. Hand., 10: 1-560.

Mayr, E. and P. D. Ashlock, 1991. Principles of Systematic Zoology. 1-475. (McGraw-Hill, Inc., New York).

McCall, J. N. & J. W. Fleeger, 1995. Predation by juvenile fish on hyperbenthic meiofauna: a review with data on post-larval *Leiostomus xanthurus*. Vie Milieu, 45: 61-73.

Mielke, W., 1992. Description of some benthic Copepoda from Chile and a discussion on the relationships of *Paraschizopera* and *Schizopera* (Diosaccidae). Microfauna Marina, 7: 79-100.

——, 1995. Species of the taxon Schizopera (Copepoda) from the Pacific coast of Costa Rica. Microfauna Marina, 10: 89-116.

Mistri, M. & R. Rossi, 2000. Levels of taxonomic resolution and choice of transformation sufficient to detect community gradients: an approach to hard-substrata benthic studies. Ital. J. Zool., 67: 163-167.

Pace, M. C. & K. R. Carman, 1996. Interspecific differences among meiobenthic copepods in the use of microalgal food resources. Mar. Ecol. Prog. Ser., 143: 77-86.

Palmer, M. A., 1984. Invertebrate drift: behavioral experiments with intertidal meiobenthos. Mar. Behav. Physiol., 10: 235-253.

——, 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. Mar. Ecol. Prog. Ser., 48: 81-91.

——, 1992. Incorporating lotic meiofauna into our understanding of faunal transport processes. Limnol. Oceanogr., 37: 329-341.

Palmer, M. A. & R. R. Brandt, 1981. Tidal variation in sediment densities of marine benthic copepods. Mar. Ecol. Prog. Ser., 4: 207-212.

Palmer, M. A. & G. Gust, 1985. Dispersal of meiofauna in a turbulent tidal creek. J. Mar. Res., 43: 179-210.

Palmer, M. A. & R. M. Molloy, 1986. Water flow and the vertical distribution of meiofauna: a flume experiment. Estuaries, 9: 225-228.

Pfannkuche, O. & H. Thiel, 1988. Sample processing. In: R. P. Higgins & H. Thiel, Introduction to the study of meiofauna: 134-145. Smithsonian Institution Press, Washington, D. C.

Rumohr, H. & I. Karakassis, 1999. Comparison of multivariate patterns: different taxonomic levels in macrofaunal analysis versus sediment profiling imagery (SPI). Mar. Ecol. Prog. Ser., 190: 125-132.

Savidge, W. B. & G. L. Taghon, 1988. Passive and active components of colonization following two types of disturbance on intertidal sandflat. J. Exp. Mar. Biol. Ecol., 115: 137-155.

Service, S. K. & S. S. Bell, 1987. Density-influenced active dispersal of harpacticoid copepods. J. Exp. Mar. Biol. Ecol., 114: 49-62.

Sherwood, C. R., B. Butman, D. A. Cacchione, D. E. Drake, T. F. Gross, R. W. Sternberg, P. L. Wiberg & A. J. Williams III, 1994. Sediment-transport events on the northern California continental shelf during the 1990-1991 STRESS experiment. Cont. Shelf Res., 14: 1057-1062.

Shirayama, Y., T. Kaku & R. P. Higgins, 1993. Double-sided microscopic observation of meiofauna using an HS-Slide. Benthos Research, 44: 1-44.

Somerfield, P. J. & K. R. Clarke, 1995. Taxonomic levels in marine community studies, revisted. Mar. Ecol. Prog. Ser., 127: 113-119.

Suderman, K. & D. Thistle, 1998. Adult female harpacticoid copepods maintain their energy reserves by feeding while suspended during storms. Mar. Ecol. Prog. Ser., 164: 245-252.

Sun, B. & J. W. Fleeger, 1994. Field experiments on the colonization of meiofauna into sediment depressions. Mar. Ecol. Prog. Ser., 110: 167-175.

Thistle, D., G. L. Weatherly & S. C. Ertman, 1995. Shelf harpacticoid copepods do not escape into the seabed during winter storms. J. Mar. Res., 53: 847-863.

Thistle, D., G. L. Weatherly, A. Wonnacott & S. C. Ertman, 1995. Suspension by winter storms has an energetic cost for adult male benthic harpacticoid copepods at a shelf site. Mar. Ecol. Prog. Ser., 125: 77-86.

Walters, K., 1991. Influences of abundance, behavior, species composition, and ontogenetic stage on active emergence of meiobenthic copepods in subtropical habitats. Mar. Biol., 108: 207-215.

Wells, J. B. J., 1967. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. Trans. Roy. Soc. Edinburgh, 67(7): 189-358.

——, 1977. *Protopsammotopa wilsoni* n. sp. (Copepoda, Harpacticoida) and the fate of the type material of *Goffinella stylifer* C. B. Wilson. Crustaceana, 32(2): 200-202.

Wells, J. B. J. & G. C. Rao., 1976. The relationship of the genus *Schizopera* Sars within the family Diosaccidae (Copepoda: Harpacticoida). Zool. Journ. Linnean Soc., 58: 79-90.

BIOGRAPHICAL SKETCH

Lori Bouck was born May 11, 1969 to Donald and Dorothy Cook in Savannah, Illinois. She graduated valedictorian from Mira Mesa High School in San Diego, California in 1987. She attended Massachusetts Institute of Technology on a Navy ROTC scholarship during her freshman year and completed her undergraduate studies at University of California, Davis. She received a Bachelor of Science with High Honors, Phi Beta Kappa, in Biological Sciences with a minor in Linguistics in 1991. She studied the following year in a teaching credential program at University of California, Davis, supported by a Paul Douglas scholarship, and received a teaching credential in Life Sciences in 1992. From 1992 to 1995 she taught middle school in Yuba City, California. She was accepted to the oceanography program at Florida State University in 1995, supported by a research assistantship. She received a Master of Science in Oceanography in 1998. After completing her doctoral dissertation, she will teach community college students and continue to describe new species of harpacticoid copepod.