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Horton H. Hobbs, Jr. (29 March 1914–22 March 1994). Biographical notes

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Abstract.—The 211 papers and abstracts published by the late Horton H. Hobbs, Jr., are cited and annotated by a list of new taxa published in each paper. An alphabetical list of taxa named by Hobbs is provided; the repository and the catalogue number are cited for each holotype. Hobbs's reminiscences of his introduction to crayfishes and his early work are summarized from an oral interview.

To many who knew him and his work, the name Horton H. Hobbs, Jr., (Figs. 1, 2) is synonymous with freshwater crayfishes of North America. Indeed, to many he was known affectionately as "crawdaddy." The enormous advances in our understanding of the systematics, distribution, and evolution of crayfishes that resulted from his studies in a career spanning six decades are well known to all astacologists. Perhaps less known are his contributions on other groups, including freshwater and cave shrimps and crabs, and ostracod associates of crayfishes.

Hobbs's studies resulted in the recognition of many new taxa: 1 new family (Cambaridae); 38 new genera and subgenera (1 genus of palaemonid shrimp, *Neopalaemon*; 8 genera of entocytherid ostracods; and 29 genera and subgenera of North American crayfishes); and 286 species (168 crayfishes, 104 entocytherids, 8 caridean shrimps, and 6 freshwater crabs).

A remarkable number of Hobbs's contributions are monographs or other book-length works on a wide variety of topics:

1942d, crayfishes of Florida, 179 pp.;

1964a, Hobbs & Villalobos, crayfishes of Cuba, 59 pp.;

1969a, Chace & Hobbs, freshwater and terrestrial decapods of the West Indies, 258 pp.;

1971b, entocytherid ostracods of Mexico and Cuba, 55 pp.;

1972a, subgenera of *Procambarus,* 22 pp.;

1972g, crayfishes of North and Middle America, 173 pp.;

1974c, checklist of North and Middle American crayfishes, 161 pp.;

1977b, Hobbs & Peters, entocytherid ostracods of North Carolina, 73 pp.;

1977c, Hobbs, Hobbs III, & Daniel, troglobitic decapods of the Americas, 183 pp.;

1981b, crayfishes of Georgia, 549 pp.;

1982e, Hobbs & Hart, revision of *Atya,* 143 pp.;

1986a, Andolshek & Hobbs, entocytherid ostracods of Georgia, 43 pp.;

1987b, revision of *Astacoides,* 50 pp.;

1989g, illustrated checklist of American crayfishes, 236 pp.

Hobbs's productivity led a European student to remark to one of us (R.B.M.) "Oh, Hobbs. He writes faster than I can read."

Hobbs III recalls (in litt.) that during the late 1930s, Hobbs's father held him by his ankles while Hobbs slithered into a vertical crack (River Bed Cave, Columbia County, Florida) to collect *Procambarus* (*O.*) *pallidus*—he then pulled him back out (for other anecdotes by and about Hobbs, see Hobbs 1986d).

Fig. 1. Hobbs collecting after the 1967 meeting of the Association of Southeastern Biologists, Columbia, South Carolina (J. F. Fitzpatrick, Jr. and Hobbs III).

J. F. Fitzpatrick, Jr. (in litt.), provided two other anecdotes. "One day, in the '60s, I think—Hobbs had stopped by to see Miss Peggy on some business while he was en route on some field excursion. Because he was in motion, he did not call or write ahead to announce his arrival. When he knocked on the door in the middle of the day in an active residential neighborhood of a small Virginia city, he found Miss Peggy home alone. The entire conversation, not short, was conducted with him standing on the porch and she behind the cracked door with the chain engaged. To her, 'It just wouldn't be proper to have a man in the house with Miss Lucille away on an errand', even such a true gentleman of long acquaintance as was Hobbs. He delighted in relating this story to those who knew her as an example of her propriety, but he never faulted her behavior; he only respected it in his amusement."

"The other goes back to his graduate student days at Gainesville and reveals a side of his character that only those of us who knew him well knew. He and Archie Carr were classmates and shared an office with a few others. Despite the reticence of his later years, a youthful Archie apparently was animated and outspoken. He had a habit during repeated discussions of rearing back on the hind legs of his wooden chair, and when he made an emphatic point, he would slam the front legs on the floor. The mischievous crew connived to play a trick on Archie with Hobbs surely one of the conspirators if not the actual perpetrator. They got a couple of fireworks 'torpedoes' and clandestinely attached them to the front legs of Archie's chair. When he came in, they led him into a topic to which they knew he would react strongly. True to form, he reared his chair and at an appropriate point slammed the front legs. Archie was attached to the ceiling by his nails as the others rolled on the floor in merriment. Despite this treatment, the group remained friends for their whole lives."

All of us who knew and worked with Horton have many fond remembrances of him. He was the quintessential southern gentleman, always rising when a woman entered his presence. It pained him not to be able to open doors for women, and his female car-poolers were trained to wait at a door if he fell behind them. Elizabeth Nelson remembers that in his last years, in frail condition and walking precariously with a cane, he rushed to open a door for her as she walked by with a small package. She knew that to refuse his offer of assistance would have pained him terribly.

Elizabeth also remembered his expression, a mixture of embarrassment and delight, when he was presented with a pair of boxer shorts with two flies at his retirement party—the idea being that having studied entocytherid ostracods so long he might have developed hemipenes.

Brian Kensley joined Horton on one of his last field trips. "In the fall of 1987, I accompanied Horton on a field trip to eastern Texas. He wanted to complete a survey of the crayfishes of this area, and also gather some data on *Fallicambarus devastator* Hobbs & Whiteman, 1987c, the burrowing crayfish that causes much destruction to fields and lawns. We drove in Horton's car. He would set the speed control, and discourse on the flora and geology of the area we were driving through. Every now and then we would have to stop, so that he could push a net through a puddle next to the road, or to show me a tree with which I was unfamiliar. Between whiles, he recounted incidents from his early days of field collecting and teaching. It was for me a natural history revelation. Arrived in Texas, we met with farmers and agricultural extension officers to gather information on *devastator,* and to dig in the bone-dry, concrete-hard fields dotted with chimneys. This was my primary role. Once I had got down to the water table, Horton would lie stretched out on the ground, one arm reaching 2–3 feet down into the hole for the couple of crayfish at the bottom. We also did a lot of (much easier) digging in stream banks, and this is where I uncovered specimens of a beautiful spotted crayfish which he eventually named for me [*Procambarus* (*Girardiella*) *kensleyi* Hobbs, 1990a]. Hunting season opened while we were in the Neches River area. On the third occasion while we were either walking through the woods, or working at a stream bank, and a

rifle shot rang out nearby, Horton turned to me (I was distinctly edgy at this point) and said: 'Let's go home', which we did, all the way back to northern Virginia, at the sedate speed limit while I absorbed yet more landscape science."

Horton thoroughly enjoyed his martini at cocktail hour (see Fig. 3, showing Horton on his boat, the martini barge, on Lake Barcroft). While one of us (R.B.M.) was living in Tunisia, Horton graciously shared his home with me. On one of my trips back, I noticed that Horton was having a clear cocktail in a 12 oz. glass rather than in his normal martini glass. This appeared strange to me, but I didn't comment on the large drink, assuming that Horton's affinity for martinis had expanded exponentially. Someone told him of my concern, and he had many laughs from the occasion, as he had shifted from martinis to a gin and tonic, with lots of ice, for the summer. I suspect that I took Horton his last martini during his last stay in the hospital. It was in a glass jar, which he gleefully accepted and hid in a drawer so that he could have it at happy hour. Later that day, his daughter Nina visited him, and Horton told her "look what I have." She smelled the jar and asked where he got it, probably knowing full well that I was involved.

Aspects of Hobbs's life and career have been summarized in other obituaries by Fitzpatrick (1995a, 1995b, 1996) and Hoffman (1994). Hobbs's southern manners were characteristic of him. One aspect of his life that was known to those who shared dinner as his guest was his interest (and ability) in baking and cooking. Alan Davidson (1979:432) in North Atlantic Seafood published his recipe for hush puppies. Davidson referred to him as "The scholarly Mr Hobbs."

Cooper & Cooper (1997:616) acknowledged Hobbs's influence: "As always, we are immensely grateful to the late Horton H. Hobbs, Jr., for the splendid lessons he taught (not all of them about decapods)."

Only his colleagues in the Department of Invertebrate Zoology at the National Museum of Natural History are aware of one highlight of Hobbs's career. In 1976 Thomas E. Bowman and Louis S. Kornicker, members of the department's self-appointed SOL Awards Committee, awarded him the "Smithsonian Order of the Lobster." The award celebrates an accomplishment or achievement of outstanding insignificance, something that usually is quite difficult to associate with Hobbs. The award was based on the following series of misadventures.

Hobbs and colleagues C. W. Hart, Jr. and Margaret Walton introduced four new names for the entocytherid ostracod, *Donnaldsoncythere donnaldsonnensis* (Klie, 1931) (see Hobbs & Peters 1977:43, 44 for a synonymy), already burdened by two synonyms, *Entocythere humesi* Hoff, 1943 and *E. pennsylvanica* Hart, 1960, as well as four unavailable names published as erroneous spellings: *E. donnaldsoni* Wolf, 1934–1938; *E. donalsonensis* Rioja, 1943; and *E. donaldsonensis* Tressler, 1947. Hobbs & Walton (1961a) named *E. hiwasseensis* from Georgia; Hart & Hobbs (1961b) named *E. tuberosa* from Tennessee (with the erroneous spelling *tuberculata* in the same paper); Hobbs & Walton (1963b) named *Donnaldsoncythere scalis* from Virginia and *D. ileata* from Virginia.

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Fig. 2. United States crawfish workers, meeting of Association of Southeastern Biologists, Memphis, Tennessee, 19 April 1969 (includes all significant workers with crayfishes and their associated biota, except for Perry C. Holt, who worked on branchiobdellids). From left to right, C. W. Hart, Jr., J. F. Fitzpatrick, Jr., Glen Gentry, Rudolph Prins, Daniel J. Peters, James F. Payne, Raymond W. Bouchard, Jean E. Pugh, Horton H. Hobbs III, Horton H. Hobbs, Jr., Marilyn Black, Martha Reiser Cooper, Joe B. Black, and John E. Cooper (J. F. Fitzpatrick, Jr., R. Prins, and Hobbs III).

Fig. 3. Horton H. Hobbs, Jr. Clockwise, from upper left: Enjoying a crayfish, 1969 (Hobbs III); Gainesville days, undated (Hobbs III); in the field, undated (Hobbs III); on the martini barge with Manning, undated (Daniel J. Peters); in the field, 4 July 1980, photo by Jean Dubois, Belgium (Daniel J. Peters).

Biographical Notes

Here we reproduce part of an Oral History Interview of Hobbs by Pamela M. Henson, Smithsonian Institution Archives, in July 1976. It and the rest of the interview, largely dealing with aspects of his career after he left the University of Florida to go to the University of Virginia in 1946, form Record Unit 9509 in the Smithsonian Institution Archives. The questions are by Henson, the answers by Hobbs.

Question: As we discussed, we can start with some biographical information about you and your education, and how you came to be interested in Crustacea.

Answer: My undergraduate, well, all of my work was done at the University of Florida. It was during the depression years, so when I received my Bachelor's degree I was able to get an assistantship in the department and took my Master's. There was no place to go, so I stayed on and joined the faculty after I took my Master's, teaching the introductory courses in biology. I stayed on for my doctorate; and it took me several years because of residence requirements and working full time, so I got my degree in 1940. I spent one summer at the Mountain Lake Biological Station during that time, doing work with Dr. [Chauncy M.] Gilbert, a course in arthropods.

You asked about my interest in crayfishes. This began when I was a freshman in college. We came to the laboratory exercise dealing with the crayfish; the first day it was external anatomy—had no difficulty whatsoever, everything was beautiful. The second day had to do with internal structures, and the crayfish that I was given apparently had demised with the flood, because it was complete soup inside. So I suppose I was an eager beaver, in part, and I knew that not far from the boarding house where I was living at the time there was a little creek. I went down after school that afternoon and I caught a few crayfishes and brought them back to the room. That evening I made my dissection and everything was as it should be, but I had some crayfish left over and I couldn't see killing them. So I found a jar to put them in (I planned to take them back to the creek the next evening) and put them on my desk where I was studying. In a few minutes I noticed a commotion, and a male and female had gotten together. I watched them for a while, and I said, "Well, maybe I'll get eggs in a few days." And sure enough, within two weeks, eggs were there. About three weeks later the female was carrying the young, and the more I watched them the more interested I became. By the end of that semester, I went to the chairman of the department and told him that I'd become interested in crayfishes and would like to do some work with them. He said, "Well, I know nothing about them but I'll be happy to help you in any way that I can." So that's the way it began, and since 1931, I've looked at not much else.

Question: That is interesting. And I suppose your room turned into a big aquarium?

Answer: No, not really. But strangely enough, I was never able after that time to rear a clutch of eggs to adulthood until after I came to the Smithsonian.

Question: Just chance?

Answer: I didn't know enough about them at that time to do the wrong thing!

Question: That's amazing. But there was no one at the university studying crayfish?

Answer: No, no, there was only one person in the United States at the time. The big crayfish men had died: [Walter] Faxon and [Arnold Edward] Ortmann; and Edwin P. Creaser at Michigan Museum [Museum of Zoology, University of Michigan] was the only person working.

That brings me to my first visit to the Smithsonian [Institution] which might be of some interest to you. In 1935, I went up to the Mountain Lake Biological Station for the summer. I had a letter of introduction from my major professor [J. Speed Rogers] at the University of Florida, and one from Dr. Ivey F. Lewis, who was Dean of the University of Virginia, introducing me to Dr. Waldo [L.] Schmitt [then Head Curator of Zoology at the U. S. National Museum]. So after my stay at the station, I came up to Washington hoping that I might be able to examine the crayfishes. Dr. Schmitt took one look at me . . . I know you wouldn't believe it now, at one time I looked a little young. At the ripe old age of twenty-one I suppose I looked like I was about fifteen. He told me that he would be glad to have me look at the crayfishes, but that I could not open any of the types, couldn't open the bottles. Well I had made that trip at some sacrifice, and Dr. Creaser couldn't identify my material.

Dr. Schmitt was very gracious but not of much help in doing so. Not until 1937, when I convinced Dr. Schmitt that I was a serious worker, did he allow me to come back and examine the type specimens. So I worked for five years on crayfishes not knowing the name of a single crayfish that I was working with!

Question: Oh my goodness! Yes, not having compared them with the ones here.

Answer: I needed to compare them with the types.

Question: Well, you must have come up with some original observations.

Answer: Oh, well, a number of my animals were new. When I started working in Florida I think there'd been about, oh maybe, four species recorded from the state; and when I finished there were forty-two of them.

Question: [Laughter] That's a difference!

Answer: Which labels me perhaps as a splitter.

Question: Yes, but still, there just hadn't been that much work done. There was a paper written by Fenner [A.] Chace [Jr.] at one point about the lack of work in systematics being done in that area during that period [reference to Chace 1951?]. I guess it was not one of the more worked on areas?

Answer: No, it never has been. Crayfishes have never attracted very many people. Those who start, most of them have fallen [by] the wayside after a little bit of work. I've worked on crayfishes I suppose longer than any other human ever has, in terms of number of years spent.

Question: What was the Smithsonian like when you first came here to work on those?

Answer: Oh, it was a delightful place. Of course, my coming from a small town and coming to Washington, in part, I suppose I was much impressed. Dr. Schmitt was most gracious, as were Mr. [Clarence R.] Shoemaker, Mr. [James O.] Maloney, and Miss [Mary Jane] Rathbun.

Question: She was still here?

Answer: She was still here. I can't remember whether I met her or not, but at least I saw her. And Dr. [Leonhard] Stejneger was a marvel. All of them were most gracious and helpful, and as I said, I do not hold it against Dr. Schmitt at all because I suppose I did look like a high school kid who thought he was going to do something.

Question: Right, take apart all the type specimens.

Answer: With this particular group, the group that's dominant in Florida, unless you look at the first pleopods of the males you can't identify the crayfish at all, and through a bottle you couldn't see them.

Question: Were the collections of crayfish at that point fairly extensive here?

Answer: Well certainly nothing in comparison with what we have at the present time. It was perhaps not even the most important collection in the country. The Museum of Comparative Zoology had many more types than we had at that time; and there were a few at the Philadelphia Academy [of Natural Sciences], but a very important collection existed here, one that formed a nucleus around which we've been building on for a number of years. Now, of course, we have the largest collection of crayfishes in the world—perhaps larger than all the other collections of crayfishes in the world combined [the collection of crayfishes now includes about 25,000 lots and 1500 lots of types].

Question: Was anyone working on them then?

Answer: No, no one at the Smithsonian

had worked on crayfishes. I'm the first person.

Question: Yes, to come in and work on it.

Answer: Faxon worked at the Museum of Comparative Zoology, and Ortmann was at the Carnegie Museum, and Creaser was at the Michigan Museum. Perhaps you know that we have the Michigan collection now. After I came here my major professor became director of the Michigan Museum, and he said, "Nobody's working on crayfishes out here, and we're crowded. Wouldn't the Smithsonian like to have it?" That was just before I came here; I was in Charlottesville at the time. He said, "You're nearby so you can use them from time to time." So we inherited that collection.

Question: How easy was it to start working in a field like that where no one else was working?

Answer: As I look back on it, I had a delightful time all the way through. I knew that I could tell the difference between what I had, and just because I didn't have a name for them at the time didn't bother me too much. The literature had not been cluttered with my group of animals that I was working on in Florida, so there was very little in the literature at all. So there was no great literature problem to face.

Question: Yes, going through the masses of descriptions.

Answer: I hate to say what has been done to it since. [Laughter.] As I frequently say, they will curse me and say all kinds of things, but they can't ignore me any longer with the crayfish.

Question: Right, you have left your mark. Were there avenues, let's say, for publishing your results?

Answer: Oh, they were very limited, of course. Again, I came along during the depression years, but Dr. Schmitt was very, very kind, and I can tell you one lovely little anecdote that happened to me in connection with publications. I used the Proceedings of the Florida Academy of Sciences—it used to be called the Journal. I used that for some of my work. Then the Charleston Museum at that time was publishing a series of Leaflets and Zoologica out of New York, and The American Midland Naturalist [also were available]. So there were a number of places that were open. But I sent one of my early papers up to Dr. Schmitt, describing seven new crayfishes from Florida—I think it was seven new ones—and redescribing, in essence, a species that had already been described. In this I used the word "crawfish." I'd always used crawfish as a name, and throughout most of the South they're still referred to as crawfish. Dr. Schmitt carefully went through my manuscript completely and changed it to crayfish everywhere. So I decided that, well, if they're going to force me to do this (I didn't raise any questions whatsoever), I'll just accept it. So since that time I have used "crayfish," and most of my students do. However, most of the other people, particularly those who've worked in the South, still write crawfishes when they write it.

Question: I hadn't even realized that there was the difference in words.

Answer: Oh yes. And one other thing occurred in that paper. I had caught crayfishes from a cave from which they had been reported in Florida. Faxon had identified the animal as *Cambarus lucifugus* [error for *acherontis* sensu Faxon, not Lönnberg; replaced by *lucifugus* Hobbs (1940a)], a species that had been described by [Einar] Lönnberg in the latter part of the nineteenth century from a well down near Orlando. Well, believing that the written word was infallible, I assumed that the specimens from this cave were what Faxon said they were. This was in the same manuscript, and Dr. Schmitt passed it on up to Dr. Stejneger, who at that time was Head Curator. Dr. Stejneger took one look at it and he said, "What right does he have to say that this is *lucifugus*?" [error for *acherontis* sensu Faxon.] He said, "He should go down to that well and catch some crayfish from that place to be sure." So Dr. Schmitt wrote back to me and gave me Dr. Stejneger's remarks. Well I was a little bit upset because I thought the possibility of my finding that well that had been dug back in the latter part of the last century was very slight, and Florida was not easy to get around in, it was certainly not like it is now—all highways. But a friend of mine, Lewis J. Marchand, who lived down near Orlando, happened to come by my office within a day or so after I'd heard from Dr. Schmitt. I asked him if he had ever seen any white crayfishes down in that area. He said, "Oh sure, I know a spring where I've seen them a number of times. So I said, "How soon can you be ready to go?" And he said, "Well, tomorrow morning will be fine." So I said, "Well, we'll start then." Palm Springs is what it was. In the meantime, I had another friend, fellow student, at the university who was very good at water goggling—that's what we called it in those days—it's modified scuba diving but you don't have air and so on. Anyway, I asked him if he didn't want to go. This was a cold November day, and, believe you me, Florida can get cold during the winter, the northern part. So we went down to Palm Springs, and when we got to this little spring I looked down—of course it hadn't been used since summer—it was covered with algae, and lying on the algae were white crayfish everywhere. So this friend of mine who went along with us took his gear and jumped off into the spring and time after time he came up, so we got forty-four of those animals that day. I got back to the laboratory, and sure enough, it was not the same as the thing from the cave, and was precisely what Lönnberg had described. So I had to redescribe it and put a new name [*Cambarus lucifugus*] on the material from the cave.

Question: Yes. You can't ever count on . . .

Answer: So Dr. Stejneger sitting in Washington certainly saved me considerable embarrassment, and taught me a good lesson not to accept the printed word.

Question: That is interesting, and you were having things published. Did you start collecting yourself at that point?

Answer: Oh, I started collecting back in 1931, when I was still a freshman.

Question: You did keep track of your different types?

Answer: Oh yes. One of the biggest helps, I suppose, was Dr. [J. Speed] Rogers, my major professor and the chairman of the department at that time, with his meticulousness in keeping notes and insisting that everything be carefully curated. So I started out being trained as a curator, I suppose. Through the years I amassed a collection of some 80,000 specimens that I brought with me when I came to the Smithsonian. All of those were catalogued and we're still using my old numbers. The collection's so tremendous that we haven't been able to incorporate nearly all of them into the Smithsonian catalogue, so we're still using my old cards.

Question: Where did you keep it all?

Answer: In my basement at home.

Question: You did?

Answer: I had a tiny little office at the University of Virginia in an old building. The office was about the size of this little anteroom out here. In one of the rooms the floor fell in, the basement where I had put so many crayfish. I had to take everything out and have the floor reconstructed to support the crayfish collection.

Question: Yes, I guess everything was pretty much alcoholic storage?

Answer: Everything was alcoholic storage, yes.

Question: Which is fairly heavy. The professors you were working under were they systematics people?

Answer: All of them were systematists, for the most part. There were four men in the department at the time, four of the full professors. All of them were graduates of the University of Michigan. One of them had taken his doctorate at, I believe, New York—I'm not sure whether it was Columbia [University] or not—but one of them had taken his doctorate elsewhere. But all of them had been trained in Michigan under [Alexander G.] Ruthven and [Robert W.] Hegner. Three of them were entomologists: Dr. Rogers worked on the Tipulidae, the crane flies; and Dr. [Theodore Huntington] Hubbell on the Orthoptera, grasshoppers, and Dr. [C. Francis] Byers on the Odonata, dragonflies. The fourth member was a mammalogist. He and I were good cronies because he was interested in bats—primarily, and bats live in caves and crayfish live in caves. So we had a delightful time teaming up going on field trips.

I'll tell you one other story of Dr. [Harley Bakwel] Sherman, the mammalogist. The library at the University of Florida had gotten a new photostat machine and had discarded the old one. Dr. Sherman and I rescued it and rebuilt it. We had heard that there had recently been aerial photographs taken of the area around Gainesville, of the entire county, that were available in the county agent's office. So we borrowed these, and made copies and placed them in our notebooks. Fortunately, those photographs had been taken during the winter months when the deciduous trees had lost their leaves. This meant that where you would see a black spot on our maps this was a cluster of live oak trees, and live oaks usually grow along some depression, frequently indicating a sinkhole or maybe a cave. In Florida, that section of the state is quite flat and the roads are built on the section lines so that they run at mile intervals, almost straight, occasionally going around a sinkhole or something of the sort. But no place are you more than a half a mile from any spot—if you were on the road—from any place within the quadrangle. So we would ride down the section lines with our maps, and if we'd see a black spot, we'd get out of the car and look to see whether this was a cave in which there might be bats or crayfishes or something of the sort.

One afternoon we'd been out, it was getting quite late and there were two graduate students with us, one of them, Dr. [Jerome] Krivanek, who's now at Vanderbilt [University], and a young man, [William M.] McLane, who has recently died. Dr. Sherman was driving, and I said, "Dr. Sherman, here's a little place right close to the road. Stop, it won't take Billy and me a moment or two to have a look." So we rushed over. It was nothing but a depression, but on our way back to the car there was a perfectly cylindrical chimney that went right down, dropped down, oh, between fifty and seventy feet. I peeked over the edge of it and saw that there was a little water in the bottom of it which excited me, so we rushed back to the car and asked them if we didn't have time to make one quick drop into this hole to see what it was. McLane and I went down into the hole and the other two stayed up above. We got down to the bottom, and I saw white crayfish on the bottom. We looked around and there was a little opening into the side, about two and a half feet in diameter; and we crawled into this opening, and that led into a fissure that was about four feet wide and some sixty or seventy feet long, with no floor, but the entire thing with water under us. It was shallow at one end, then it dropped off rather quickly. Even to this day we don't know how deep it really goes, it just continues on. I saw the white crayfish down there and I turned to this graduate student, and I said, "Billy, if you'll catch one of those crayfishes and it's a new one, I'll name it for you." Well, I knew what they were so I was perfectly safe. So Billy jumped into the water with a dip net and started scurrying around, but he was missing them. I said, "Well, let's go." The water had gotten so cloudy you couldn't do anything. So we crawled back up to the top, and when we reached the top of the cave, he turned to me and said, "Well, Doc, I didn't get any of the big ones but I got this little one." He handed me a vial with a little tiny crawfish [*Troglocambarus maclanei*; in his dedication of this species to McLane, Hobbs (1942b:349, footnote) commented: "It is a pleasure to name this species for Mr.

McLane, who has been a companion on many collecting trips, and who has added numerous valuable specimens to my collection."] in it, the most amazing animal I had ever seen in my life. I couldn't believe that it was anything except a mutant or something had gone wrong somewhere.

We went on back into Gainesville, and I immediately got the binocular scope on it and saw that it was really something out of this world. So the next day I was anxious to get back and get some more of them. Most of the young men who usually went with me were tied up in classes, they couldn't go. I found one man who'd go, and we had gone out to the car; we had our ropes and collecting equipment and so on. About that time I spotted the same man who had caught the crayfish down in Palm Springs, going across the campus. I called to him, and told him that we were going out to a cave, and wouldn't he like to go, and he said no, that he had an organic exam the next day. "Well, that's too bad," I said, "it's a wonderful place to water goggle." I knew that would get him, no question. "Oh?," he said, "All right, I'll go." I called him Jelly, so that gives you some idea as to his size. He wasn't all that obese, he was pretty wide, he had some flesh on him and I was worried all this time about his getting through that side of the pit.

Question: That's true, yes.

Answer: But, we got out to the cave, we went down it, . . . and he said, "Now where's that place to dive?" I said, "It's right through there." He looked at the hole and he said, "I can make it." So into the hole he went, all of us. It was such that we could prop our feet against one wall and lean our back against the other one, no place to stand whatsoever. He said, "Now where's that place to dive?" I said, "You're there." Well, if looks could have killed anyone, well of course, I would have been dead. But he was a good sport so he said, "All right." So he put on his goggles, and he went down, and he came up time after time with this big white crayfish, *Procambarus pallidus,* which I had recognized all along—but none of the little fellow. He said, "Well, I've about had it." I said, "Jelly, go down just one more time," and this time when he came up he rotated just before he surfaced and his light beam hit the submerged ceiling, and he saw one of them and picked it off and brought it up. After that, he went down and he got either three or four more that afternoon, all of them collected from the ceiling. So this little animal was highly adapted for living on submerged ceilings of caves; down below it would have been in competition, with a much less chance of survival certainly than it has above, a very small animal. What had happened, of course, McLane, when he jumped into the water, had jarred the water so that the animal became dislodged and on the way down Billy happened to catch it.

Question: Going down without ever looking up.

Answer: I finally caught one when Marchand, the man who had caught so many of them, jumped in one day and another one was dislodged and I saw it come loose and grabbed it with my dip net. That's the only one I've ever caught.

Question: But it was, I guess, a completely new type?

Answer: Oh, it was a completely new genus [*Troglocambarus*]. It is the most fantastic crayfish that we know at the present time. Most crayfishes have teeth on their third maxilliped for chewing. In the first place the maxillipeds have tremendously large and long setae that interlock, and by carrying water through the gill chamber over this setal net, it filters its food out of the water. There is no other crayfish that utilizes this technique.

Question: Fascinating, too, that you did find it. Were there many students in systematics at Florida at that time?

Answer: At that time, ecology was the thing, as it has become in recent years. I was trained as an ecologist; of course, the kind of ecology that we did then had little resemblance to the kind that exists at the present time. All of us were a combination systematist and ecologist. I was trained in ecology, and the only reason I got into systematics was that I couldn't identify my animals and there was no one to help me, and I had it to do.

Question: Yes, because that had not been done before. So you stayed there until 1946?

Answer: That's right.

Question: And then you moved to the University of Virginia.

Answer: While I was there I came up here many weekends to work in the collection.

Question: You were using these collections?

Answer: Oh, yes, I was using them from the outset. At one time Dr. Schmitt was able to get a little funds to help me to come up and work on weekends. At that time, too, he did another very nice thing for me. Most of the people had to be out of the building by a certain hour, and I was permitted to stay on until midnight. Some way he managed to help me out to that extent, because it was so rare—I could only work on Saturday night. Sometimes I would come up on Friday, I could work Friday night and Saturday night, or on holidays when I came.

Question: I guess you got to know the collections here fairly well. Were they in fairly good condition—identified or catalogued?

Answer: Oh, yes, all of the old material was, and much of the time that I was here, when I would come up on weekends, I was working up collections that had accumulated and identifying them so that they could be catalogued by the time that I came back and they were very nice in sending me duplicate cards for everything that I identified.

Question: Were there many collections coming in during those years, were there expeditions or collecting trips?

Answer: No, not a great many. There had been a considerable backlog because, as I said, no crayfish man had been here since [William Perry] Hay worked at the museum. He also taught high school here in the Washington area, as I understand it. He's one of the few older members—crayfish people—that I met, but he had retired and was quite an old man when I met him. He lived in Florida and made a special trip to come up to Gainesville to see me one time, so I was delighted. He subsequently gave me his library, so I have many of his old notes, things that will go to the archives eventually.

Co-authors of Horton H. Hobbs, Jr.

Hobbs published many papers with co-authors, acknowledging help in the field and collaborating with students and colleagues. Here we list his co-authors and, where possible, their institution (usually as of the dates), to demonstrate the breadth of his association with others with similar interests. As pointed out by Hoffman (1994: 37) some of his papers are co-authored "sometimes for no other reason than to reward the collector of a new species."

Andolshek, M. D. (1986a). Hobbs's research assistant at the museum. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (see also Margaret A. Daniel).

Banner, Albert H. (1959d). Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe.

Barr, Thomas C., Jr. (1960b, 1972b). University of Kentucky, Lexington.

Bedinger, M. S. (1964b, 1965a). U.S. Geological Survey.

Bouchard, Raymond W. (1973a, 1976b, 1994). Academy of Natural Sciences of Philadelphia.

Brown, Arthur V. (1987d). University of Arkansas, Fayetteville.

Burr, Brooks M. (1984b). Southern Illinois University, Carbondale.

Carlson, Paul H. (1983c, 1985a). Department of Health and Environmental Control, Columbia, South Carolina.

Chace, Fenner A., Jr. (1959d, 1969a). National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Cooper, Martha R. (1972e, 1980c). North Carolina State Museum of Natural History, Raleigh.

Daniel, Margaret A. (1977c) (nee Margaret D. Andolshek).

Fitzpatrick, Joseph F., Jr. (1962d, 1970a, 1971d). University of South Alabama, Mobile. Hobbs's last student.

Franz, Richard (1983a, 1986b, 1991b, 1992). Florida State Museum, University of Florida, Gainesville.

Freeman, Harry W. (1956d). College of Charleston, South Carolina.

Grubbs, Andrew G. (1982b, 1986c). Southwest Texas State University.

Hall, Edward T., Jr. (1969d, 1972f, 1974d). Georgia Water Quality Control Board, Atlanta.

Hart, C. Willard, Jr. (1956e, 1959b, 1961b, 1966d, 1982e). National Museum of Natural History, Smithsonian Institution, Washington, D.C. One of Hobbs's students.

Hobbs, Horton H., III (1962a, 1970c, 1973c, 1976e, 1977c, 1989e, 1990b, 1991d, 1995a, 1995b). Hobbs's son, referred to herein as Hobbs III. Wittenberg University, Springfield, Ohio.

Holt, Perry C. (1967d, 1968b). Virginia Polytechnic Institute, Blacksburg. Hobbs's first student. Fitzpatrick recalls that Holt liked to refer to himself and Fitzpatrick as "alpha and omega."

Hubricht, Leslie (1959d). Missouri Botanical Garden, St. Louis; Louisville, Kentucky.

Lee, David S. (1976c). North Carolina State Museum of Natural History, Raleigh.

Mackin, J. G. (1959d). Texas A&M University, College Station.

Manning, Raymond B. (1977d). National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Marchand, Lewis J. (1943a). University of Florida, Gainesville.

Massmann, William H. (1952b). Virginia Fisheries Laboratory.

McClure, Auden C. (1983e). McLean, Virginia.

Means, D. Bruce (1972c). Tall Timbers Research Station, Tallahassee, Florida.

Page, Charles H. (1953b). Charlottesville, Virginia.

Parish, Claude E. (1949b). University of Alabama.

Penn, George Henry, Jr. (1958h). Tulane University, New Orleans, Louisiana.

Perkins, F. O. (1967c). Virginia Institute of Marine Science, Gloucester Point.

Peters, Daniel J. (1977b, 1979a, 1982c, 1989b, 1991c, 1993). New Horizons Governor's School for Science and Technology, Hampton, Virginia.

Pflieger, William L. (1988c). Fish and Wildlife Research Center, Missouri Department of Conservation, Columbia.

Prins, Rudolph (1972d). Western Kentucky University, Bowling Green.

Robison, Henry W. (1982d, 1985b, 1988b, 1989f). Southern Arkansas University, Magnolia.

Rodríguez, Gilberto (1989c, 1989d). Instituto Venezolano de Investigaciones Científicas, Caracas.

Shoup, C. S. (1942c, 1947b). Vanderbilt University, Nashville, Tennessee.

Villalobos (Figueroa), Alejandro (1958f, 1964a, 1974b, 1981a). Instituto de Biología, Universidad Nacional Autónoma de México, México.

Walton sisters, Lucille ("Miss Lucille") and Margaret ("Miss Peggy") (1957b, 1958d, 1959a, 1959c, 1960a, 1960c, 1961a, 1962b, 1963a, 1963b, 1966c, 1966e, 1967d, 1968b, 1968d, 1970b, 1971e, 1975b, 1976d, 1977f). Danville, Virginia and Mountain Lake Biological Station, Pembroke, Virginia. J. F. Fitzpatrick, Jr. (in litt.) notes that "They were—or at least Hobbs thought of them as—the quintessential 'Old Maid Schoolteachers.' Both were older than he, Miss Lucille by a greater margin . . . . To the best of my knowledge they met at the Mountain Lake Biological Station where the sisters were summer fixtures. They succumbed to his characteristic charm, and Miss Peggy, "who knew not a thing about crayfishes," took great satisfaction in contributing to science by inking the pencil drawings. This seemed to be her contribution to the joint papers."

Whiteman, Mike (1987c, 1991a). Texas Agricultural Extension Service, Lufkin.

Word, Benjamin H. (1958e). University of Virginia, Charlottesville. An undergraduate, now a M.D., who did a research project under Hobbs that was never published. At the time of his death Hobbs was preparing this report for publication; Hobbs III is preparing this final study (see also remarks at end of Hobbs's bibliography).

Zinn, Donald J. (1948c). University of Rhode Island, Kingston.

Publications of Horton H. Hobbs, Jr.

Here we provide a complete bibliography of Hobbs's publications, in chronological order, annotated with the names of new taxa in each publication. The citations are cross-referenced to the list of taxa named by Hobbs, given below. If the name of a taxon is given in the title, it is not repeated in the list of taxa named in that article.

1937. Some Florida crawfishes and their habitat distribution. [Abstract].—Proceedings of the Florida Academy of Sciences for 1936 1:154.

1938a. Two new crawfishes from Florida. *Cambarus hubbelli, Cambarus acherontis pallidus.* [Abstract].—Proceedings of the Florida Academy of Sciences 2:90, 91. [Nomina nuda].

1938b. A new crawfish from Florida.—Journal of the Washington Academy of Sciences 28(2):61–65. *Cambarus rogersi.*

1940a. Seven new crayfishes of the genus *Cambarus* from Florida, with notes on other species.—Proceedings of the United States National Museum 89: 387–423. *C. hubbelli, C. kilbyi, C. lucifugus alachua, C. lucifugus lucifugus, C. pallidus, C. pictus, C. rathbunae.*

1940b. A new crayfish from South Carolina.—The Charleston Museum Leaflet 14:3–7. *Cambarus lunzi.*

1941a. A new crayfish from San Luis Potosí, México (Decapoda, Astacidae).—Zoologica, New York 26(1):1–4. *Cambarus blandingii cuevachicae.*

1941b. Three new Florida crayfishes of the subgenus *Cambarus* (Decapoda, Astacidae).—The American Midland Naturalist 26(1):110–121. *C. byersi, C. cryptodytes, C. floridanus.*

1942a. On the first pleopod of the male Cambari (Decapoda, Astacidae).—Proceedings of the Florida Academy of Sciences (for 1940) 5:55–61.

1942b. A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with the description of a new genus and species.—The American Midland Naturalist 28(2):334–357. *Troglocambarus, T. maclanei.*

1942c. Hobbs, H. H., Jr., & C. S. Shoup. On the crayfish collected from the Big South Fork of the Cumberland River in Tennessee during the summer of 1938.—The American Midland Naturalist 28(3): 634–643.

1942d. The crayfishes of Florida.—University of Florida Publication, Biological Science Series 3(2):179 pp., pls. 1 (frontispiece), 2–24. *Cambarellus schmitti, Procambarus apalachicolae, P. bivittatus, P. econfinae, P. escambiensis, P. geodytes, P. latipleurum, P. leonensis, P. okaloosae, P. pubischelae, P. pycnogonopodus, P. pygmaeus, P. rogersi campestris, P. r. ochlocknensis, P. seminolae, P. shermani, P. youngi.*

1943a. Hobbs, H. H., Jr., & L. J. Marchand. A contribution toward a knowledge of the crayfishes of the Reelfoot Lake area.—Journal of the Tennessee Academy of Science 18(1):6–35.

1943b. Two new crayfishes from the panhandle of Florida (Decapoda, Astacidae).—Proceedings of the Florida Academy of Sciences 6(1):49–58. Note by Hobbs given in footnote (p. 56): "Due to inadvertent delay in publication of this volume diagnoses of these species [*Procambarus leonensis, P. pycnogonopodus*] appeared earlier in 'The Crayfishes of Florida' (Hobbs: Univ. Fla. Pub. Biol. Series 3(2): 114–115, 117) and thus actually constitute the original descriptions."

1943c. Two new crayfishes of the genus *Procambarus* from Mexico (Decapoda, Astacidae).—Lloydia 6: 198–206. *P. rodriguezi, P. toltecae.*

1944. Notes on the subterranean waters of the Florida Peninsula with particular reference to their crustacean fauna.—The Biologist 26(1&2):6–8.

1945a. Notes on the first pleopod of the male Cambarinae (Decapoda, Astacidae).—Quarterly Journal of the Florida Academy of Sciences 8(1):67–70.

1945b. The subspecies and intergrades of the Florida burrowing crayfish, *Procambarus rogersi* (Hobbs).—Journal of the Washington Academy of Sciences 35(8):247–260. Note by Hobbs given in footnote (p. 260): "This paper was originally accepted for publication in the Proceedings of the United States National Museum, and it was cited as 'in press' in my *Crayfishes of Florida* (Hobbs, 1942). Wartime restrictions, however, so delayed publication by the Museum that the manuscript was withdrawn and submitted to this JOURNAL in order that the full descriptions of the two new subspecies of *Procambarus rogersi* might appear more promptly."

1945c. Two new species of crayfishes of the genus *Cambarellus* from the Gulf coastal states, with a key to the species of the genus (Decapoda, Astacidae).—The American Midland Naturalist 34(2):466–474. *C. diminutus, C. puer.*

1947a. Two new crayfishes of the genus *Procambarus* from Georgia, with notes on *Procambarus pubescens* (Faxon) (Decapoda, Astacidae).—Quarterly Journal of the Florida Academy of Sciences 9(1):1–18. *P. enoplosternum, P. litosternum.*

1947b. Hobbs, H. H., Jr., & C. S. Shoup. Two new crayfishes (Decapoda, Astacidae) from the Obey River drainage in Tennessee.—Journal of the Tennessee Academy of Science 22(2):138–145. *Cambarus obeyensis, C. parvoculus.*

1947c. A key to the crayfishes of the Pictus subgroup of the genus *Procambarus,* with the description of a new species from South Carolina.—The Florida Entomologist 30(3):25–31. *P. lepidodactylus.*

1947d. A preliminary report on the crayfishes of Virginia. [Abstract].—Proceedings of the Virginia Academy of Science 1946–1947:72.

1948a. On the crayfishes of the *Limosus* section of the genus *Orconectes* (Decapoda: Astacidae).—Journal of the Washington Academy of Sciences 38(1):14–21. *O. shoupi.*

1948b. Two new crayfishes of the genus *Orconectes* from Arkansas, with a key to the species of the Hylas group (Decapoda: Astacidae).—The American Midland Naturalist 39(1):139–150. *O. leptogonopodus, O. marchandi.*

1948c. Hobbs, H. H., Jr., & D. J. Zinn. Crayfish in southern Nevada.—Science 107(2780):369.

1948d. The crayfish genus *Cambarellus* in the United States. [Abstract].—Proceedings of the Virginia Academy of Science 1948:88.

1948e. A new crayfish of the genus *Orconectes* from southern Tennessee (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 61:85–91. *O. wrighti.*

1948f. A new crayfish of the genus *Cambarus* from Texas, with notes on the distribution of *Cambarus fodiens* (Cottle).—Proceedings of the United States National Museum 98:223–231. *C. hedgpethi.*

1949a. The cave crayfishes of North America. [Abstract].—Journal of the Tennessee Academy of Science 24(3):170.

1949b. Hobbs, H. H., Jr., & C. E. Parish. Notes on the life history of a Virginia crayfish. [Abstract].—Proceedings of the Virginia Academy of Science 1948–1949:97.

1949c. Observations on the emergence of a stonefly of the genus *Taeniopteryx* in Virginia. [Abstract].—Proceedings of the Virginia Academy of Science 1948–1949:101.

1949d. A new crayfish of the genus *Orconectes* from the Nashville Basin in Tennessee, with notes on the range of *Orconectes compressus* (Faxon) (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 62:17–25. *O. rhoadesi.*

1950a. A new crayfish of the genus *Cambarellus* from Texas (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 63:89–94. *C. ninae.*

1950b. A new crayfish of the genus *Procambarus* from Oklahoma and Arkansas (Decapoda, Astacidae).—Journal of the Washington Academy of Sciences 40(6):194–198. *P. tenuis.*

1950c. Observations on the ecological distribution of three Virginia crayfishes. [Abstract].—The Virginia Journal of Science for 1949–1950, new series 1(4): 349.

1951a. A new crayfish of the genus *Orconectes* from southeastern Virginia (Decapoda, Astacidae).—The Virginia Journal of Science, new series 2(2):122–128. *O. virginiensis.*

1951b. A new crayfish of the genus *Procambarus* from Louisiana, with a key to the species of the Spiculifer group.—Journal of the Washington Academy of Sciences 41(8):272–276. *P. penni.*

1952a. A new crayfish from Alabama, with notes on *Procambarus lecontei* (Hagen).—Proceedings of the United States National Museum 102:209–219. *P. verrucosus.*

1952b. Hobbs, H. H., Jr., & W. H. Massmann. The river shrimp, *Macrobrachium ohione* (Smith), in Virginia.—The Virginia Journal of Science, new series 3(3):206, 207.

1952c. A new crayfish of the genus *Procambarus* from Georgia with a key to the species of the Clarkii subgroup.—Quarterly Journal of the Florida Academy of Sciences 15(3):165–174. *P. howellae.*

1952d. A new albinistic crayfish of the genus *Cambarus* from southern Missouri with a key to the albinistic species of the genus (Decapoda, Astacidae).—The American Midland Naturalist 48(3): 689–693. *C. hubrichti.*

1952e. A preliminary report on the crayfishes of the Atlantic Slope from New Brunswick to South Carolina. [Abstract].—The Virginia Journal of Science, new series 3(4):295.

1953a. Two new crayfishes from the Highland Rim in Tennessee (Decapoda, Astacidae).—Journal of the Tennessee Academy of Science 28(1):20–27 [also published in Report of the Reelfoot Lake Biological Station, vol. 17, 1953]. *Cambarus brachydactylus, C. friaufi.*

1953b. Hobbs, H. H., Jr., & C. H. Page. Additional records of the occurrence of the freshwater jellyfish, *Craspedacusta sowerbii,* in Virginia.—The Virginia Journal of Science, new series 4(3):137.

1953c. The epizootic associates of the crayfishes of the New River system with particular reference to the ostracods. [Abstract].—Journal of the Tennessee Academy of Science 28(3):180, 181.

1953d. A new crayfish of the genus *Procambarus* from Alabama and Florida (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 66:173–178. *P. suttkusi.*

1953e. On the ranges of certain crayfishes of the Spiculifer group of the genus *Procambarus,* with the description of a new species (Decapoda: Astacidae).—Journal of the Washington Academy of Sciences 43(12):412–417. *P. raneyi.*

1954a. Apparent competition between two groups of crayfishes in the southeastern states. [Abstract].—The Virginia Journal of Science, new series 4(4): 230.

1954b. A new crayfish from the upper coastal plain of Georgia (Decapoda, Astacidae).—Quarterly Journal of the Florida Academy of Sciences 17(2):110–118. *Procambarus truculentus.*

1954c. A redescription of *Procambarus ruthveni* (Pearse) from La Laja Creek at Cuatatotolapam, Veracruz, Mexico (Decapoda, Astacidae).—Occasional Papers of the Museum of Zoology, University of Michigan 559:1–5.

1954d. Studies on the geographic distribution of the crayfishes of the genus *Procambarus.* [Abstract].—Journal of the Tennessee Academy of Science 29(3): 181.

1954e. Notes on the evolution of the Longulus group of the crayfish genus *Cambarus.* [Abstract].—The Virginia Journal of Science, new series 5(4):261.

1955a. A new crayfish of the genus *Cambarus* from Mississippi.—Proceedings of the Biological Society of Washington 65:95–100. *C. cristatus.*

1955b. Ostracods of the genus *Entocythere* from the New River system in North Carolina, Virginia, and West Virginia.—Transactions of the American Microscopical Society 74(4):325–333. *E. daphnioides, E. runki.*

1955c. A tendency towards cyclic dimorphism in female crayfishes. [Abstract].—The Virginia Journal of Science, new series 6(4):248.

1955d. Two crayfish highways to Florida. [Abstract].—Association of Southeastern Biologists Bulletin 2(1):7.

1956a. A new crayfish of the genus *Cambarus* from North Carolina and South Carolina (Decapoda, Astacidae).—Journal of the Elisha Mitchell Scientific Society 72(1):61–67. *C. reduncus.*

1956b. A new crayfish of the Extraneus section of the

genus *Cambarus* with a key to the species of the section (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 69:115–121. *C. spicatus.*

1956c. A new crayfish of the genus *Procambarus* from South Carolina (Decapoda: Astacidae).—Journal of the Washington Academy of Sciences 46(4):117–121. *P. echinatus.*

1956d. Hobbs, H. H., Jr., & H. W. Freeman. The decapod crustaceans of the Wateree River system in North Carolina and South Carolina. [Abstract].—Association of Southeastern Biologists Bulletin 3(1):10.

1956e. Hart, C. W., & H. H. Hobbs, Jr. The crayfish of the Lower Flint-Chattahoochee River system. [Abstract].—The Virginia Journal of Science, new series 7(4):292.

1957a. Observaciones acerca de las especies del género *Entocythere* (Crustaceos, Ostracodos) de Cuba.—Anales del Instituto de Biología, Universidad Nacional Autónoma de México 27(2):431–436. *E. hamata.*

1957b. Hobbs, H. H., Jr., & M. Walton. Three new crayfishes from Alabama and Mississippi (Decapoda: Astacidae).—Tulane Studies in Zoology 5(3): 39–52. *Procambarus hybus, P. jaculus, P. mancus.*

1958a. The evolutionary history of the Pictus group of the crayfish genus *Procambarus* (Decapoda, Astacidae).—Quarterly Journal of the Florida Academy of Sciences 2(1):71–91.

1958b. Two new crayfishes of the genus *Procambarus* from South Carolina.—Journal of the Washington Academy of Sciences 48(5):160–168. *P. ancylus, P. hirsutus.*

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At the time of his death, Hobbs was completing a manuscript entitled "A comparative study of functional morphology of the male reproductive systems in the Astacidea (Crustacea: Decapoda) with emphasis on the freshwater crayfishes." Hobbs III plans to complete preparing this manuscript for publication.

Taxa Named by Horton H. Hobbs, Jr.

The family, genera and subgenera, species and subspecies named by Hobbs and colleagues are listed alphabetically and are cross-referenced to Hobbs's bibliography, above. We provide the repository and catalogue number for all holotypes of species and subspecies. Most of the holotypes of taxa named by Hobbs are in the collections of the National Museum of Natural History, Smithsonian Institution, Washington (USNM). One holotype is in The Natural History Museum, London (BMNH) and several are in the Muséum National d'Histoire Naturelle, Paris (MNHN) as well as The Academy of Natural Sciences of Philadelphia (ANSP). When a holotype has been deposited in a museum other than the USNM, catalogue numbers of USNM paratypes are provided.

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Alpheopsis stygicola Hobbs, 1973d. Holotype USNM 143629.

Ankylocythere barbouri Villalobos Figueroa & Hobbs, 1974b. Holotype USNM 149159.

Ankylocythere carpenteri Hobbs & McClure, 1983e. Holotype USNM 204402.

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Ankylocythere maya Hobbs, 1971b. Holotype USNM 128822.

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Ascetocythere batchi Hobbs & Walton, 1968d. Holotype USNM 123321.

Ascetocythere bouchardi Hobbs & Walton, 1975b. Holotype USNM 150640.

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Ascetocythere lita Hobbs & Hobbs III, 1970c. Holotype USNM 126251.

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Ascetocythere triangulata Hobbs & Walton, 1975b. Holotype USNM 150643.

Ascetocythere veruta Hobbs & Walton, 1975b. Holotype USNM 150645.

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Aviticambarus Hobbs, 1969c.

Barbicambarus Hobbs, 1969c.

Bouchardina Hobbs, 1977a.

Bouchardina robisoni Hobbs, 1977a. Holotype USNM 147146.

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Cambarellus diminutus Hobbs, 1945c. Holotype USNM 81554.

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Cambarus floridanus Hobbs, 1941b. Holotype USNM 79341.

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Cambarus gentryi Hobbs, 1970d. Holotype USNM 130283.

Cambarus georgiae Hobbs, 1981b. Holotype USNM 118944.

Cambarus halli Hobbs, 1968a. Holotype USNM 129288.

Cambarus harti Hobbs, 1981b. Holotype USNM 148348.

Cambarus hedgpethi Hobbs, 1948f. Holotype USNM 85146.

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Cambarus howardi Hobbs & Hall, 1969d. Holotype USNM 129866.

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Cambarus hubbelli Hobbs, 1940a. Holotype USNM 76593.

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Cambarus nerterius Hobbs, 1964c. Holotype USNM 111295.

Cambarus nodosus Bouchard & Hobbs, 1976b. Holotype USNM 146756.

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Cambarus pallidus Hobbs, 1940a. Holotype USNM 76591.

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Creaserinus Hobbs, 1973e.

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Dactylocythere jeanae Hobbs, 1967a. Holotype USNM 113475.

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Dactylocythere myura Hobbs & Walton, 1970b. Holotype USNM 126975.

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Depressicambarus Hobbs, 1969c.

Distocambarus Hobbs, 1981b.

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Entocythere ambophora Walton & Hobbs, 1959c. Holotype USNM 105953.

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Entocythere asceta Hobbs & Walton, 1962b. Holotype USNM 108174.

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Entocythere costata Hobbs & Peters, 1977b. Holotype USNM 155334.

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Entocythere daphnioides Hobbs, 1955b. Holotype USNM 98406.

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Entocythere hiwasseensis Hobbs & Walton, 1961a. Holotype USNM 105963.

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Entocythere phyma Hobbs & Walton, 1962b. Holotype USNM 108178.

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Entocythere prisma Andolshek & Hobbs, 1986a. Holotype USNM 213649.

Entocythere reddelli Hobbs & Walton, 1968d. Holotype USNM 123330.

Entocythere runki Hobbs, 1955b. Holotype USNM 98410.

Entocythere simondsi Hobbs & Walton, 1960a. Holotype USNM 105956.

Entocythere steevesi Hart & Hobbs, 1961b. Holotype ANSP 6236.

Entocythere tuberosa Hart & Hobbs, 1961b. Holotype ANSP 6340.

Entocythere tyttha Hobbs & Hobbs III, 1970c. Holotype USNM 126258.

Entocythere ungulata Hart & Hobbs, 1961b. Holotype ANSP 6234.

Entocythere xania Hart & Hobbs, 1961b. Holotype ANSP 6237.

Erebicambarus Hobbs, 1969a.

Exilicambarus Bouchard & Hobbs, 1976d.

Fallicambarus Hobbs, 1969c.

Fallicambarus caesius Hobbs, 1975c. Holotype USNM 144921.

Fallicambarus danielae Hobbs, 1975c. Holotype USNM 145997.

Fallicambarus devastator Hobbs & Whiteman, 1987c. Holotype USNM 218546.

Fallicambarus gilpini Hobbs & Robison, 1989f. Holotype USNM 219511.

Fallicambarus harpi Hobbs & Robison, 1985b. Holotype USNM 217946.

Fallicambarus hortoni Hobbs & Fitzpatrick, 1970a. Holotype USNM 129895.

Fallicambarus jeanae Hobbs, 1973e. Holotype USNM 144672.

Fallicambarus petilicarpus Hobbs & Robison, 1989f. Holotype USNM 219507.

Fallicambarus spectrum Hobbs, 1973e. Holotype USNM 144674.

Fitzcambarus Hobbs, 1983d.

Geocythere nessoides Hobbs & Hobbs III, 1970c. Holotype USNM 126259.

Hagenides Hobbs, 1972a.

Harpagocythere baileyi Hobbs & Peters, 1977b. Holotype USNM 155332.

Harpagocythere tertius Hobbs & Walton, 1968d. Holotype USNM 123329.

Hiaticambarus Hobbs, 1969c.

Jugicambarus Hobbs, 1969c.

Lacunicambarus Hobbs, 1969c.

Leconticambarus Hobbs, 1972a.

Litocythere Hobbs & Walton, 1968d.

Litocythere lucileae Hobbs & Walton, 1968d. Holotype USNM 123327.

Lonnbergius Hobbs, 1972a.

Lordocythere Hobbs & Hobbs III, 1970c.

Lordocythere petersi Hobbs & Hobbs III, 1970c. Holotype USNM 126262.

Macrobrachium catonium Hobbs & Hobbs III, 1995a. Holotype USNM 260328.

Macrobrachium villalobosi Hobbs, 1973d. Holotype USNM 143633.

Mexicambarus Hobbs, 1972a.

Neopalaemon Hobbs, 1973b.

Neopalaemon nahuatlus Hobbs, 1973b. Holotype USNM 143120.

Odontothelphusa monodontis Rodriguez & Hobbs, 1989c. Holotype USNM 230078.

Orconectes chickasawae Cooper & Hobbs, 1980c. Holotype USNM 144926.

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Orconectes incomptus Hobbs & Barr, 1972b. Holotype USNM 130299.

Orconectes leptogonopodus Hobbs, 1948b. Holotype USNM 82262.

Orconectes marchandi Hobbs, 1948b. Holotype USNM 82072.

Orconectes propinquus erismophorous Hobbs & Fitzpatrick, 1962d. Holotype USNM 107597.

Orconectes rhoadesi Hobbs, 1949b. Holotype USNM 87953.

Orconectes shoupi Hobbs, 1948a. Holotype USNM 84072.

Orconectes virginiensis Hobbs, 1951a. Holotype USNM 91659.

Orconectes wrighti Hobbs, 1948e. Holotype USNM 85144.

Ornithocythere Hobbs, 1967a.

Ornithocythere thomai Hobbs & McClure, 1983e. Holotype USNM 204405.

Ornithocythere waltonae Hobbs, 1967a. Holotype USNM 113472.

Palaemonetes lindsayi Villalobos Figueroa & Hobbs, 1974b. Holotype USNM 149161.

Pennides Hobbs, 1972a.

Phymocythere Hobbs & Hart, 1966d.

Phymocythere lophota Hobbs & Peters, 1993. Holotype USNM 260074.

Plectocythere johnsonae Hobbs & Hart, 1966d. Holotype USNM 113454.

Plectocythere kentuckiensis Hobbs & Peters, 1991c. Holotype USNM 235517.

Potamocarcinus leptomelus Rodríguez & Hobbs, 1989c. Holotype USNM 230080.

Procambarus ancylus Hobbs, 1958b. Holotype USNM 115050.

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Procambarus attiguus Hobbs & Franz, 1992. Holotype USNM 220683.

Procambarus bivittatus Hobbs, 1942d. Holotype USNM 81274.

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Procambarus geminus Hobbs, 1975c. Holotype USNM 145756.

Procambarus geodytes Hobbs, 1942d. Holotype USNM 82263.

Procambarus gibbus Hobbs, 1969e. Holotype USNM 129804.

Procambarus hirsutus Hobbs, 1958b. Holotype USNM 101148.

Procambarus horsti Hobbs & Means, 1972c. Holotype USNM 132043.

Procambarus howellae Hobbs, 1952c. Holotype USNM 93158.

Procambarus hybus Hobbs & Walton, 1957b. Holotype USNM 99581.

Procambarus jaculus Hobbs & Walton, 1957b. Holotype USNM 99584.

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Procambarus medialis Hobbs, 1975c. Holotype USNM 144942.

Procambarus milleri Hobbs, 1971f. Holotype USNM 131257.

Procambarus morrisi Hobbs & Franz, 1991b. Holotype USNM 220374.

Procambarus nechesae Hobbs, 1990a. Holotype USNM 219733.

Procambarus nigrocinctus Hobbs, 1990a. Holotype USNM 219426.

Procambarus niveus Hobbs & Villalobos, 1964a. Holotype USNM 109076.

Procambarus nueces Hobbs & Hobbs III, 1995b. Holotype USNM 260326.

Procambarus oaxacae oaxacae Hobbs, 1973b. Holotype USNM 144341.

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Procambarus rogersi expletus Hobbs & Hart, 1959b. Holotype USNM 102125.

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Procambarus shermani Hobbs, 1942d. Holotype USNM 81287.

Procambarus steigmani Hobbs, 1991e. Holotype USNM 220525.

Procambarus strenthi Hobbs, 1977e. Holotype USNM 147725.

Procambarus suttkusi Hobbs, 1953d. Holotype USNM 93730.

Procambarus talpoides Hobbs, 1981b. Holotype USNM 115002.

Procambarus tenuis Hobbs, 1950b. Holotype USNM 90390.

Procambarus texanus Hobbs, 1971c. Holotype USNM 131457.

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Franconictis (Mammalia: Carnivora) from the Late Oligocene of eastern Kazakstan

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Abstract.—The right dentary of a small carnivore from near Ayaguz in eastern Kazakstan is identified as *Franconictis* sp. aff. *F. vireti* (Dehm). *Franconictis* has previously been reported only from the early Miocene of Europe. Previous reports of *Plesictis* from Asia are not well founded. *Franconictis* from Ayaguz extends the geographic range of the genus into Asia and its temporal range back to the late Oligocene.

Fossil mammals from eastern Kazakstan are best known from the richly fossiliferous Paleogene-Neogene strata of the Zaysan basin (Fig. 1). Some Paleogene and more extensive Neogene mammalian assemblages are also known from the intermontane basins of the northern Tien Shan drained by the Ily River and its tributaries (Tleuberdina et al. 1993, Lucas & Bayshashov 1996, Emry et al. 1997). However, between the Ily and Zaysan basins, relatively few Cenozoic fossil mammals are known, in part because outcrops are limited in the relatively low topography of the Balkash-Alakol drainage basin. Here, we add to this sparse record a jaw of the mustelid carnivore *Franconictis,* collected near Ayaguz. *Franconictis* has previously been known only from the early Miocene of Europe (Wolsan 1993, Morlo 1996); this specimen is the first record of the genus from Asia and extends its temporal range back to the late Oligocene.

Abbreviations used.—When used in dental notations, upper case letters denote upper (skull) teeth and lower case letters denote lower (dentary) teeth. Institutional abbreviations used are: AMNH–American Museum of Natural History, New York; KAN–Kazak Academy of Sciences, Almaty.

Systematic Paleontology

Order Carnivora Bowdich, 1821
Family Mustelidae Fischer von Waldheim, 1817
Genus *Franconictis* Wolsan, 1993
Franconictis sp. aff. *F. vireti* (Dehm 1950)
Fig. 2

Referred specimen.—KAN 401-67, horizontal ramus of right dentary with p1–m1, from lower Miocene strata termed "Aral svita" near Ayaguz, Kazakstan.

Description.—The dentary is narrow and shallow with two mental foramina on its labial aspect—one under the anterior root of the p2 and the other under the center of the p3. The ascending ramus is broken, but appears to have been tall and thin, with the anterior border of the coronoid fossa sharply defined.

There is a dorso-ventrally oval alveolus for the canine at the anterior edge of the dentary as preserved. Evidently the postcanine diastema was either short or nonexistent. The p1 is a small, well worn trenchant tooth with a single root. The crown consists

Fig. 1. Map of Kazakstan showing location of the Zaysan basin, the Ayaguz fossil mammal locality and the Ily basin in the eastern part of the country.

of an anteriorly situated main cusp (protoconid) with a long posterior surface sloping to a low heel. The p1 length = 2.4 mm, width = 1.3 mm.

The p2 has two distinct roots and a trenchant crown dominated by the tall protoconid. There is a very small anterior cingulid and a low, broad heel defined by the lingual cingulid which continues around the posterior margin of the tooth. The p2 length = 3.3 mm, width = 1.6 mm.

The p3 is similar to the p2 but larger and has a relatively longer anterior slope. A very slight swelling low on the posterior slope of the protoconid is an incipient postprotoconid cuspid. The p4 has a similar overall shape, except the anterior cingulid bears a distinct cuspid, there is a small cuspid (?metaconid) on the posterior slope of the protoconid, and the posterolingual cingulid is a sharp ridge produced into a small posterior accessory cuspid. The p3 length = 3.8 mm, width = 1.8 mm; p4 length = 4.6 mm, width = 2.1 mm.

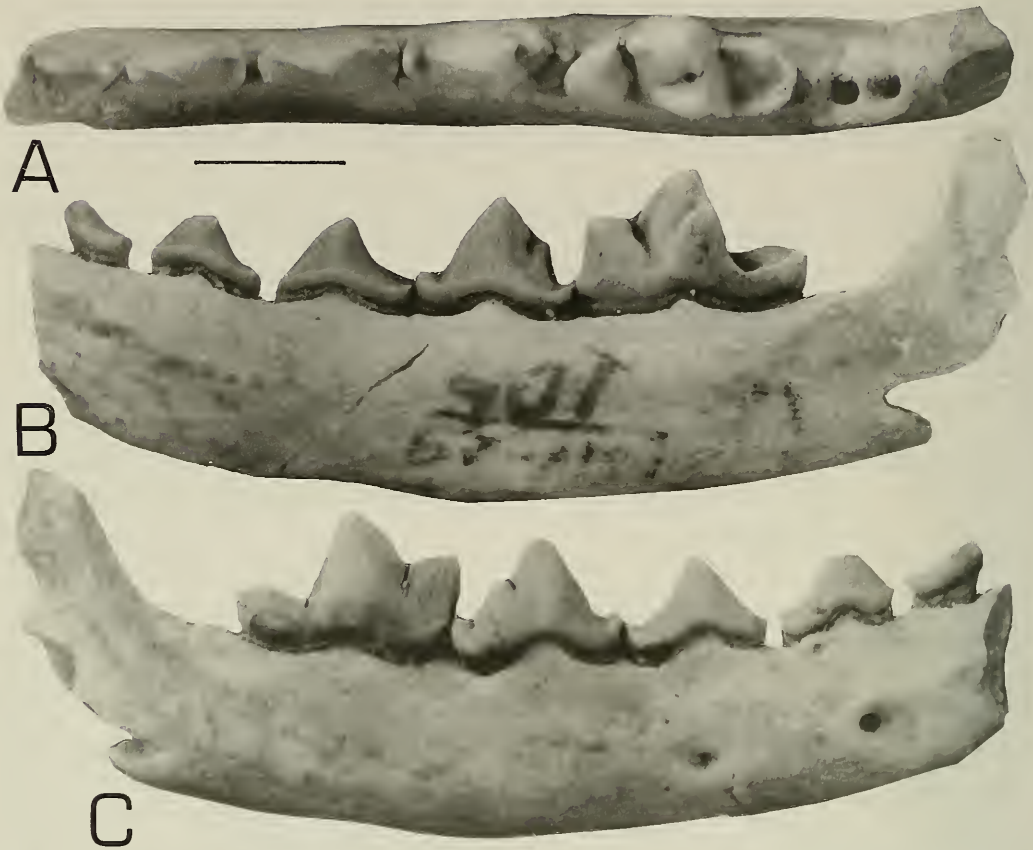

Fig. 2. *Franconictis* sp. aff. *F. vireti* (Dehm) from eastern Kazakstan, KAN 401-67, right dentary with p1–m1, occlusal (A), lingual (B) and labial (C) views. Bar scale = 5 mm.

The m1 is the only molar tooth remaining in the jaw, and it is substantially larger than the other teeth. The large, postero-labially canted protoconid dominates the trigonid. A relatively small and low metaconid is directly lingual to the protoconid, and a larger but lower paraconid projects antero-lingually, so that the trigonid basin is broadly open lingually. A carnassial notch interrupts the paracristid. The low talonid consists of a basin surrounded by a relatively sharp rim, which is much lower lingually than labially. The hypoconid is relatively large and the entoconid is present but poorly differentiated as a small cuspid on the posterolingual rim of the talonid; between the hypoconid and entoconid are two small, bead-like cuspids. The m1 length = 6.4 mm, width = 2.9 mm.

The m2 is missing, but its position is indicated by two alveoli, the posterior of which is well up on the slope of the ascending ramus. It was obviously a much smaller tooth than the m1.

Identification.—The presence of a single-rooted p1 supports assignment of KAN 401-67 to the Mustelidae *sensu* Wolsan (1993). Among mustelids, its closest similarity is to "*Plesictis,*" particularly the relatively small species "*P.*" *vireti* from Wintershof-West, Germany (e.g., Dehm 1950, figs. 92–99). Points of close resemblance include the shallow dentary, single-rooted p1, lack of a posterior cuspid on p2 or p3, m1 trigonid less than three times as long as the talonid, m1 protoconid relatively low, broad and posteriorly inclined, m1 metaconid higher than paraconid, m1 entoconid and entoconulid poorly differentiated, m2 two-rooted, and m2 alveoli on the ascending ramus.

In a re-evaluation of the phylogeny and classification of European mustelids, Wolsan (1993) recently removed *Plesictis vireti* from *Plesictis* and placed it in the new genus *Franconictis.* Given its strong similarity to *P. vireti,* we identify KAN 401-67 as *Franconictis,* but do not attempt a definite species-level identification of so incomplete a specimen. Therefore, we identify KAN 401-67 as *Franconictis* sp. aff. *F. vireti.* M. Wolsan (in litt., 1997) notes that KAN 401-67 is slightly smaller and "more primitive" than *F. vireti* and probably represents a new species of *Franconictis,* but we believe the specimen is inadequate material upon which to base a new species.

Plesictis in Asia

To our knowledge (also see Russell & Zhai 1987, Werdelin 1996), *Plesictis* has been reported only twice from Asia. Gabuniya (1964) first reported *Plesictis* based on an isolated canine, fragment of a distal humerus and partial metacarpal (Gabuniya 1964, figs. 17–19) from the Benara locality (late Oligocene) in western Georgia. These fossils represent a small carnivore, but are not sufficient to identify *Plesictis.* Therefore, we identify them as Carnivora, indeterminate.

Mellett (1968) reported cf. *Plesictis* sp. from the upper part of the Hsanda Gol Formation (Mongolia, late Oligocene) based on AMNH 21654, a right dentary with m1–2 (Fig. 3). In this specimen, m1 is much larger than m2 and has a long, tall trigonid with the basin broadly open lingually. Its protoconid is large, tall and inclined postero-labially, and the metaconid is a much lower, pointed cuspid lingual to the protoconid. The paraconid is intermediate in size between the protoconid and metaconid and is massive and projects anteriorly. A carnassial notch interrupts the paracristid. The talonid is very low and cup-like with a distinct hypoconid. The m1 length = 8.4 mm, width = 4.0 mm.

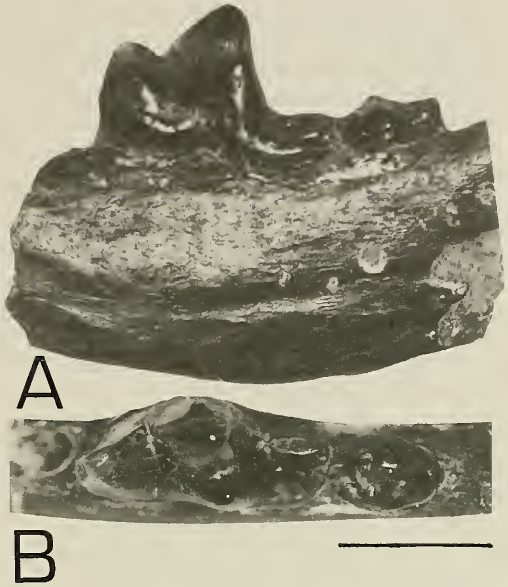

Fig. 3. AMNH 21654, *Stenoplesictis constans* from the Hsanda Gol Formation of Mongolia, right dentary fragment with m1–2, lingual (A) and occlusal (B) views. Bar scale = 5 mm.

The m2 is a small, oval tooth with a three-cusped trigonid and a low talonid with a shelf-like posterior rim. The m2 length = 3.6 mm, width = 2.8 mm.

This specimen conforms well to *Stenoplesictis,* particularly in its relatively tall m1 trigonid, prevallid shear on m1, small m2 with a well developed trigonid and narrow, trenchant talonid, and lack of m3 (Dashzeveg 1996). Indeed, AMNH 21654 closely resembles *Stenoplesictis constans* from the Hsanda Gol Formation (Matthew & Granger 1924, fig. 6F), to which we assign it. Therefore, there are no well founded reports of *Plesictis* in Asia.

Biostratigraphy and Biochronology

The locality from which KAN 401-67 was collected is on the right bank of the Ayaguz River, 29 km downstream from the town of Ayaguz, in eastern Kazakstan. The vertebrate-producing strata (Fig. 4) here rest with erosional unconformity on red beds

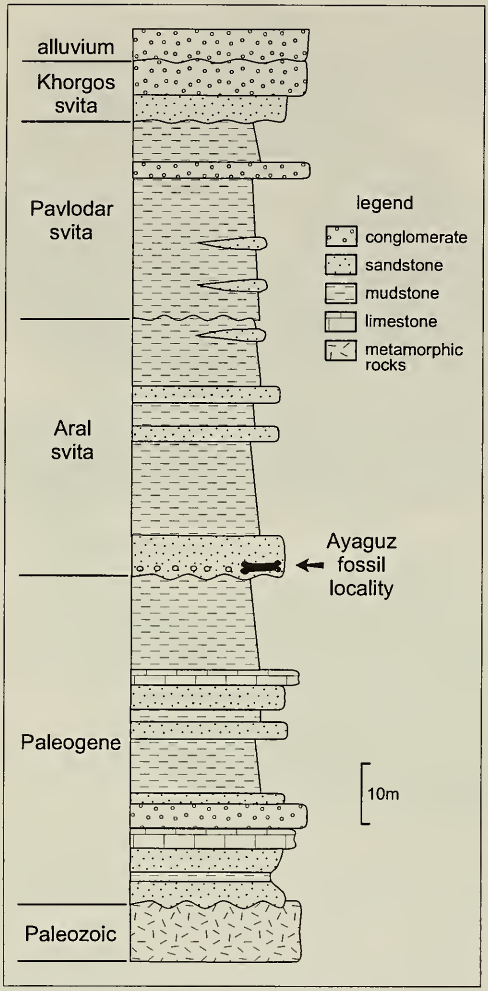

Fig. 4. Measured section of strata exposed in the Ayaguz River basin showing the stratigraphic position of the Ayaguz fossil mammal locality (after Tolochko & Aubekerova 1971).

that elsewhere in the Balkash-Alakol basin produce middle Eocene (Irdinmanhan) mammals (on the Shinzhaly River to the south: Didenko-Kislitsina 1990; Lucas et al. 1997). The fossiliferous bed at the Ayaguz River locality is composed of rusty green sandy clays and sandy gravel lenses at the base of a section referred to as "Aral svita" by Tolochko & Aubekerova (1971). In addition to *Franconictis,* the following taxa have been reported from this site: the lagomorphs *Sinolagomys* cf. *S. major* Bohlin and *Desmatolagus* cf. *D. robustus* Matthew & Granger; the castorids *Asiacastor antecedens* Lychev and *Steneofiber depereti* Mayet; and an indeterminate tragulid artiodactyl (Musakulova 1971, Erbayeva 1982, Lychev 1982).

Desmatolagus ranges in age from Ergilian to Shandgolian in China-Mongolia, and is a characteristic Oligocene genus (Russell & Zhai 1987, Qiu & Qiu 1995). The ochotonid *Sinolagomys* is a characteristic late Oligocene taxon in China and Mongolia, though it has its youngest occurrence (*S. pachygnathus*) in the early Shanwangian (early Miocene) of China (Qiu & Qiu 1995). Therefore, Erbayeva (1982) assigned the Ayaguz mammal locality a late Oligocene age.

Lychev (1982, 1987, *in* Lychev & Aubekerova 1971) described *Asiacastor* from localities in eastern Kazakstan that he assigned a Miocene age, although there is no clear basis for the age assignment. Indeed, *Asiacastor* is known from the late Oligocene Aral local fauna, north of the Aral Sea in western Kazakstan (Lucas et al. 1998). In Asia, the genus *Steneofiber* is of Oligocene and Miocene age (Russell & Zhai 1987). Tragulids range through the Oligo-Miocene boundary, so the indeterminate tragulid from the Ayaguz locality is of no precise biochronological significance. We thus support Erbayeva's (1982) assignment of a late Oligocene age to the Ayaguz mammal locality.

Franconictis is known in European early Miocene (MN 1–4) mammal assemblages (Mein 1989, Bruijn et al. 1992, Wolsan 1993, Morlo 1996, Steininger et al. 1996). Its occurrence in eastern Kazakstan thus is an extension of its temporal range back to the late Oligocene. Wolsan's (in litt. 1997) interpretation of the Kazak specimen of *Franconictis* as more primitive than European *Franconictis vireti* is consistent with an older age for the Kazak occurrence. Furthermore, given that the distribution of *Franconictis* in Asia is largely unknown, an older age for the genus in Asia than in Europe is quite plausible. On face value it might suggest an Asian origin of the genus during the Oligocene, and subsequent immigration to Europe in the early Miocene.

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 6. An intergeneric hybrid, *Aglaiocercus kingi* × *Metallura tyrianthina*, from Venezuela

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Abstract.—An intergeneric hybrid hummingbird, *Aglaiocercus kingi* × *Metallura tyrianthina,* is described. External measurements of the hybrid are intermediate of those of the parental species. Back plumage iridescence is bluer (511 nm) in the hybrid than in either of the parental species (553–571 nm). This color shift is thought to be caused by a developmental aberrancy or mutation which affects melanin granules that produce iridescence in feather keratins.

Under certain circumstances, interspecific hybridization may be an important source of genetic exchange among avian lineages that may create favorable conditions for rapid and significant evolutionary change (Grant & Grant 1992). From an analysis of data in Panov's (1989) catalog of avian hybrids, Grant & Grant (1992) reported that 19.1% (61 of 319) of hummingbird species has hybridized in nature. A surprising 69.2% (36 of 52) of the hybridizing pairs is intergeneric (taxonomy of Sibley & Monroe 1990), a finding consistent with Prager & Wilson's (1975) thesis that interspecific hybridization potential is slowly lost during avian evolution. The true extent of hybridization among hummingbirds, however, is imperfectly known. Panov's (1989) compilation includes numerous poorly documented or erroneous records, as did its antecedent (Gray 1958). Moreover, many new hybrid combinations have been reported recently (e.g., Graves 1990, 1996a, 1998a; Graves & Zusi 1990; Hinkelmann 1996; Weller & Schuchmann 1997). A definitive analysis of hybridization and phyletic reticulation must await a robust phylogeny and a systematic survey of purported hybrids, type specimens, and museum collections. Here I describe an intergeneric hybrid combination, *Aglaiocercus kingi* × *Metallura tyrianthina.*

Materials and Methods

The unsexed specimen (American Museum of Natural History [AMNH] 146645) was collected by S. Gabaldon in Estado Mérida, Venezuela. The exact locality, elevation, and date of collection are unknown. The specimen appears to be a male in subdefinitive plumage as evidenced by the faint striations on the maxillary ramphotheca (see Ortiz-Crespo 1972) and by its elongated tail (Fig. 1 & 2). Five different identifications have been written in ink and pencil (in quotations below) on the two attached AMNH labels since the specimen was cataloged in 1927 (in probable order of occurrence): (a) "*Cyanolesbia*" [=*Aglaiocercus*]; (b) "*Aglaiocercus ?caudata*" [=*Aglaiocercus kingi caudatus*]; (c) "*Metallura purpureicauda*" [=*Chalcostigma purpureicauda*]; (d) "?Hybrid?, *Aglaiocercus caudata* × *Ramphomicron*" [=*Aglaiocercus kingi caudatus* × *Ramphomicron microrhynchum*]; and (e) "*Aglaiocercus emmae caudata,* (melanistic aberration),

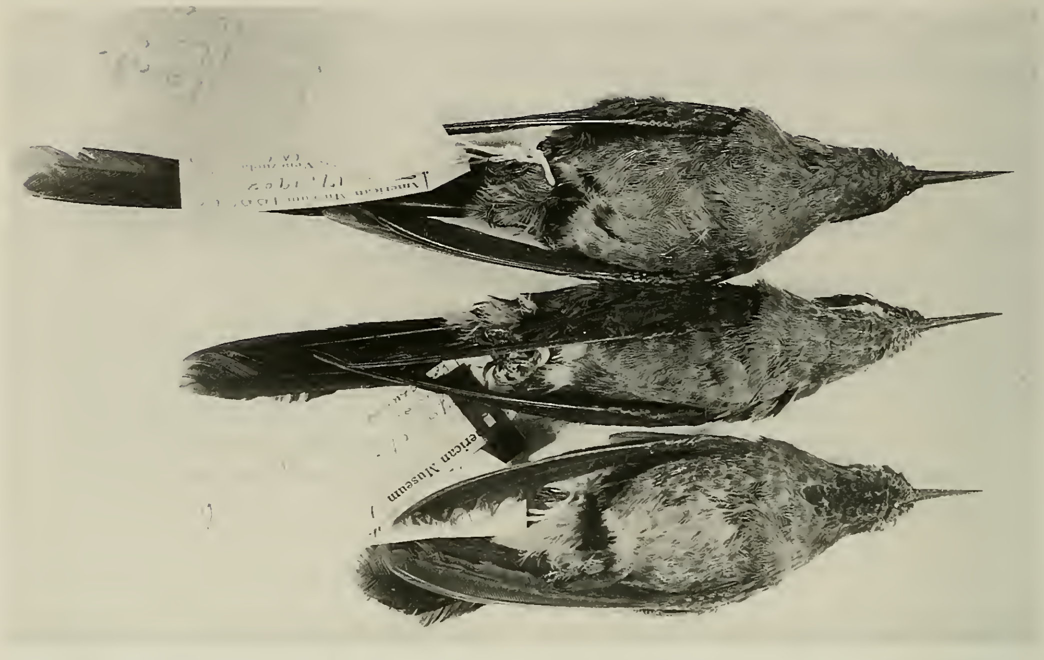

Fig. 1. Ventral views of male *Aglaiocercus kingi caudatus* (top), *Metallura tyrianthina oreopola* (bottom), and a probable hybrid, *A. kingi caudatus* × *M. tyrianthina oreopola* (AMNH 146645).

Fig. 2. Probable hybrid, *Aglaiocercus kingi caudatus* × *Metallura tyrianthina oreopola* (AMNH 146645).

fide J. Berlioz, Apr. 1975" [=*Aglaiocercus kingi caudatus*].

I compared the oft-identified specimen with series of all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), in the collections of the American Museum of Natural History and the National Museum of Natural History (USNM), Smithsonian Institution. For the purpose of hybrid diagnosis, I considered all hummingbirds (Trochilinae; taxonomy of Sibley & Monroe 1990) that occur in Estado Mérida as potential parental species (Phelps & Phelps 1958, Meyer de Schauensee & Phelps 1978) (Appendix 1). In addition, I compared the specimens directly with the holotypes of *Chalcostigma purpureicauda* (AMNH 483931), *Lesbia ortoni* (AMNH 156651), *Zodalia thaumasta* (USNM 173911), and *Aeronympha prosantis* (Field Museum of Natural History, FMNH 11852), and with notes, photographs, and videotape of the holotype of *Heliangelus zusii* (Academy of Natural Sciences of Philadelphia, ANSP 159261).

Color descriptions given in Appendix 2 were made under natural light. I evaluated the color of dorsal plumage (center of back) and the ventral surfaces of the rectrices with a reflectance spectrophotometer equipped with a 11.0 mm aperture (Color Mate Colorimeter, Milton Roy). The colorimetric characters were described in terms of opponent-color coordinates (*L, a, b*) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (*L*), red-green (*a*), and yellow-blue (*b*). The rationale is that a color cannot be red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value *a,* which is positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by *b* for yellows and $-b$ for blues. The third coordinate *L,* ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. In other words, the more light reflected from the plumage the higher the *L* value will be. It should be noted that visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. Dominant wavelengths reflected from plumage surfaces are listed for comparison. Data in Table 1 were compiled from the averages of five independent measurements (specimen moved from aperture between trials) for each plumage area per specimen.

Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 2). Measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

There are three alternatives to consider– the specimen represents an aberrant color morph of *A. kingi* or some other species, a hybrid, or an undescribed species. The specimen differs significantly in size and shape from all species in Appendix 1. In particular, the rectrices of the specimen are considerably wider, flatter in cross section, and more iridescent on the ventral surfaces than in *A. kingi,* indicating that it is not simply a melanistic example of that species as suggested by Berlioz on the specimen label. Because hybrids have no standing in zoological nomenclature, the burden of proof rests on the investigator to refute this possibility before bestowing species status on a unique specimen. Because the evidence points to hybridization, I refer to the specimen as a hybrid in the remainder of the paper.

The diagnosis was approached in a hierarchical manner. The presumed parental species of the hybrid first were hypothesized through the comparative analysis of plumage pattern, as well as from feather

Table 1.—Ranges and means (±standard deviation) of opponent color coordinates (*L, a, b*) and dominant wavelength reflected from dorsal plumage (center of back) and the ventral surface of rectrices in male *Aglaiocercus kingi caudatus, Metallura tyrianthina oreopola,* and their probable hybrid (AMNH 146645).

Variables		*A. kingi* (*n* = 12)	*M. tyrianthina* (*n* = 12)	Hybrid
Back plumage				
L (Lightness)	(*L*)	23.6–30.1 27.1 ± 1.8	21.5–26.6 24.2 ± 1.4	24.1
a (Red [+]/Green [−])	(*a*)	−14.8–(−6.6) −10.9 ± 2.9	−7.1–(−0.6) −3.7 ± 1.8	−7.9
b (Yellow [+]/Blue [−])	(*b*)	15.4–20.2 17.8 ± 1.4	12.6–20.9 17.3 ± 2.3	2.9
Dominant Wavelength (nm)		553.1–563.8 557.8 ± 3.5	562.8–570.5 566.7 ± 2.6	511.3
Ventral surface of rectrices				
L (Lightness)	(*L*)	18.8–21.1 20.1 ± 0.7	20.3–23.9 21.7 ± 1.0	20.6
a (Red [+]/Green [−])	(*a*)	3.8–5.9 4.9 ± 0.6	11.5–17.0 14.6 ± 1.6	10.6
b (Yellow [+]/Blue [−])	(*b*)	−4.3–1.5 −0.9 ± 1.9	5.5–14.9 9.5 ± 2.9	−7.1
Dominant Wavelength (nm)		487.2–652.1 520.7 ± 47.7	588.9–622.7 602.5 ± 11.2	541.0

and bill shape. The restrictive hypothesis then was tested with a quantitative analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, Graves & Zusi 1990).

Table 2.—Ranges and means (±standard deviation) of measurements (mm) of males of *Aglaiocercus kingi caudatus* (subdefinitive plumage, see Appendix 2), *Metallura tyrianthina oreopola,* and their presumed hybrid (AMNH 146645).

Character	*A. kingi* (*n* = 21)	*M. tyrianthina* (*n* = 20)	Hybrid
Wing chord	59.7–63.6 61.8 ± 1.0	54.0–61.5 57.7 ± 2.2	61.4
Bill	11.0–13.6 12.3 ± 0.7	9.1–10.6 9.9 ± 0.4	11.1
Rectrix 1	22.8–25.3 24.1 ± 0.8	33.7–38.9 36.1 ± 1.6	32.1
Rectrix 2	29.0–33.6 31.3 ± 1.2	34.3–41.3 37.9 ± 1.8	36.9
Rectrix 3	38.9–46.7 42.8 ± 1.9	36.0–43.6 39.9 ± 1.8	43.1
Rectrix 4	53.7–61.5 58.0 ± 2.2	38.4–45.3 41.5 ± 2.1	49.0
Rectrix 5	67.5–102.7 81.5 ± 8.7	37.9–46.3 42.2 ± 2.7	55.8

Results and Discussion

Plumage characters.—Salient characters of the hybrid that permit its parental species to be identified include: (a) moderately elongated outer rectrices (fork depth = 23.7 mm), nearly flat in cross section; (b) unmarked rectrices exhibiting metallic iridescence on the dorsal and ventral surfaces; (c) short tibial plumes (not extending to hallux); and (d) short straight bill (11.1 mm). Two species in the pool of potential parental species (Appendix 1) possess elongated tails (length of rectrix 5 > 55 mm): *Ocreatus underwoodii* and *Aglaiocercus kingi. Ocreatus* can be deleted from the list of possibilities because the hybrid lacks evidence of spatulate rectrices or lengthened tibial plumes. *Aglaiocercus kingi* is thus identified as one of the parental species.

Determination of the other parental species is equally straightforward. The intensity of the metallic iridescence reflected

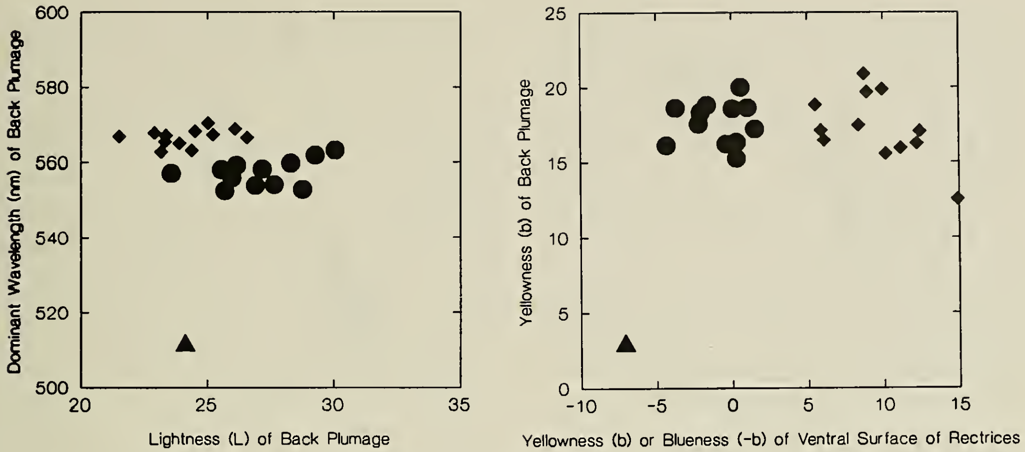

Fig. 3. Bivariate plots of spectrophotometric data from male hummingbirds: *Aglaiocercus kingi caudatus* (circles); *Metallura tyrianthina oreopola* (diamonds); and a probable hybrid, *A. kingi caudatus* × *M. tyrianthina oreopola* (triangle; AMNH 146645).

from the ventral surfaces of the hybrid's rectrices is matched or exceeded only in *Metallura tyrianthina.* Details of plumage pattern and feather shape are sufficient to suggest that the parentage of the hybrid is *Aglaiocercus kingi* × *Metallura tyrianthina* (see Appendix 2). None of the other species in Appendix 1, considered two at a time, can account for the characters observed in the hybrid. In particular, the ventral rectricial surfaces of the hybrid are metallic reddish-purple as opposed to dull black or purplish-black in both *Ramphomicron microrhynchum* and *A. kingi,* effectively eliminating this pair of species from contention.

The question of plumage color.—Iridescence in hummingbirds is caused by the interference of light reflected from the upper and lower surfaces of gas-filled vacuoles in melanin granules in the keratin of feather barbules, which are compactly stacked in 7–15 layers in the barbule keratins (Dorst 1951; Greenewalt et al. 1960a, 1960b; Lucas & Stettenheim 1972). Carotenoid pigments have not been extracted from iridescent feathers. Employing transmission electron microscopy and micro-spectrophotometry, Greenewalt et al. (1960a, 1960b) found melanin granules to be elliptical in shape, about 2.5μ long, 1.5μ wide, and 0.15μ thick. Briefly summarized, they found that granules contain a fairly uniform layer of gas-filled vacuoles that resemble a monolayered foam. The melanin matrix and gas-filled vacuoles have refractive indices of ~2.0 and 1.0, respectively. The color of iridescence varies according to the thickness of the granule and the amount of gas in the vacuoles. Iridiscent colors change from blue to green to orange and finally to red, as the effective refractive index of granules advances from 1.45 to 1.90 (figure 4 of Greenewalt et al. 1960a). Melanin granules in noniridescent parts of feathers lack vacuoles.

The pattern of bluish-green iridescence in the hybrid corresponds precisely to that of green iridescence in the parental species, suggesting a single mutational or developmental aberrancy that affects plumage color. The dominant wavelength reflected from dorsal plumage is shorter in the hybrid (511 nm) than in the parental species: *Aglaiocercus kingi* (553–564 nm) and *Metallura tyrianthina* (563–571 nm) (Table 1, Fig. 3). The premise that "hybridization produces no traits characteristic of genera or species other than those involved in the particular cross" (Banks & Johnson 1961:3) was extended to spectrophotometric measures of

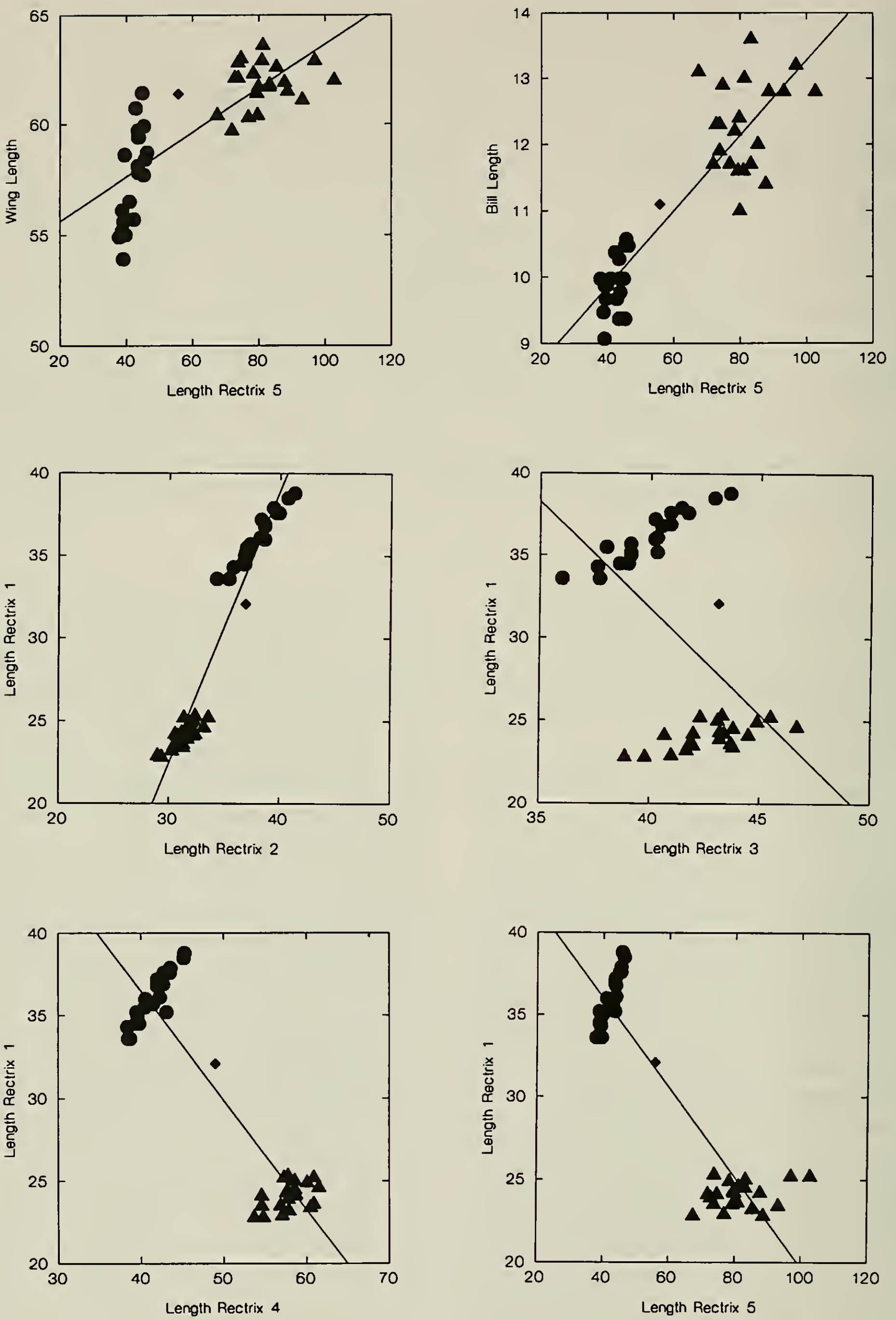

Fig. 4. Bivariate plots of mensural characters of male hummingbirds: *Aglaiocercus kingi caudatus* (triangles); *Metallura tyrianthina oreopola* (circles); and a probable hybrid, *A. kingi caudatus* × *M. tyrianthina oreopola* (diamond; AMNH 146645). Least squares regression lines are projected for comparison.

plumage color (Graves 1996b). Both assumptions are violated in the present example.

Elucidation of the micro-structure and spectrophotometric properties of melanin granules in *Aglaiocercus kingi, Metallura tyrianthina,* and the hybrid is beyond the scope of this paper. Several observations on hummingbird plumages, however, are worth noting. A variety of plumage aberrations, unassociated with hybridization, has been observed in hummingbirds, including leucism, albinism, schizochroism, erythrism, and melanism (Salvin 1892, Banks & Medina 1963, Greenway 1978, Graves 1998b). Subtle within-population variation in iridescent color is commonly observed whenever large series of species are assembled. Although post-mortem effects may be partially responsible in some cases (Graves 1986, 1991), most of the observed variation in iridescence among individuals, factoring out the effects of sex and age (see Bleiweiss 1992), is due to genetic and developmental factors. Pronounced color shifts of the magnitude observed in this hybrid are rare but not unknown (e.g., Salvin 1892, Greenway 1978). The example described here seems to be the first in which a hybrid hummingbird exhibits a major plumage aberrancy.

External measurements.—One of the guiding principles of hybrid diagnosis is that hybrids are not larger or smaller than their parental species (Graves 1990). Morphological luxuriance or dwarfism in hybrid hummingbirds has not been recorded. Male *Aglaiocercus kingi* and *Metallura tyrianthina* are similar in bill length (cumulative range, 9.1–13.6 mm) and wing chord (cumulative range, 54.0–63.6 mm), but differ markedly in tail size and shape (Table 2, Fig. 4). Bivariate plots of rectrix length of the parental species exhibit positive (1 vs. 2) or negative (1 vs. 3, 1 vs. 4, 1 vs. 5) allometry. Except for rectrix 3, measurements of the hybrid fall between the character means for *A. kingi* and *M. tyrianthina,* and, in several cases, approximate the values predicted by least squares regression on bivariate plots (Table 2, Fig. 4). In summary, plumage pattern, distribution and intensity of iridescence, rectrix shape, and mensural characters provide strong support for the hypothesis of hybridity (*Aglaiocercus kingi* × *Metallura tyrianthina*).

Previous records.—A hybrid of *Aglaiocercus kingi* and *Metallura tyrianthina* was reported once before by Meyer de Schauensee (1947:108), who described a specimen (No. 134) obtained in Bogotá, circa 1909, from the Brother Nicéforo María collection:

> "... fore-crown glittering brassy green, hind crown and back dark bluish green, rump and upper tail coverts bluer; chin dusky, throat patch shaped as in *Metallura tyrianthina* but blue instead of green; breast dark bluish green, bases and edges of the feathers buffy; belly dark green, the bases of the feathers white, showing through and giving a somewhat barred appearance; tail purple, deeply forked, the outermost tail feathers 50 mm., the central ones 30 mm., wing 61 mm., culmen 12.5 mm."

The brief description of Nicéforo's specimen differs in minor details from the Venezuelan specimen (AMNH 146645). The two specimens are similar in size. Nicéforo's specimen possesses a bluish gorget as might be expected in an adult male hybrid of *Metallura t. tyrianthina* and *Aglaiocercus k. kingi* from the Cordillera Oriental of the Colombian Andes. Whereas I characterized the back color of the Venezuelan specimen as "greenish-blue," Meyer de Schauensee used the term "bluish-green" for Nicéforo's specimen. This and other discrepancies might reflect semantics or real differences in color. Unfortunately, the whereabouts of Nicéforo's specimen is unknown, although another mentioned in Meyer de Schauensee's paper was deposited in the Academy of Natural Sciences of Philadelphia (Nicéforo no. 148, now ANSP 159261; Graves 1993).

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Appendix 1

Species of hummingbirds that occur in Estado Mérida, Venezuela: *Campylopterus falcatus, Colibri thalassinus, C. coruscans, Klais guimeti, Lophornis delattrei, L. stictolophus, Chlorestes notatus, Chlorostilbon mellisugus, C. poortmani, Thalurania furcata, Hylocharis cyanus, Chrysuronia oenone, Amazilia versicolor, A. fimbriata, A. viridigaster, Chalybura buffonii, Heliodoxa leadbeateri, Sternoclyta cyanopectus, Coeligena coeligena, Ocreatus underwoodii, Aglaiocercus kingi, Heliomaster longirostris, Chaetocercus jourdanii.*

Appendix 2

Comparative description of plumages of male *Aglaiocercus kingi caudatus, Metallura tyrianthina oreopola,* and their presumed hybrid, AMNH 146645. The molts and plumages of male *Aglaiocercus* spp. are incompletely known. Young males (>6 months?) acquire a plumage that differs from the definitive plumage of adult males. This subdefinitive plumage is characterized by shorter outer rectrices, an incompletely developed crown patch (8 of 20 examined), and remnants of a white rump patch (see Zimmer 1952). One quarter (5 of 20) of the males in subdefinitive plumage retain a few striations on the maxillary ramphothecum, a character usually interpreted as a sign of immaturity (Ortiz-Crespo 1972). The descriptions of *Aglaiocercus kingi* given below refer to the subdefinitive plumage.

Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

The dark bluish-green crown of young *kingi* is replaced (from anterior to posterior) by an ovate crown patch composed of brilliant bluish-green feathers. The hindneck, back, and rump are dark green; feathers are gray, tipped with green. Upper-tail coverts are bluish-green. A few white feathers form an indistinct patch on the lower back.

The dorsal plumage of *tyrianthina* is dark dusky green, brighter on the crown, and with coppery highlights on the lower back and rump. Feathers are gray, banded subterminally with coppery-green, and tipped broadly with dark green. When viewed head-on in direct light, plumage posterior to the midcrown region appears sooty black. Immature *tyrianthina* lack a contrasting rump patch.

Under a diffuse light source, the dorsum of the hybrid is a rich greenish-blue (paler on the crown), a color that is distinctly different from that of the presumed parental species. Feathers on the left side of the forecrown are discolored, possibly by a preservative chemical. Dorsal feathers are dark gray, tipped with greenish-blue. Crown feathers are not modified as in adult *kingi.* When light is reflected obliquely (>90 from the observer), the dorsal plumage appears purple; when viewed head-on the hindcrown, back, and rump appear black. A few rump feathers are tipped with buff.

The ventral plumage of *kingi* is medium green exhibiting subdued iridescence. A few small shining green disks occur on the throat of more mature individuals. The barbs of ventral feathers are narrowly tipped with buff or grayish-buff, especially along the midline of the abdomen. Some males in juvenile and subdefinitive plumage (e.g., AMNH 484067) have a white or buffy-white line extending from the base of the bill posterior to below the eye. Downy vent feathers are dark gray tipped with white or pale gray. Undertail coverts are dark green broadly edged with buff. Tibial feathers are short (extending half way to the hallux from the tibiotarsal joint), dark olive-gray and narrowly tipped with scattered grayish-buff barbs.

The venter of *tyrianthina* is dark dull green; feathers are tipped with buff or grayish-brown, especially along the midline. Feather tipping imparts a mottled appearance to the underparts. A narrow ovate gorget extends from the chin to the upper breast in *tyrianthina.* When view head-on in direct light, the auriculars and sides of the throat appear matte black and contrast greatly with the brilliant green gorget. Subadult males have a buffy line extending from the bill to below the eye.

Vent feathers are dark gray tipped with white or pale gray. Under-tail coverts are buff with a large broadly lanceolate spot (coppery- or bronzy-red) along the midline. Tibial feathers (dark gray tipped with buff) extend to the base of the hallux.

The venter of the hybrid is similar in pattern to *kingi,* but with the green portions replaced with bluish-green (paler than dorsum). A small brilliant feather occurs along the midline at midthroat (deep blue tip separated from the gray base by narrow blending bands of light blue and coppery-gold). A buffy-white stripe extends from the bill to below the eye (Fig. 2). Vent feathers are dark gray tipped with white. Undertail coverts are buff with a lanceolate subterminal spot (purple) near the midline. Tibial feathers (dark gray broadly tipped with buff) of the hybrid extend about halfway to the hallux, but may have been damaged by knotting of the specimen label string.

The remiges of *kingi* are brownish-black faintly tinted with purple. The outer vanes of the primary coverts and the innermost secondaries are edged with shining green or bluish-green; secondary coverts are broadly tipped with bluish-green. The remiges of *tyrianthina* are very similar in color but faintly tinted with bronze or olive. Wing coverts and the innermost secondaries are bronzy-green.

The remiges of the hybrid resemble those of *kingi.* Wing coverts and innermost secondaries are purple tipped with dark bluish-green.

The tail of *kingi* is deeply forked. The basal portions of the rectrices that are obscured in the folded tail are black. The exposed dorsal sections of the inner rectrices (1–4) are deep brilliant purple tipped with bluish-green. The outermost rectrices (5) lack bluish-green tips, are greatly elongated, narrow (5–6 mm wide, 25 mm from tip), and bowed in cross-section. Inner rectrices are smoothly tapered; rectrix 5 is bluntly tipped. Ventrally, the vanes are dull purplish-black. The rachises in *kingi* are blackish-brown dorsally, medium brown ventrally.

The tail of *tyrianthina* is shallowly forked. Rectrices are wide (10–11 mm), nearly flat in cross-section, abruptly truncate at the tip, and metallic coppery-red above and below. Rachises are dark brown above and below.

The tail of the hybrid is moderately forked. Feather size and shape are intermediate between *kingi* and *tyrianthina.* The outermost rectrices (5) are slightly bowed in cross-section (ca. 9.3 mm at widest point). Rectrices are metallic reddish-purple, above and below, the innermost (1–2) are diffusely tipped with purple. This iridescence, especially from the ventral surfaces, is similar in visual essence to that of *tyrianthina.* Rachises are dark brown above, medium brown ventrally.

Bill color is black in *kingi, tyrianthina,* and hybrid. In dorsal profile, the bills of both parental species are abruptly tapered, more so in *kingi.* The bill profile of the hybrid is similar to that of *tyrianthina.*

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A new species of *Alsodes* (Amphibia: Anura: Leptodactylidae) from southern Chile

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Abstract.—A new species of frog, *Alsodes kaweshkari*, is described from the temperate *Nothofagus* forests of South America in Southern Chile. From the karyological point of view this species is included in the *monticola* group (2N = 26) of the genus *Alsodes.*

The genus *Alsodes* Bell 1843, is distributed in central and southern Chile and along the eastern slope of the Andes, in Argentina (south of Mendoza city). Frost (1985) included the following species in the genus: *A. barrioi, A. gargola, A. illotus, A. laevis, A. montanus, A. monticola, A. nodosus, A. pehuenche, A. tumultuosus, A. vanzolinii,* and *A. verrucosus.* Formas (1989) studied the identity and synonymy of the Chilean frog *Eupsophus vittatus* and concluded that this species must be included in the genus *Alsodes* as *A. vittatus.* The taxonomic status of *A. illotus* is not clear (Cei 1980) and according to Frost (1985) *A. laevis* has not been collected since its description by Philippi (1902). The most remarkable characteristic of the males of this genus is the presence of thorny structures on the fingers and round spiny patches on the chest.

During the course of collecting frogs in southern Chile we found a new species of *Alsodes* which is here described. Moreover, we describe the karyotype and C-banded chromosomic pattern of the new taxon. The bands of hemoglobin of the new species were characterized electrophoretically and compared with those of *A. monticola* (type species of the genus).

Methods and Materials

Specimens were deposited in the Instituto de Zoología, Universidad Austral de Chile (IZUA). Adults were measured with a dial caliper to the nearest 0.1 mm according to Cei (1962). The following measurements were taken: snout–vent length (SVL), head length, head width, nostril-snout distance, tibia length, and foot length. Internarial distance was measured according to Cei (1980) and eye diameter according to Duellman (1970).

The chromosomal characteristics were obtained from the holotype (IZUA 1624) according to the following methods: the animal was treated with 0.1% colchicine for two hours, then anaesthetized with diethyl ether, cut open ventrally under sterile conditions and its intestine carefully removed. Metaphase plates were obtained by squashing intestinal epithelium fragments that were hypotonically treated with distilled water, then fixed in acetic-alcohol (1:3), and finally placed in 45% acetic acid. Small tissue fragments were squashed between a glass slide and cover slip and dipped in liquid nitrogen; thereafter, the cover slip was removed with a razor blade to allow chromosomes to air dry. After 3 days, the chromosomes were stained for 15 minutes in Sorensen's phosphate buffer (pH 6.8), containing 4% Giemsa solution (Formas 1991). Centromeric positions were determined according to Levan et al. (1964). Secondary constrictions were included in the measurements. Chromosomes were stained to reveal C-band pattern position (Sumner 1972). Microscopic slides and the specimen (IZUA

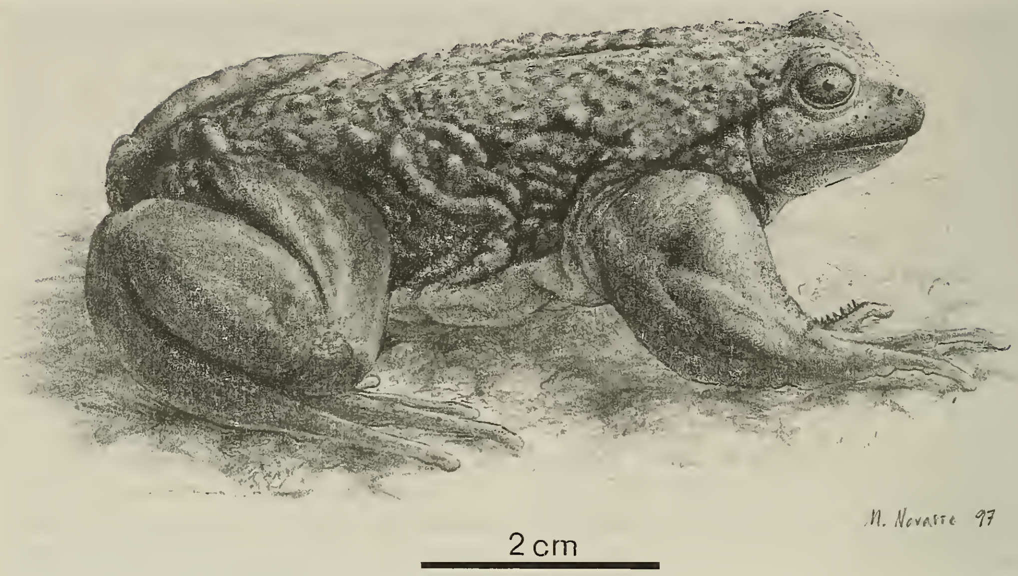

Fig. 1. *Alsodes kaweshkari* Holotype, IZUA 1624.

1624) were deposited in the amphibian collection of the Instituto de Zoología, Universidad Austral de Chile.

Hemoglobin was obtained according to the following methodology: blood was collected by cardiac puncture from the holotype and a specimen of *Alsodes monticola* (control species) using a sterile syringe with 3.8% of sodium citrate as anticoagulant; the red cells were washed 3 times with 0.85% NaCl and centrifuged at 700 g for 5 minutes at room temperature (20°C). The packed cells were hypotonically treated with distilled water (10 volumes) for 30 minutes and centrifuged at 3500 g for 10 minutes. The supernatant was stored at −70°C. The hemolyzate was treated according to the method described by Muir (1981) with modifications. We used a minicolumn (5 × 70 mm) of Sephadex G-50 equilibrated with 1.0 mM of potassium phosphate (pH 7.0). Fractions of 500 μl were collected and their absorbances measured at 410 nm, the wave length at which the porphyrin ring of the hemoglobin molecule absorbs specifically. Those fractions with the highest absorbance value were used for the electrophoretic analysis of the hemoglobin of the new species and *A. monticola.* To proceed with the electrophoresis the samples were denatured by heating (100°C, 5 minutes) in presence of 2% of betamercaptoethanol. Electrophoresis of the hemoglobins from *Alsodes kaweshkari* and *A. monticola* was carried out individually in vertical slab gels of polycrilamide (15%) in denaturant conditions at 20 mA for 20 hours (Laemmeli 1970). Gels were stained with Coomassie Blue R-250 for 2 hours and destained with acetic acid (7%). The molecular weight of the hemoglobin bands was estimated using a protein standard for molecular weight (Sigma Co).

Systematics

Alsodes kaweshkari, new species.
Fig. 1

Holotype.—IZUA 1624, an adult male collected by J. Ramón Formas on 8 March 1995, at Puerto Edén (49°8′S, 74°25′W, 10 m), Wellington Island, Ultima Esperanza Province, Magallanes and Chilean Antartic Region (XII Región), Chile (Fig. 2).

Paratype.—IZUA 1625, an adult male collected by Pablo Corti on 21 Oct 1995,

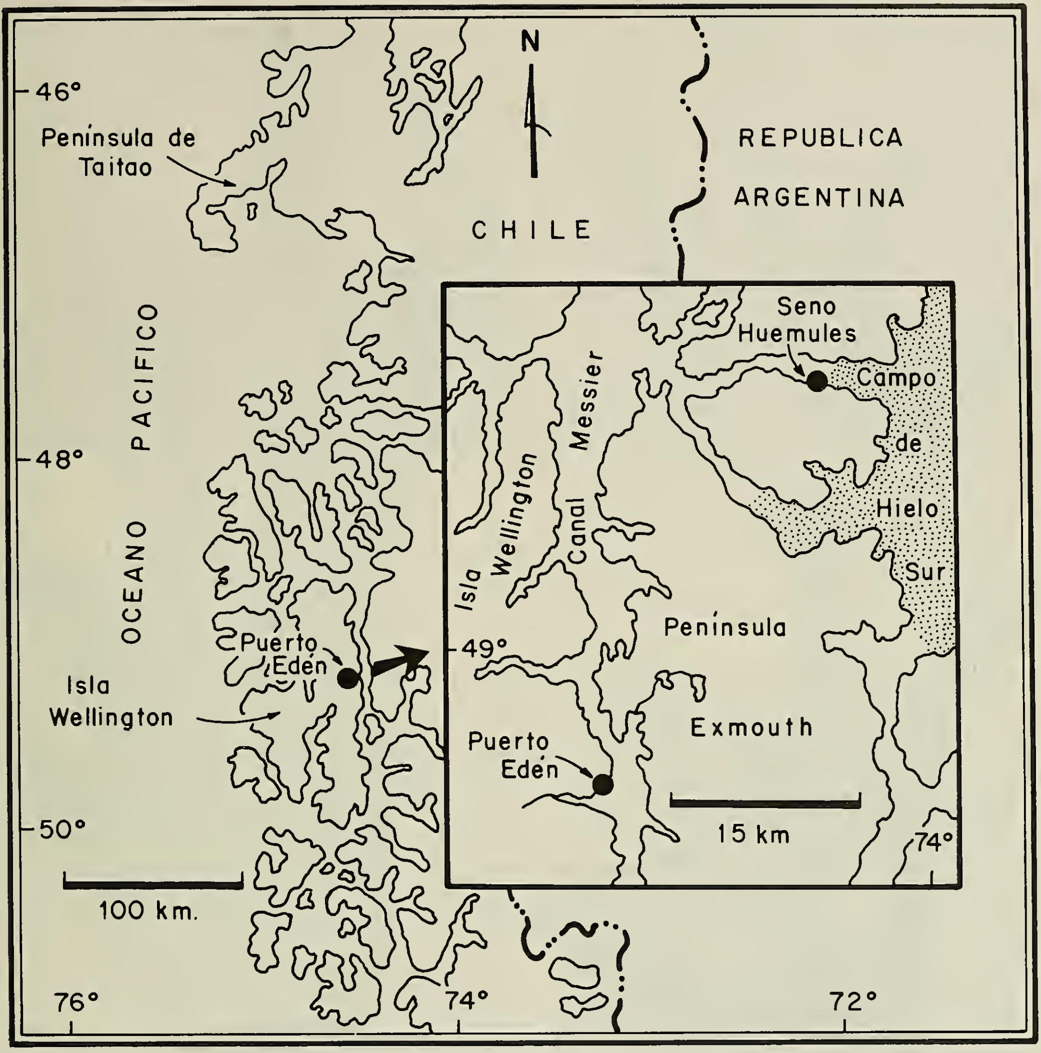

Fig. 2. Type locality of *Alsodes kaweshkari.*

at Seno Huemules (48°43'5S, 74°25'W, 8 m), Ultima Esperanza Province, Magallanes and Chilean Antartic Region (XII Región), Chile (Fig. 2).

Diagnosis.—*Alsodes kaweshkari* can be distinguished from its congeneric species by the following combination of characters: SVL 56.5–62.2 mm; toes totally fringed; webbing of feet present between all toes, but reduced; dorso-lateral surfaces granular; skin around vent and posterior thighs granular.

Description.—Based on the type series. Body robust, arms and legs well developed. Head depressed, slightly wider than long, its length 29% of snout–vent length. Snout truncated from above, rounded in lateral profile; canthus rostralis slightly rounded, loreal region concave in cross section; nostrils anterolateral, midway between tip of snout and anterior border of eye; eye diameter greater than distance between eye and nostril; internarial distance less than interorbital distance. Tympanum absent; postocular fold evident, reaching insertion of arm. Tongue rounded, without notch at tip.

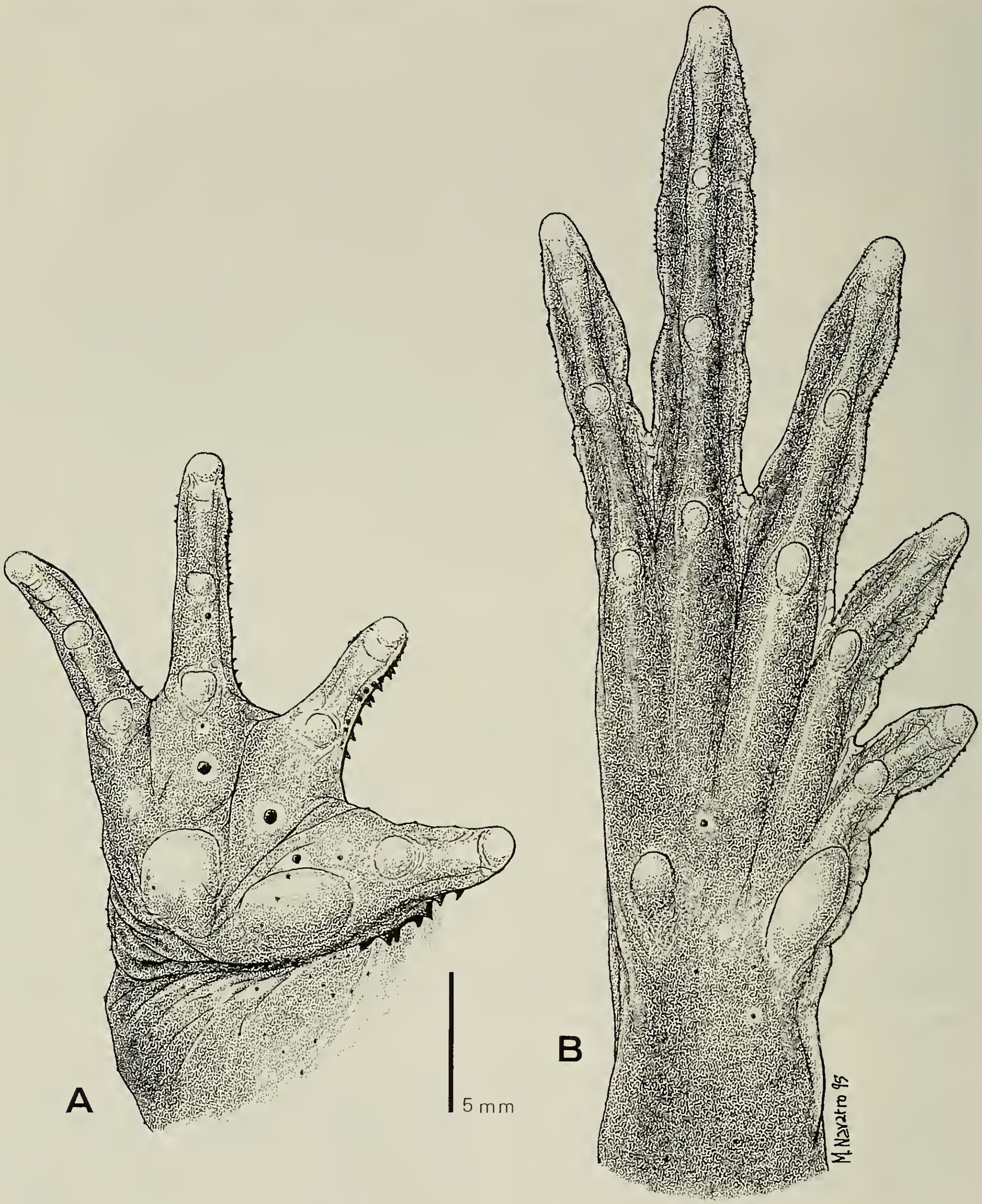

Fig. 3. Morphological details of the holotype. (A) Palmar view of the right hand. (B) Plantar view of the right foot.

Choanae oval-shaped; dentigerous processes of vomer between choanae. Forelimbs of males robust. Fingers in order of increasing length: II, I, IV, III. Webbing of hand absent. Fingers long with moderately globular tips. Inner palmar tubercle ovoid, outer palmar tubercle rounded; subarticular tubercles rounded, (Fig. 3A). First finger with strong thorny excrescences; second finger with narrow band of spines (Fig. 4B). Palmar

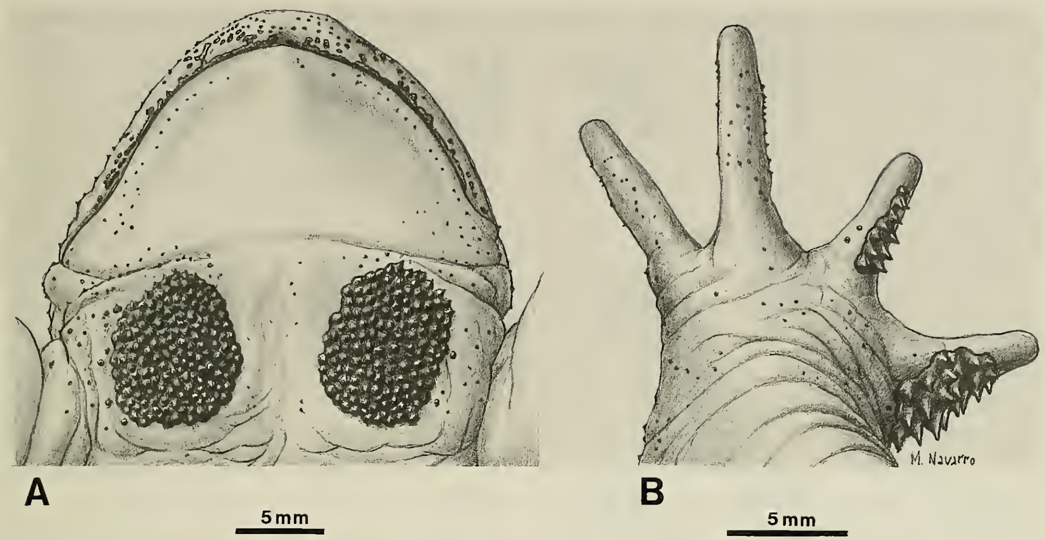

Fig. 4. Secondary sexual characters of the holotype. (A) Ventral view of the chest and throat. (B) Dorsal view of the left hand.

surface with few thorns irregularly distributed. Spines also present at lower border of mandible (Fig. 4A). Toes long, thick and fringed; in order of increasing length: I-II-III-V-IV; tips moderately rounded. Webbing present, thick, but reduced. Inner metatarsal tubercle oval, elongate; outer tubercle smaller than the inner, oval. Tarsal fold present; reaching middle of tarsus. Flanks and dorsal surface granular; ventral skin smooth with minute granules; skin around vent and posterior thighs granular. Chest of males with two bilateral rounded black patches of keratinous spines (Fig. 4A). Dorsal surfaces of head and areas below dorsolateral fold with granules.

The measurements of the holotype and the paratype are given in Table 1.

Coloration.—In alcohol, dorsal surfaces of ground, arms and legs dark gray. Venter whitish, gular area dark gray. Arms and legs whitish ventrally. The granular surface around posterior thighs dark gray. In life, dorsal surface, arms and legs brown. Belly whitish yellow. Areas around nostrils, lips and eyes light brown. The iris with a coppery reticulum.

Distribution and ecology.—The species is known from two Chilean localities (Puerto Edén and Seno Huemules) (Fig. 2). The type locality (Puerto Edén) is a small beach of the Wellington Island, near a small fishing town. There are small forests (*Nothofagus betuloides, Embothrium coccineum, Maytenus magellanicus,* and *Drymis winteri*) surrounded by typical tundra with plants of the genera *Donatia, Astelia,* and *Azorella* and rushes of the families Cyperaceae and Juncae. This area is situated in the oceanic cold temperate region (di Castri 1968). The annual mean temperature of this region is 8.8°C; the relative humidity is

Table 1.—Measurements (mm) of the type series of *Alsodes kaweshkari.*

Character	Holotype IZUA 1624 male	Paratype IZUA 1625 male
Snout–vent length	62.2	59.9
Head length	17.7	16.4
Head width	24.2	22.8
Eye diameter	7.0	6.7
Nostril–snout distance	4.0	3.6
Internarial distance	5.7	5.4
Tibia length	27.7	27.4
Foot length	33.8	30.9

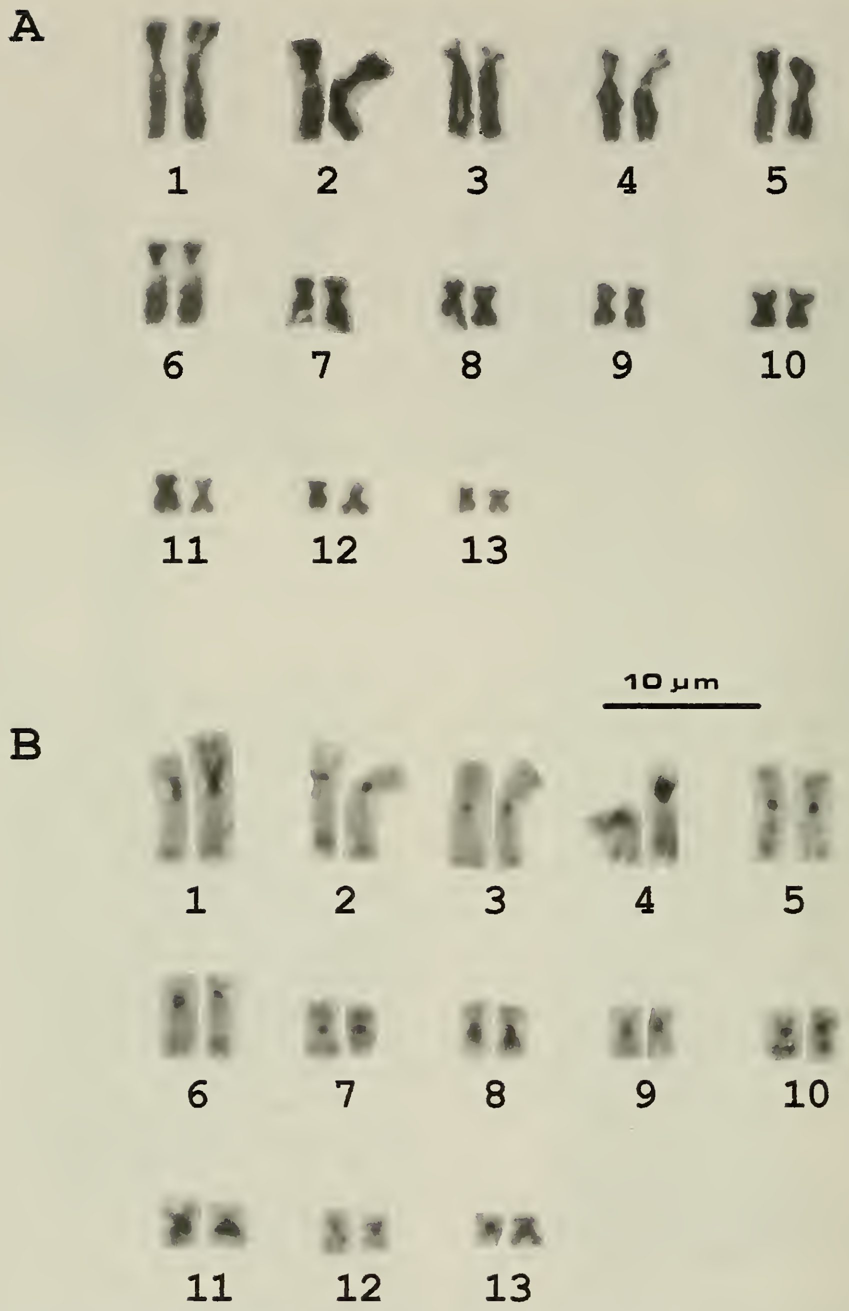

Fig. 5. Chromosomes of the holotype. (A) Karyotype. (B) C-banded karyotype.

87%, and the rain fall ranges from 2000–2500 mm per annum. The frog was collected under a log between the forest and the tundra. The male holotype shows its remarkable thorny excrescences on the chest and fingers (Fig. 4A, B). The following amphibians were also collected in this area: *Bufo variegatus, Batrachyla antartandica* and *Eupsophus calcaratus.* Lynch (1975) pointed out the presence of *Atelognathus*

Table 2.—Relative length, arm ratio (mean and standard deviation), and type of chromosomes (m = metacentric; sm = submetacentric; st = subtelocentric) of metaphase chromosomes of *Alsodes kaweshkari*. Relative length was calculated according to Bogart (1970). Arm ratio was calculated by dividing the short arm into the long arm. *Chromosomes with secondary constrictions.

Pair n°	Relative length	Arm ratio	Type
1*	148.72 ± 18.32	1.97 ± 0.20	sm
2	135.58 ± 18.76	1.71 ± 0.63	sm
3	126.80 ± 10.50	4.69 ± 0.48	st
4*	116.74 ± 12.13	2.28 ± 0.74	sm
5	102.27 ± 12.27	1.43 ± 0.50	m
6*	92.39 ± 7.21	2.05 ± 0.60	sm
7	74.03 ± 8.03	2.10 ± 0.32	sm
8	66.16 ± 6.46	1.42 ± 0.24	m
9	61.76 ± 6.00	1.30 ± 0.27	m
10	57.29 ± 6.43	1.20 ± 0.18	m
11	51.95 ± 5.54	1.90 ± 0.15	sm
12	48.73 ± 3.71	1.50 ± 0.27	m
13	39.75 ± 5.59	1.40 ± 0.12	m

grandisonae and Diaz & Nuñez (1988) reported *Alsodes verrucosus* (adult and tadpoles). The other locality where *Alsodes kaweshkari* was collected is Seno Huemules. This area has the same ecological characteristics as Puerto Edén. The male paratype, collected at a border of a cold stream, also has the nuptial asperities on fingers and chest.

Chromosomes.—Examination of 10 metaphase plates from the holotype revealed a diploid number of 2N = 26. All chromosomes are bi-armed and the fundamental number (NF) is 52. Pairs 5, 8–10, 12, 13 are metacentric, pairs 1, 2, 4, 6, 7, 11 are submetacentric, and pair 3 is subtelocentric. Pairs 1 and 4 have secondary constrictions on the smaller arm, and pair 6 exhibits secondary constrictions on the longer arm. The karyotype of *Alsodes kaweshkari* is shown in Fig 5A. A summary of the relative length, arm ratio, and type of chromosomes is presented in Table 2.

The C-banded karyotype, based on five plates (Fig 5B) shows constitutive heterochromatin in the pericentromeric region of all chromosomes. Thin heterochromatic bands can be discerned at some telomeres, especially in those of pairs 1, 2, 6 and 10. A thin insterticial band was observed in the long arm of pair 5. Pair 4 presents a polymorphic situation: one chromosome shows a remarkable band of pericentromeric position, but in the other the band is located in the centromeric region. This situation was observed in all the examined plates.

Hemoglobin.—Figure 6A shows the chromatographic profiles of the hemolysates of *Alsodes kaweshkari* and *A. monticola* obtained from the fractions collected in the Sephadex G-50 minicolumn. The fractions with the higher absorbance values at 410 nm (fraction 9 in *Alsodes kaweskari* and fraction 8 in *A. monticola*) were electrophoretically analyzed under the experimental conditions used in this study. Figure 6B indicates the electrophoretical patterns obtained for these species. Both taxa share a similar two-banded pattern with an anodal band (Hb_1) of 14.2 KDa an other catodal one (Hb_2) of 16.8 KDa.

Etymology.—The new taxon is named for the Kaweshkar indians, a brave people, hunters of sea-lions, who still live in Puerto Edén, the type locality of the new species.

Comparisons

When the adult snout–vent length of *Alsodes kaweshkari* (males, 59.9–62.2 mm) is compared with that of the other *Alsodes* species, it is observed that this frog is as large as *A. nodosus* (58.5 mm), *A. barrioi* (59.9 mm) and *A. tumultuosus* (61.5 mm). Other members of the genus are small [*A. vittatus* (37.4 mm), *A. gargola* (40.8 mm), and *A. verrucosus* (42.4 mm)] and medium-sized [*A. monticola* (49.1 mm), *A. montanus* (50.2 mm), *A. vanzolinii* (51.1 mm), and *A. pehuenche* (52.3 mm)]. Among the large-sized frogs, the external morphology of the foot provides useful characteristics to identify each taxon. One example of this is *A. nodosus,* a species characterized by the absence of lateral fringes (present on the toes of *A. barrioi, A. kaweshkari,* and *A.*

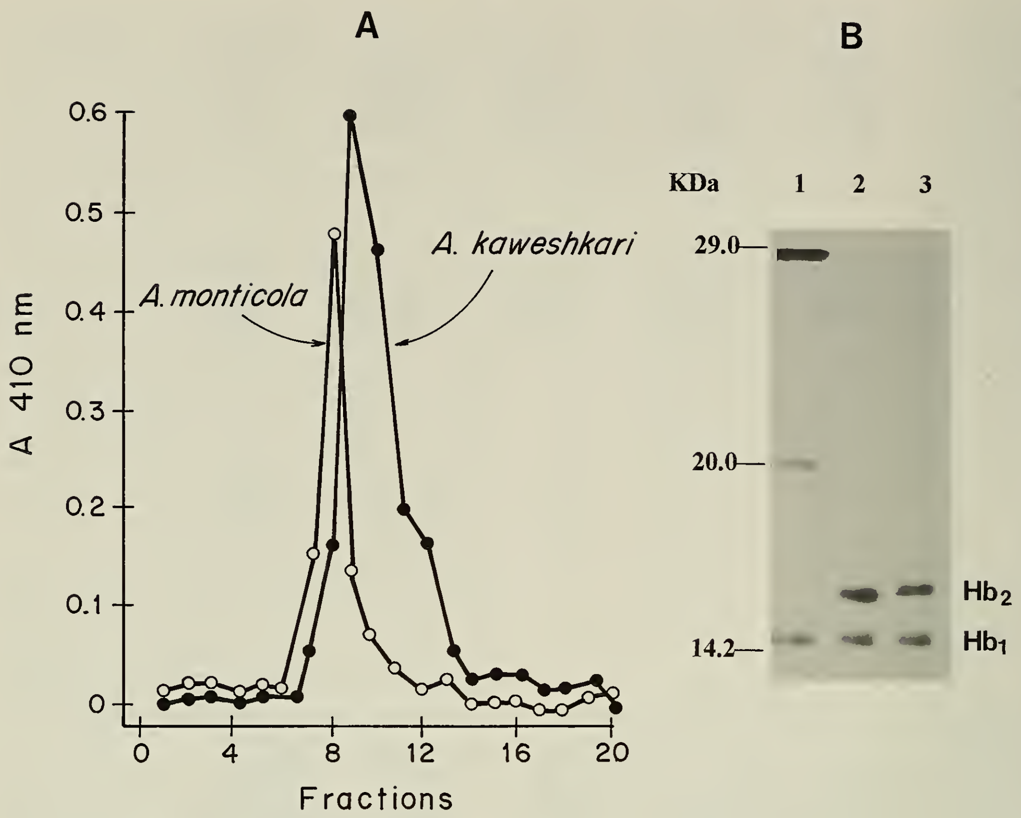

Fig. 6. Hemoglobins of *Alsodes kaweshkari* and *A. monticola.* (A) Chromatographic elution profiles of *A. monticola* and *A. kaweshkari* in Sephadex G-50 minicolumn (B) Electrophoretical patterns of *Alsodes kaweshkari* and *A. monticola.* (1) Standard of molecular weight, (2) *A. monticola,* (3) *Alsodes kaweshkari.*

tumultuosus). In the case of this latter species, its toes are long and thin, whilst in *Alsodes kaweshkari* and *A. tumultuosus* they are thick and strongly fringed. These frogs also differ in characteristics of the outer metatarsal tubercle (large in *Alsodes kaweshkari* and small in *A. tumultuosus*). On the other hand, both species differ in webbing; reduced in *Alsodes kaweshkari* and moderately developed in *A. tumultuosus* (Fig. 7A, B).

Formas & Vera (1983) studied the karyological relationships among the member of the genus *Alsodes.* They recognized three groups within the genus: the *barrioi* group (2N = 34) (*A. barrioi*), the *monticola* group (2N = 26) (*A. gargola, A. monticola, A. tumultuosus, A. vanzolinii,* and *A. verrucosus*), and the *nodosus* group (2N = 22) (*A. nodosus*). The presence of 26 chromosomes in *Alsodes kaweshkari* allows its inclusion in the *monticola* group.

Muir (1981) studied the electrophoretical patterns of the hemoglobin molecule of 14 taxa of the frogs of the genus *Xenopus.* The species and subspecies were characterized and grouped according the number of bands obtained in the electrophoretical profiles. *Xenopus borealis, X. fraseri, X. muelleri, X. ruwenzoriensis, X. tropicalis, X. vestitus* and *X. witteii* show an electrophoretical pattern of two bands (Hb_1, Hb_2). *Alsodes kaweshkari* and *A. monticola* show a similar two-banded electrophoretical pattern like that found in some *Xenopus* species. Though our biochemical study was unable to differenciate *Alsodes kaweshkari* and *A. monticola,* this is the first attempt to char-

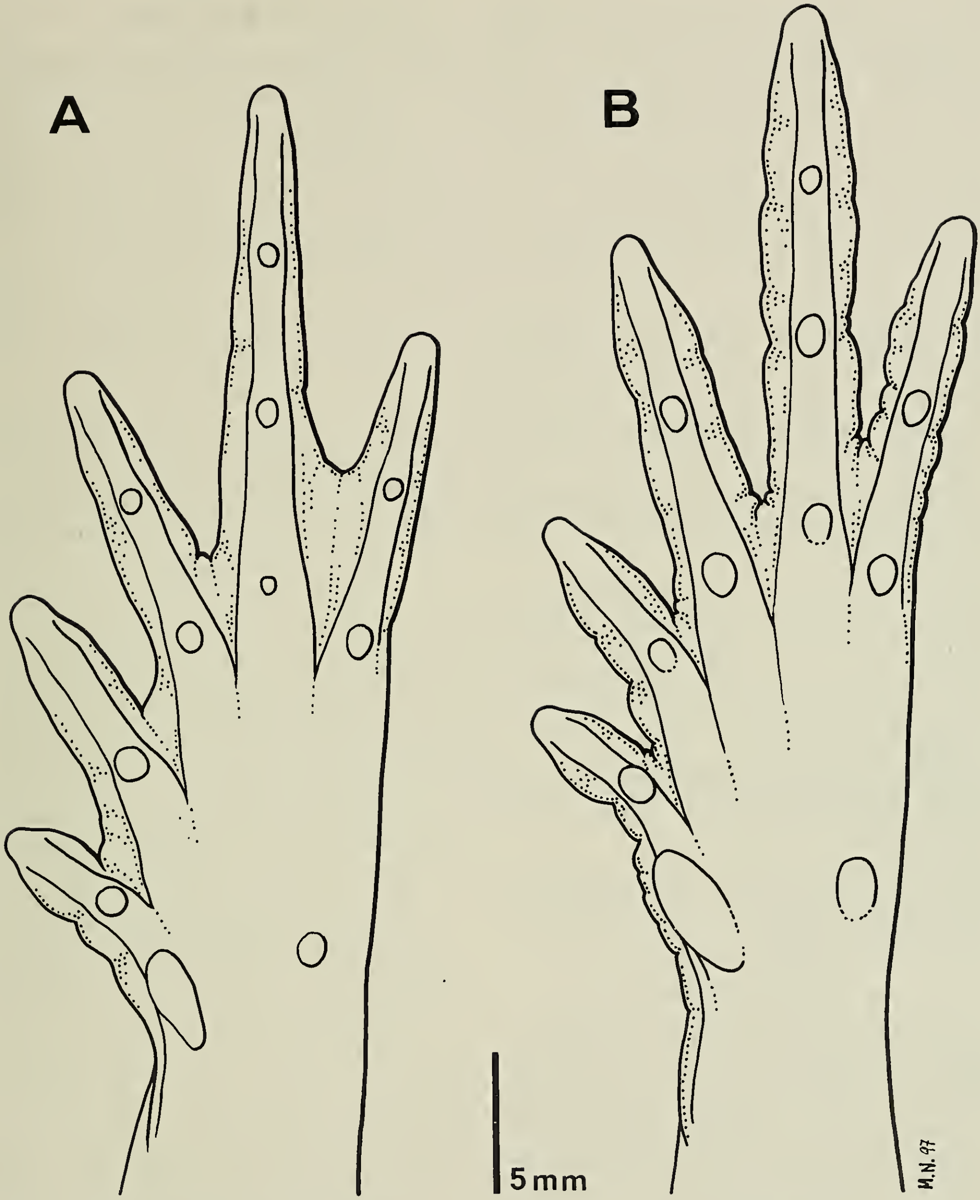

Fig. 7. Schematic plantar views of the left foot of *Alsodes kaweshkari* (A) and *A. tumultuosus* (B).

acterize the molecule of hemoglobin of frogs of the genus *Alsodes.*

Specimens Examined

Abbreviations.—Carmen Ubeda (personal collection) (CU), Argentina; Departamento de Biología Celular y Genética, Universidad de Chile (DBCG), Chile; Instituto de Biología Animal, Universidad Nacional de Cuyo (IBA), Argentina; Instituto de Zoología, Universidad Austral de Chile (IZUA), Chile; Museo Nacional de Historia Natural (MNHN), Chile; Museo de Zoología, Universidad de Concepción (MZUC), Chile.

Alsodes barrioi: IZUA 1629–1630; Cordillera Pelada, Provincia de Valdivia, 1020 m, Chile.

Alsodes gargola: CU 6; Macizo Loncoluán, Provincia de Neuquén, 1900 m, Argentina.

Alsodes montanus: IZUA 824; Estero Cobarrubias, Provincia de Santiago, 2400 m, Chile.

Alsodes monticola: IZUA 1550,1749; Cordillera Pelada, Provincia de Valdivia, 1020 m, Chile.

Alsodes nodosus: IZUA 756,700; Aguas Claras, Provincia de Petorca, 150 m, Chile.

Alsodes pehuenche: IBA 1643; Valle del Pehuenche, Provincia de Mendoza, 2500 m, Argentina.

Alsodes tumultuosus: DBCG 161–162; La Parva, Provincia de Santiago, 2600 m, Chile.

Alsodes vanzolinii: MZUC 12063–12070; Ramadillas, Provincia de Arauco, 100 m, Chile.

Alsodes verrucosus: MNHN 1506; Puerto Edén, Provincia de Ultima Esperanza, 10 m, Chile.

Alsodes vittatus: MZUC (untagged); Cordillera de Pemehue, Provincia de Malleco, 1152 m, Chile.

Acknowledgments

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Helicoprion nevadensis (Wheeler, 1939) from the Pennsylvanian–Permian Antler Peak Limestone, Lander County, Nevada (Pisces: Selachii: Helicoprionidae)

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Abstract.—A new specimen of *Helicoprion nevadensis* (Wheeler 1939) is described from the Antler Peak Limestone of Lander County, Nevada. The occurrence is significant as the only other individual of the species known has no geographic or stratigraphic information. The new specimen is dated as Wolfcampian (Early Permian) using associated fusulinids. Presence of *H. nevadensis* in Nevada and similar species in California confirms open-marine connections between the Permian shelf of North America and coeval island arcs to the west.

A new specimen of the spiral tooth-whorl shark fossil, *Helicoprion nevadensis* (Wheeler 1939) is described from the Pennsylvanian-Permian Antler Peak Limestone of Lander County, Nevada. This is only the second individual of the species discovered. The original geographic and stratigraphic location of the holotype are unknown. In contrast, this specimen is precisely located and accurately dated for the first time. It is Wolfcampian (Lower Permian) based upon cooccurrence of fusulinids. Although this occurrence does not resolve the controversy surrounding longitudinal separation between the North American continental margin and coeval island arcs to the west (Harwood and Miller 1990), this accurate locality and biostratigraphic information does allows us to conclude that open marine connections existed between North American (autochthonous) shelf seas and island arc (allochthonous) deposits during the Early Permian.

Systematic Paleontology

Family Helicoprionidae Bendix-Almgreen, 1966

Genus *Helicoprion* Karpinsky, 1899

Helicoprion nevadensis Wheeler, 1939

Fig. 1

Helicoprion nevadensis.—Wheeler, 1939: 109–112, fig. 3.

Description.—The symphysial whorl of the specimen consists of 1.5 volutions and is broken off at both juvenile and adult ends (Fig. 1). The maximum preserved diameter (tooth crown tip to tooth crown tip) is 100.35 mm. Description is compromised by the fact that the enclosing rock is broken so that most of the specimen is split laterally, and several tooth crowns are broken off at the shaft and missing. 47 tooth crowns are preserved in one volution. For a well-preserved tooth at approximately 1 volution, the volution height (V) is 20.2 mm, the shaft height (S) is 2.3 mm, with an S/V ratio of 0.11. No serration denticles are preserved.

Depository.—The specimen is deposited in the University of California Museum of Paleontology (UCMP) as specimen 140632.

Location.—From UCMP Locality V94012, in western Lander County, Nevada, with a Township/Range coordinate of T32N, R44E, in NE ¼ of SE ¼ of Section 21 on the Snow Gulch, Nevada, 7.5-minute U.S. Geological Survey quadrangle, 1991 edition. The specimen occurs in pale brown

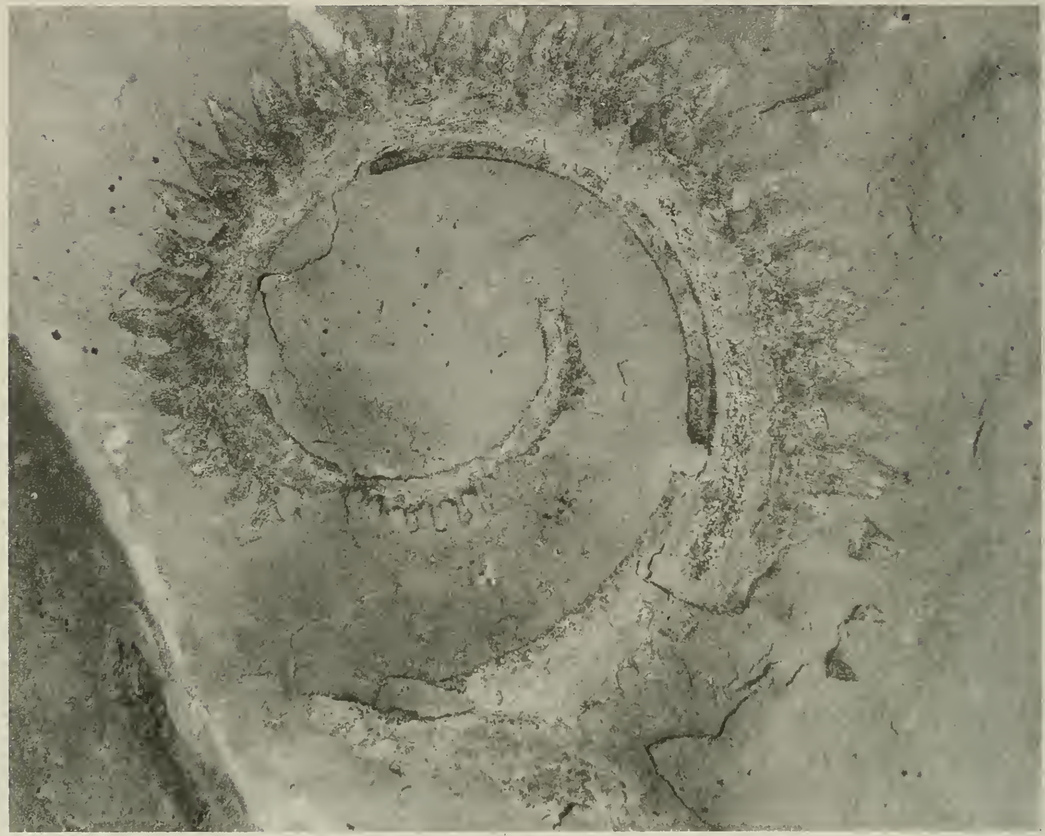

Fig. 1. *Helicoprion nevadensis.* (UCMP 140632) from the Antler Peak Limestone, Lander County, Nevada, X 1.1.

siltite of the siliclastite-dominated facies of the Antler Peak Limestone (Theodore 1994).

Comparison.—Several workers (Bendix-Almgreen 1966, Siedlecki 1970) have noted the very strong similarities of all described *Helicoprion* species. Unfortunately, *Helicoprion* fossils are always found as isolated specimens, not populations. The possibility exists that much of the published species diversity of the genus actually reflects the range of morphologic variation of very few, or even a single species. Because of this taxonomic imprecision and the incompleteness of UCMP 140632, specific taxonomic placement is difficult. For S/V ratio and number of tooth crowns/volution, UCMP 140632 is most like Wheeler's (1939) holotype *H. nevadensis,* UCMP 1001.

Biostratigraphy.—UCMP Locality V94012 occurs between strata containing fusulinid foraminifera (Verville et al. 1986). Several species of *Schwagerina* confirm a Wolfcampian age for UCMP 140632, consistent with the established geologic range of *Helicoprion* (Wolfcampian–Guadalupian).

Biogeography.—The genus *Helicoprion* has a worldwide distribution, with species described from Russia (Karpinsky 1899, Obruchev 1953, for summary), Japan (Yabe 1903, Araki 1980), Laos (Hoffet 1933), Australia (Teichert 1940), Spitsbergen (Siedlecki 1970), Arctic Canada (Nassichuk & Spinosa 1970, Nassichuk 1971), British Columbia, Alberta (Logan & McGugan 1968), Idaho, Wyoming (Hay 1907, 1909; Williams & Dunkle 1948; Bendix-Almgreen 1966), Nevada, California (Wheeler 1939, Larson & Scott 1955, this report) West Texas (Kelly & Zangerl 1976, Chorn 1978), and Mexico (Mulleried 1940), Thus, *Helicoprion* is found within rocks of many Permian benthic faunal provinces (see for example, Shi et al. 1995, Yancey 1975, Bambach 1990). Collectively, these provinces span polar to equatorial paleolatitudes in both hemispheres, a remarkable distribution, even for a nektic organism, suggesting that temperature was not a limiting factor for *Helicoprion.*

Paleogeography.—Documenting the occurrence of *Helicoprion* is problematic in the paleogeographically "suspect" accreted terrane region of western North America. Besides UCMP 140632, only three individual specimens are known. The holotype of *H. nevadensis* Wheeler, 1939, described originally as from the Koipato Group of the Humboldt Range, Nevada, is considered by Silberling (1973) not to have been obtained from the Koipato Group because of discrepancies between the lithology of the rock fragments attached to the fossil and the diagnostic lithologies of the Koipato Group. *Helicoprion sierraensis* Wheeler, 1939 is said to be found by an amateur "in a glacially transported boulder in the valley of Frazier Creek, California." Convoluted interpretations have to be proposed to attempt to determine provenance for the fossil. A third reported specimen from Nevada, *H.* sp., is reasonably located, but comes from autochthonous rocks near Elko, Nevada (Larson & Scott 1955). This specimen is not figured in any publication, nor is its museum deposition mentioned. The current location of the specimen is unknown.

Heretofore, lack of adequate documentation for the genus has prevented reliable paleogeographic inference. The joint occurrence of *Helicoprion* in autochthonous rocks of the Early Permian continental margin (Wheeler 1939, Larson & Scott 1955, Roberts et al. 1958, this report) and in the allochthonous Northern Sierra terrane of McCloud Belt faunal affinity (Harwood 1992, Miller 1987) should not be taken as evidence of original paleogeographic proximity of the McCloud Belt to North America during the Permian, nor can it resolve the problem of longitudinal separation. However, presence of the nektic genus in both areas does suggest presence of open marine conditions between these tectonic elements.

Acknowledgments

R. T. Ashinhurst of the Battle Mountain Gold Company, Battle Mountain, Nevada kindly donated the specimen to UCMP.

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Pentamera rigida and *P. pediparva,* two new species of sea cucumber from the west coast of North America (Echinodermata: Holothuroidea)

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Abstract.—Two new species of the genus *Pentamera* from the west coast of North America are described, and all known species from the west coast of North and South America are reviewed. *Pentamera rigida* is a slender, stiff, U-shaped species with five rows of podia. It occurs in sand-gravel substrata from 18 to 421 m between British Columbia and California. The table ossicles of the skin have an angular disc with a broad, low, convoluted spire. *Pentamera pediparva* has a soft, curved body with five rows of fine podia. It is known from central British Columbia to northern California from 8 to 120 m in mud-gravel or sand-gravel. The table ossicles are small and oval with small, two pillared spires. The taxonomic characters of fourteen species of *Pentamera* are summarized.

Twelve species of *Pentamera* have been described from the west coast of North and South America (Stimpson 1851, 1864; Ludwig 1886a, 1886b; Clark 1924; Deichmann 1938a, 1938b). Panning (1949) placed the genus *Pentamera* in Thyoninae, a new subfamily of Cucumariidae. Based on the presence of posterior processes composed of a mosaic of small pieces, Pawson & Fell (1965) transferred Thyoninae Panning to the family Phyllophoridae. No new species of *Pentamera* have been added to the west coast fauna since Deichmann (1938a, 1938b), with the exception of those transferred to the genus by Panning (1949). The purpose of this paper is to describe two new species of *Pentamera* from the Pacific coast of North America and present a summary table of morphological characters for species from the west coast of North and South America.

Materials and Methods

Ossicle slides were prepared by the method described in Lambert (1985). At least 30 ossicles per specimen were measured on transects across each slide. Length and width of disc, and width of central spire were recorded for tables. Length, height of curve, and height of spire were recorded for supporting tables (Fig. 7). Only ossicles that were totally within the field of vision, lying flat, and not broken, were measured. Via a drawing tube attached to a Wild M20 microscope, the image of each ossicle was visualised on a digitising tablet (Summasketch II, Summagraphics Corporation). Measurements were made with the cursor and automatically saved to a file using SigmaScan software (Jandel Scientific). That file was then transferred to a statistical package (Systat, Systat, Inc.) for analysis. External measurements of the whole specimen were made with an ocular micrometer, calipers, or in the case of strongly curved specimens, a string was used to trace the distance from the base of the tentacles to the anus, around the outer side of the curve, usually the ventral side.

Institutions mentioned in this paper are abbreviated as follows: Allan Hancock

Fig. 1. Preserved specimen of *Pentamera rigida* dredged from type locality, 115 m, off Nootka Sound, B.C., length 7 cm, RBCM 984-199-3.

Foundation (AHF) now housed at LACM; California Academy of Sciences, San Francisco (CASIZ); Fisheries Research Board of Canada (FRB) now known as Department of Fisheries and Oceans, (DFO); Canadian Museum of Nature, Ottawa (CMNI or NMC); Natural History Museum of Los Angeles County (LACM); Royal British Columbia Museum, Victoria (RBCM); National Museum of Natural History (USNM), Washington, D.C.

Results

Order Dendrochirotida Grube

Family Phyllophoridae Oestergren

Diagnosis.—Dendrochirotid holothurians without a test. Tentacles 10–25 (usually 10 or 20), well branched. Pedicels either restricted to the ambulacra or scattered, but fewer and usually papilliform dorsally. Calcareous ring complex, often tubular, with long or short posterior processes, both ring and processes always composed of a mosaic of small pieces. Ossicles usually plates or buttons, rods, tables or derivatives of tables (after Thandar 1990).

Remarks.—Thandar modified the diagnosis of Pawson (1982) by adding that the podia may be in rows or scattered and that the ossicles may be tables or derivatives of tables in the form of plates, rods or buttons.

Subfamily Thyoninae Panning, 1949

Diagnosis.—Small to medium-sized phyllophorids, rarely more than 100 mm long. Body soft. Pedicels numerous, usually scattered all round, but often most crowded ventrally. Tentacles 10, ventral two always reduced. Calcareous ring tubular with long paired posterior processes on radial plates. Ossicles of body wall usually in the form of tables or plates (buttons), or absent (after Thandar 1990).

Genus *Pentamera* Ayres, 1852

Diagnosis.—Small to medium sized forms. Ten tentacles with two smaller ventral tentacles. Nonretractile podia in five series, not scattered. Radials of the calcareous ring with long forked tails. In the skin two pillared tables or derivatives of these with the spire reduced or absent. Podia with large endplates and curved supporting tables with spires varying from low to high. Tentacles usually with rods, plates or both. (After Deichmann 1941)

Type species: *Pentamera pulcherrima* Ayres

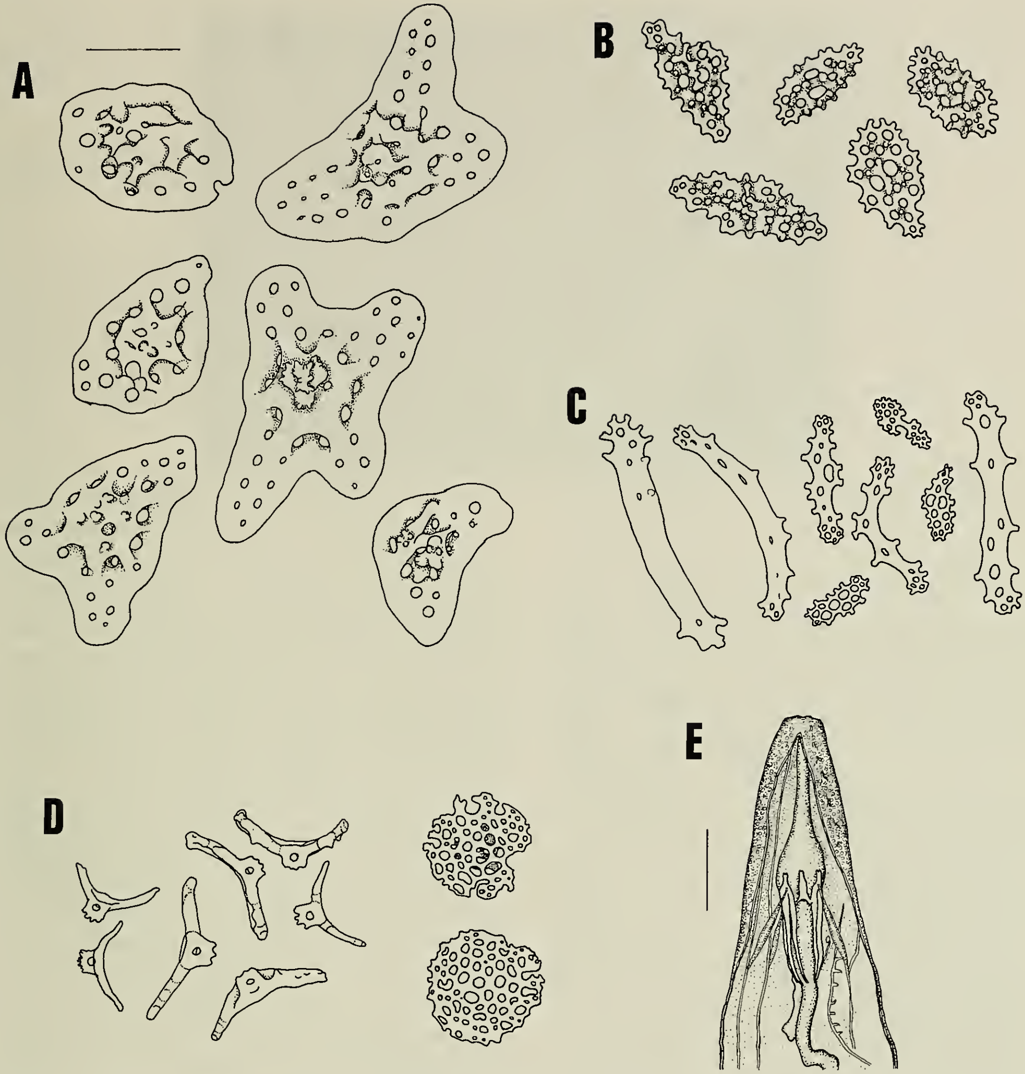

Fig. 2. Ossicles and calcareous ring of *Pentamera rigida.* (A) Tables of the dorsal skin. (B) Plates from the introvert. (C) Tentacle ossicles. (D) Supporting tables and end plates of podia. (E) Calcareous ring and retractor muscles; scale bar 5 mm. All from holotype (RBCM 997-123-1) except for the podial end plates (RBCM 983-1658-30) and the calcareous ring of paratype (RBCM 984-199-3). Top scale bar 100 μm applies to all ossicles.

Pentamera rigida, new species
Figs. 1–3

Pentamera lissoplaca.—Bergen 1996 (partim):239, fig. 9.23B. Specimens described as having "large tables" may be *P. rigida.*

Pentamera sp. A Lambert, 1997:101, figs. 52–53, photo 24.

Diagnosis.—Body U-shaped; skin usually stiff and white. Podia in five series, longer and more abundant in midventral region than distally. Ten small dendritic tentacles including smaller ventral pair; often speckled with brown. Calcareous ring long and tubular with forked tails on the radials; made up of a mosaic of smaller pieces; ratio of radial to interradial length approximately 4:1. Skin ossicles circular, triangular or star-shaped tables (100–300 μm) with a broad

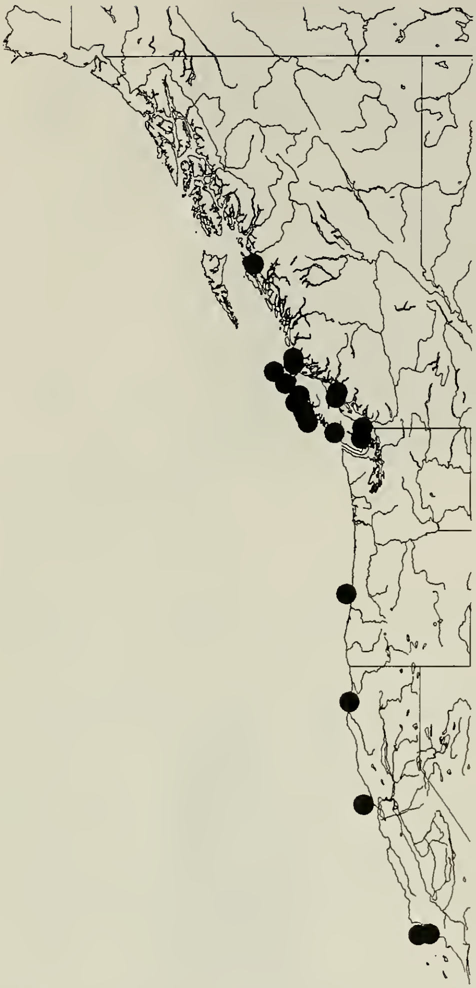

Fig. 3. Collection sites for *Pentamera rigida.*

convoluted spire covering about one-half width of disk; small, curved supporting tables (100 μm) with low spire. Introvert with oval knobbed perforated plates, some with remnant of a spire. Tentacle ossicles in two forms, finer curved oval plates and large robust rods with a few holes.

Material examined.—Eighty-one specimens from 15 localities in British Columbia, one locality in Oregon, four in California, and one from an unknown locality on the west coast of U.S.A. Number of specimens in parentheses after the catalogue number; depth in metres (m).

Holotype.—RBCM 997-123-1 (1), collected by F. Bernard and T. C. Lambert, FRB station 63-91, 8 Sep 1964, length 6.8 cm (measured along the outside of the curved body), female.

Type locality.—British Columbia, Vancouver Island, Nootka Sound, 49°32′N, 127°03′W, 115 m, sandy mud.

Paratypes.—RBCM 984-248-1 (1), collected by D. B. Quayle, FRB Haul No. 1, 7 Jul 1962, British Columbia, Kitkatla Inlet, Porcher Island, 53°51′N, 130°W, 37 m, sand and gravel, specimen 10.8 cm long. RBCM 984-200-1 (7), FRB station 63-204, 10 Sep 1964, British Columbia, Vancouver Island, Quatsino Sound, 50°19.6′N, 128°06.5′W, 119 m, sand, specimen lengths from 2.8 to 5.1 cm. RBCM 984-199-3 (12), collected by F. Bernard and T. C. Lambert, FRB station 63-91, 8 Sep 1964, British Columbia, Vancouver Island, Nootka Sound, 49°32′N, 127°03′W, 115 m, sandy mud, from same lot as holotype, specimen lengths from 3 to 8 cm (mean 5.5). USNM E16915 (32), collected by A. Carey, Oregon State University, Cruise C 700810, BMT 239, 17 Aug 1970, Oregon, off Hecata Head Light, 44°08.8′N, 124°24′W, 100 m, specimen lengths from 1.5 to 5.7 cm. CASIZ 50227 (1), Sta. 20, 28 Sep 1949, California, off Point Reyes, south of Cordell Bank, 37°55.75′N, 123°19.25′W, 110–113 m, specimen 6 cm long. AHF 440.61 (1), Velero 6131-59, California, Ventura Co., Oxnard, Port Hueneme Lighthouse, 34°8.1′N, 119°21.5′W, 165 m.

Other collections.—British Columbia: RBCM 989-564-4 (1), collected by D. B. Quayle, FRB station 70-24, Jul 1970, Bramham Island near Pine Island, 51°05′N, 27°39′W, 82 m. RBCM 984-213-1 (1), collected by D. B. Quayle, FRB station 71-14, Apr 1971, Gordon Channel, near Nigei Island, 50°53.1′N, 127°36.5′W, 421 m. RBCM 990-939-11 (2), FRB station 67-66, Aug 1967, Vancouver Island, Cape Scott, 50°39.8′N, 128°47.2′W, 200 m, gravel. RBCM 984-249-1 (1), collected by J. Fleury, FRB Drag #7 + #8, 27 Jun 1962, Baker Pass, near Cortes Island, 50°04.0′N,

Fig. 4. Holotype of *Pentamera pediparva* collected by scuba from 7.5 m in Quatsino Sound, B.C., length 8 cm, RBCM 997-124-1.

124°59.0′W, 117 m, gravel. RBCM 980-344-1 (1), collected by P. Lambert, station L80-61, 6 Jul 1980, Vancouver Island, Kyuquot Channel, Sandy Bay, Rugged Point, 49°58.2′N, 127°14.6′W, 9 m, clean sand and algae. RBCM 55-56 (1), collected by D. Ellis, 16 Aug 1965, Strait of Georgia, 49°54.05′N, 125°04′W, 178 m, sand. RBCM 983-1658-30 (3), collected by Gordon Green, 23 Nov 1983, Vancouver Island, off Kyuquot Sound, 49°45.7′N, 127°30.1′W, 150 m, sand. RBCM 974-570-6 (3), FRB station 2231-33, 17 Jul 1934, Vancouver Island, Estevan Point, 49°22.3′N, 126°55′W, 137 m, sand. RBCM 986-93-27 (3), collected by P. Lambert, on Endeavour, Station L86-9, 19 Mar 1986, Vancouver Island, Estevan Point, 49°11′N, 126°45.2′W, 120 m, sand. RBCM 983-1397-1 (1), collected by M. Byrne, 11 Feb 1983, east of Galiano Island, 49°01.48′N, 123°29.45′W, 50–230 m. RBCM 991-10-1 (2), collected by S. Carson, 22 Feb 1990, Barkley Sound, Trevor Channel, 48°52′N, 125°08′W, 54 m, mud. RBCM 988-758-10 (1), collected by P. Lambert, G. Green, D. Bright, Station L88-27, 22 Jun 1988, Satellite Channel, Boatswain Bank, 48°42.2′N, 123°32.1′W, 18 m.

California: CASIZ uncatalogued (1), 9 Aug 1940, 2.5 mi. off Mad River, Eureka, 37 m. USNM E2371 (4), Albatross St. 2902, California, Channel Islands, Santa Cruz Channel, Santa Rosa Island, 34°6.0′N, 120°2.0′W, 97 m. USNM 30563 (1), Albatross St. unknown, West Coast United States, depth unknown.

Description.—Total length 1.5–10.5 cm (measured along the outer curve of the body); mean length (cm ± 1 *SD*) 4.6 ± 1.6 cm ($n = 72$). Holotype 6.8 cm long. Body typically bent in a tight U-shape with long slender anterior and posterior ends (Fig. 1). Skin stiff with ossicles. Podia slender and probably non-retractile because of their heavy complement of ossicles. Podia form five bands, each consisting of two rows, crowed together in the middle of the body on ventral side but sparse distally and on dorsal side. Specimens typically white in life and in alcohol. Ten tentacles arranged in five pairs with a smaller ventral pair.

Madreporite in dorsal mesentery about two-thirds of distance from anterior end of calcareous ring. Semi-circular madreporite with a long narrow stone canal, connects to the ring canal near posterior tip of calcareous ring. One polian vesicle usually on ventral side of ring.

Two respiratory trees emerge from cloaca on left and right sides; each one splits into a dorsal and ventral branch; dorsal

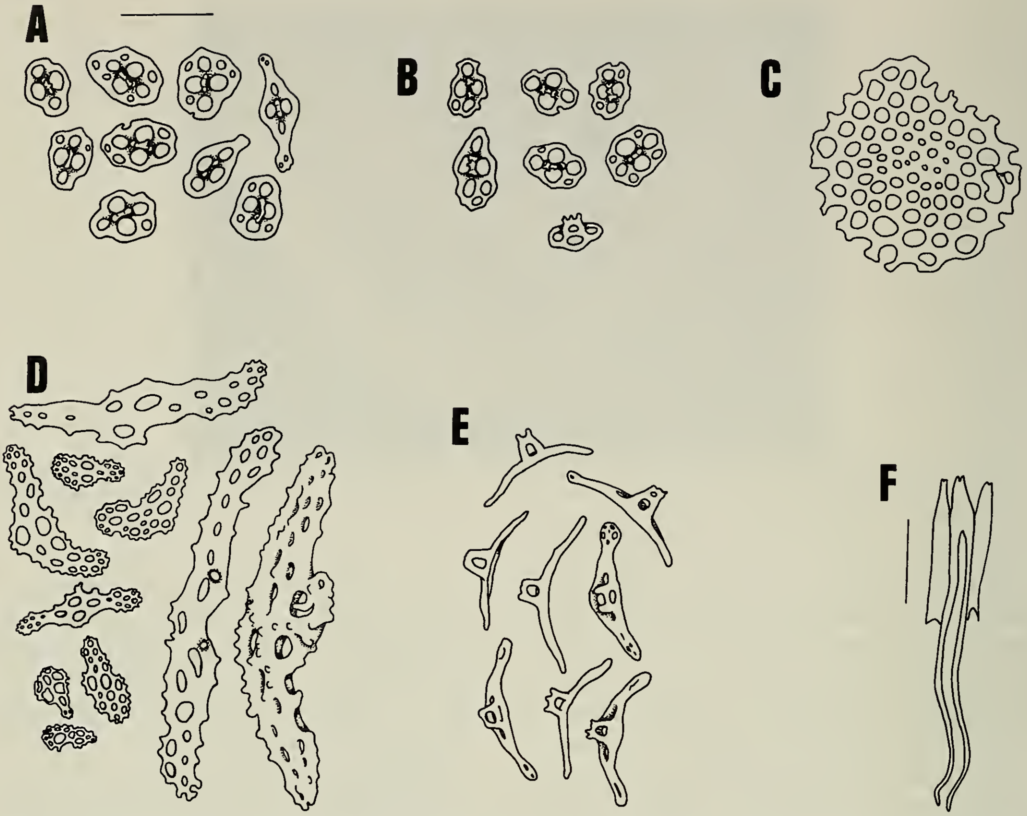

Fig. 5. Ossicles and calcareous ring of *Pentamera pediparva.* (A) Tables of the dorsal skin. (B) Plates from the introvert. (C) End plate of podia (D) Tentacle ossicles. (E) Supporting tables of podia (F) Calcareous ring; scale bar, 5 mm. All from holotype (RBCM 997-124-1). Top scale bar (100 μm) applies to all ossicles.

branch runs full length of body, ventral branch only to mid body. Respiratory trees usually brown, with a main trunk and simple, short side branches. Cloaca occupies most of narrow "tail."

Gonad has two tufts of unbranched tubules, one tuft on each side of dorsal mesentery where it joins the dorsal body wall.

Thin retractor muscles attach to body wall at a point level with posterior end of calcareous ring. Five thin longitudinal muscles. Radial plates of calcareous ring with long posterior prolongations; interradials with no tails, shaped like an elongate triangle (Fig. 2E). Transverse thickenings indicate joints between mosaic of pieces that make up the tails. Ratio of interradial to radial length about 1:4.

Tables of mid skin circular to roughly triangular or star-shaped, with a mean diameter (μm ± 1 *SD*) of 194 ± 45 ($n = 141$) with a complex central spire (width 102 ± 32, $n = 140$) that covers about one-half the surface area of table (Fig. 2A). Supporting tables of podia small (length 110 ± 15, $n = 90$) and tightly curved with a low spire (height 16 ± 5, $n = 90$) with three or four teeth. Ratio of length (L) to total height (TH) of supporting tables 1.9 ± 0.3, $n = 90$ (see Fig. 7 for explanation of dimensions). Podial end plates small (diameter 115–135 μm, $n = 5$) (Fig. 2D). Ossicles in tail region not significantly different from mid skin. In juveniles (<2 cm) tables tend to be more star-shaped and spires not as robust. Introvert has oval perforated plates with two larger central holes and knobs on the surface of plate (Fig. 2B). In tentacles,

Fig. 6. Collection sites for *Pentamera pediparva.*

ossicles range in size from large flat rods (length 230 μm) with a few knobs and holes to smaller curved perforated plates with scalloped edges (Fig. 2C).

Etymology.—The species name, *rigida,* is based on the Latin word *rigidus,* meaning stiff or inflexible and refers to the typically stiff ossicle-filled body of this species.

Distribution and habitat.—*Pentamera rigida* is known from Porcher Island near Prince Rupert, British Columbia (53°51′N, 130°W) south to Santa Cruz Channel, Santa Rosa Island, Channel Islands, California (34°6.0′N, 120°2.0′W) (Fig. 3). It ranges in depth from 18 to 421 m on the continental shelf. The majority of collections are from less than 200 m. The one specimen from 421 m is from a deep trench between Vancouver Island and the mainland. So far none have been collected on the continental slope or deeper. Usually occurs in sand or gravel substrata.

Pentamera pediparva, new species
Figs. 4–6

Pentamera sp. B Lambert, 1997:104, figs. 54, 55, photo 25.

Diagnosis.—Body curved; up to 7 cm long; skin usually soft; colour white to

Table 1.—*Pentamera* of the west coast of North and South America (ossicle measurements in micrometers ± 1 *SD*; L = length, H = height of spire, TH = total height, *n* = 15 unless otherwise indicated).

Pentamera species	Distribution	Body shape	Podia	Colour
P. beebei Deichmann 1938	Costa Rica	Small form	Typical	White
P. calcigera (Stimpson 1851) as *Pentacta*	Arctic; eastern Russia; Alaska, Bering Sea, Chukchi; 7–25 fm; 33–80 m	Curved with tapered posterior; 50–60 mm	Single pairs in 5 rows; non-retractible	White or yellowish
P. charlottae Deichmann 1938	Monterey Bay to southern California (Bergen); intertidal to 642 m	Few cm long; body straight. Up to 6.5 cm, cylindrical (Bergen)	5 double rows; cylindrical, non-retractile	White or coffee (preserved)
P. chierchia (Ludwig 1886) as *Cucumaria*	Panamic region; Mexico and Costa Rica; shallow water	Small 3–6 cm; soft-skinned	Numerous cylindrical feet in 5 bands	Dark brown almost black.
P. chiloensis (Ludwig 1886) as *Cucumaria*	Cape Horn to Lower California; 8–60 fm (Deichmann)	Curved, about 5 cm; skin thin and wrinkled	"Resembles genus type"; conspicuous cylindrical podia in 5 well-defined bands	White
P. lissoplaca (Clark 1924) as *Cucumaria*	Southeast Alaska south to Baja California; 9–82 m	Curved, tapering to posterior	5 crowded double series; non-retractile stiff with ossicles	Yellowish white in preservative
P. montereyensis Deichmann 1938	Pacific Grove, Long Beach & Santa Rosa I. California, intertidal & shallow on rocks	Moderate-size form, up to 5 cm; cylindrical	5 bands, cylindrical, non-retractile	White, tentacles and introvert with few pigment spots

Table 1.—Extended.

Calcareous ring	Mid-dorsal Ossicles	Introvert	Tentacles
Not stated in original description	Minute tables (L = 37, *n* = 2) with four+ holes, 2-pillared spire with tuft of spines; curved support tables (L = 65 ± 9, *n* = 6) with tall spire, ratio of L to TH 0.8 ± 0.3; large endplate. Data from illustrations.	Unknown	As for genus
Radial with long posterior processes; shorter inter-radial	Mostly oval plates (L = 162 ± 35); fewer oval or squarish tables with central spire. Curved supporting tables (L = 163 ± 20) with moderate spire (H = 36 ± 6), ratio of L to TH = 1.8 ± 0.3 Well developed end plates with indented perimeter (136–177, *n* = 7).	Oval perforated plates with meshwork at center (this study)	Ten; 8:2 small
Radials with long posterior processes; interradial ½ length, no tails	Small oval tables (L = 91 ± 9) with 2-pillared spire. Curved supporting tables similar to tables but with a taller spire (H = 59 ± 9), having 2 or 3 crossbeams and topped with a few teeth. Large end-plates (130–225, *n* = 7).	Tables with oblong disk, dentate margin and low spire	Ten (8:2); with rods, plates, and tables
Long posterior processes	Ossicles vary in number but not crowded; tables (L = 70, *n* = 3) with 4 central holes and dentate margin, low 2 pillared spire often lacking; few spectacle rods, trace of spire; podia with large end-plate.	No specimen examined; introvert unknown	Ten (8:2); curved perforated plates and rods
Not stated in original description	Tables with oval to squarish disk (L = 69 ± 13, *n* = 6) with 4 or 8 holes; 2 pillared spire, and 1 or 2 crossbeams short teeth on top; podia with large end-plate & curved supporting tables (L = 90 ± 105, *n* = 2) with low spire few flat teeth; ratio of L to TH = 1.5; data derived from illustrations of ossicles.	Rosettes	Tentacles missing in type, Deichmann—typical for genus; with delicate rods
Ring rather high; interradials about 2 mm high and half as wide concave behind, radials with posterior processes. Interradial to radial 1:3	Ossicles in two layers; scattered delicate tables (diameter 30–50) with fine spire; inner layer smooth, crowded, diamond-shaped plates (L = 120 ± 15); curved supporting tables (L = 103 ± 10) with moderate spire (H = 36 ± 6), ratio of L to TH = 1.9 ± 0.3; podia end plates 90–110, *n* = 4.	Oval perforated plates (100-200) with 2 larger central and numerous smaller holes, many knobs on surface	Ten (8:2); ossicles of two classes: large (~300) robust perforated rods and delicate (~100) oval perforated plates with 2 large central holes, wavy edge
?	Small oval buttons (diameter 25–55 μm) with 2 central and up to 8 marginal knobs; supporting tables with marginal knobs, reduced spire; well developed end-plates (235–275, *n* = 4), perforated rods.	Round to oblong perforated plates with 2 larger central holes and 6–20 other holes; 2 central knobs	Ten (8:2)

Table 1.—Continued.

Pentamera species	Distribution	Body shape	Podia	Colour
P. populifera (Stimpson 1864) as *Pentacta*	Kodiak I. to southern California perhaps Baja; to 60 fm	Thick fusiform up to 6 cm, skin thin and flexible; curved with tapering posterior or nipple-like	5 bands small numerous podia full length of body	Creamy white
P. pseudocalcigera Deichmann 1938	Southeast Alaska to San Benitos Island, Baja California, 7–250 fm	Medium sized, U-shaped, tapering to blunt ends, rather stiff	In 5 raised bands, podia conical in shape, non-retractile	Podia usually lighter than the pinkish inter ambulacrum
P. pseudopopulifera Deichmann 1938	Southern California; shallow water to 57 fm (Bergen)	Medium size to 6.5 cm variable fusiform curved and skin usually wrinkled	5 crowded bands of podia, up to 8 across; non-retractile; cylindrical	Straw-colored podia, beige in alcohol
P. trachyplaca (Clark 1924) as *Cucumaria*	Queen Charlottes to Channel Is, California, to 33 m	Small cylindrical, up to 3 cm; blunt subequal ends	5 bands stout podia	Yellowish white in alcohol, tentacles darker
P. zacae Deichmann 1938	Tangola Bay, Mexico; 23 fm	Small (few cm) with strongly curved body tapering toward ends	Numerous cylindrical, non-retractile podia in 5 bands, more on ventrum than at oral or anal ends	Dirty white
P. rigida, new species	Porcher I., B.C. south to Santa Rosa I., Channel Islands, California	U-shaped, stiff, elongate, fatter in middle and tapering at both ends, posterior more so	5 bands fine, stiff podia, usually more abundant midventrally	Whitish

Table 1.—Continued. Extended.

Calcareous ring	Mid-dorsal Ossicles	Introvert	Tentacles
Radials with long posterior processes about twice length of interradials	Oval to star-shaped tables (L = 213 ± 58) a few reduced in size, with scalloped edge; 25–40 holes; narrow central spire (width at base 48 ± 14); curved supporting tables (L = 119 ± 14) with a tall spire (H = 41 ± 7) topped with teeth, ratio of L to TH = 1.4 ± 0.2; podia have smallish endplates with notched perimeter (90–105, *n* = 6).	Elongate diamond-shaped plates with 2 larger central holes, some with bumps or low pillar arch	Ten (8:2); ossicles long thin curved rods and narrow perforated plates
Long posterior processes	Skin filled mostly with large, oval or triangular plates (L = 228 ± 41), rarely star-shaped tables; supporting tables (L = 143 ± 11) with moderate spire (H = 23 ± 11), ratio of L to TH = 2.1 ± 0.4; podia endplates (130–160).	Oval perforated plates with serrated edge and blunt spines on surface	Ten; 8:2 small, 1 spec had 9:1 small. Dark around mouth, brown specks on oral disk and tentacles
Radials with long posterior processes, radial about 3 times longer than interradial	Usually small (L = 111 ± 18) circular tables with small two-pillared spire; supporting tables (L = 96 ± 11) with medium spire (H = 19 ± 5) often topped with 2 "horns"; ratio of L to TH = 2.1 ± 0.4; podia endplates (114–123, *n* = 3).	Delicate perforated plates with a few knobs; approaching rosettes	8:2 small; brown spots; oblong plates and rods (Bergen)
Posterior processes of medium length, interradials an elongate triangle	Thick oval, knobbed, perforated plates (L = 147 ± 34, *n* = 20) with meshwork of bumps covering one side; curved supporting tables with wide low spire covering half length; well developed end-plates (120–140, *n* = 4).	Oblong reticulated plates (Bergen)	8:2 tentacles; various sized plates often with two enlarged central holes
No calcareous ring in type	Crowded layer of acornlike cups (~60) with 2 pillared, tapering spire rising from a cupshaped base; curved supporting tables with medium tall spire topped with few blunt teeth; podia with large endplates.	Unknown	Tentacles missing
Typical *Pentamera* with very long posterior processes; approximately 1:4	Circular to triangular or star-shaped tables (L = 194 ± 45, *n* = 140) with a wide central spire (width at base 102 ± 32, *n* = 140); supporting tables (L = 110 ± 15, *n* = 90) with low bumpy spire (H = 16 ± 5, *n* = 90), ratio of L to TH 1.9 ± 0.3; podia endplates (115–135, *n* = 5).	Elongate oval perforated plates with numerous bumps and in some, raised central rods; two larger central holes	8:2 small; speckled brown; ossicles of two forms, finer curved, elongate oval plates and large robust rods with a few holes

Table 1.—Continued.

Pentamera species	Distribution	Body shape	Podia	Colour
P. pediparva, new species	Fitz Hugh Sound, B.C. to northern California; 7–120 m	Curved and tapering at ends; skin wrinkled; not as stiff as *P. rigida*	Numerous fine podia in 5 bands, reduced at oral and anal ends	Whitish

brown in preserved state. Podia in five series, of up to 8 rows each at the midbody. Ten small dendritic tentacles including smaller ventral pair. Calcareous ring long and tubular with forked tails on the radials; a mosaic of smaller segments; ratio of interradials to radials approximately 1:3. Skin ossicles small oval tables (<100 μm diameter) with a simple, two-pillared spire in the form of a low arch; 4 central holes adjoin the spire. Curved supporting tables (length about 150 μm) with low spire. Introvert has smaller oval tables with spires having a spiny tip. Tentacle ossicles in two forms, finer, curved oval plates and large robust rods with a few larger holes. End plates of podia 200–250 μm in diameter.

Material examined.—Twenty-five specimens from 12 localities in British Columbia, two localities in Washington and one in California. Number of specimens in parentheses after the catalogue number; depth in metres (m).

Holotype.—RBCM 997-124-1 (1), length 8 cm, female, collected by Philip Lambert with SCUBA, station L80-50, 29 June 1980.

Type locality.—British Columbia, Vancouver Island, Quatsino Sound, Forward Inlet, Hall Bank, 50°29.7′N, 128°1.5′W, 7.5 m, cobble-gravel.

Paratypes.—RBCM 980-333-10 (1), length 8.2 cm, male, collected by P. Lambert with scuba, station L80-50, 29 Jun 1980, British Columbia, Vancouver Island, Quatsino Sound, Forward Inlet, Hall Bank, 50°29.7′N, 128°1.5′W, 7.5 m, cobble-gravel. RBCM 981-197-2 (1), length 2.5 cm, male, collected by P. Lambert aboard Strickland, Station L81-13, 20 Aug 1981, British Columbia, Fitz Hugh Sound, Fairmile Pass, 51°38′N, 127°51′W, 70 m. CMNI 1998-0001 (1), length 7.4 cm, female, collected by D. B. Quayle, 14 Jul 1946, British Columbia, Klucksiwi, Seymour Inlet, 51°05′N, 127°39′W, 82 m, sand-gravel. RBCM 973-235-24 (1), length 3.5 cm, sex undet., collected by P. Lambert with scuba, 14 Aug 1973, British Columbia, Barkley Sound, Treble Island, 48°56′N, 125°16.9′W, 9–12 m, sand-shell slope. RBCM 987-253-11 (1), length 3.2 cm, collected by G. Green and K. Sendall on Parizeau, Station G87-17, 23 Jul 1987, Washington, off Cape Flattery, 48°20.9′N, 125°21.39′W, 115–120 m, gravel. CASIZ 50222 (2), collected by Lloyd Barker, 13 Nov 1970, California, Eureka, west of Big Lagoon, 41°10.7′N, 124°7.0′W, 18–37 m.

Other collections.—British Columbia: RBCM 982-326-2 (1), on G. B. Reed, FRB station 70-24, Jul 1970, Bramham Island, 51°05′N, 127°39′W, 82 m, sand-gravel. RBCM 977-444-8 (4), collected by D. B. Quayle, FRB station 63-2, 12 Jan 1963, Cormorant Channel, Malcolm Island, 50°36.9′N, 126°57.7′W, 26 m, sand. NMC 1979-1529 (1), FRB St. 18, Comox Bay 49°39′N, 124°55′W, 27 m. RBCM 975-189-5 (1), formerly BMS 496 (1), St.91/75, 18 Apr 1975, Barkley Sound; Verbeke Reef, 48°52.2′N, 125°22.6′W, 31–46 m, cobble and gravel. RBCM 984-246-1 (6), FRB #8, 23 Jun 1961, Vancouver Island, Barkley Sound, 48°49′N, 125°34.3′W, 73 m, mud-gravel. RBCM 106-49 (1), collected by D. Ellis, 11 Mar 1965, Saanich Inlet, Mill Bay, 48°38.8′N, 123°32.3′W, 18 m, sand. RBCM 975-294-5 (2), collected by D. Ellis, 3 Nov

Table 1.—Continued. Extended.

Calcareous ring	Mid-dorsal Ossicles	Introvert	Tentacles
Very long posterior processes; 1:3	Small, round tables (L = 70 ± 11, *n* = 70) with 4 main holes and 4 or more smaller holes, low 2-pillared spire; in addition, larger diamond-shaped tables (L = 123 ± 21, *n* = 29); slightly curved supporting tables (L = 139 ± 18, *n* = 100) with low spire (H = 19 ± 8, *n* = 100); ratio of L to TH 2.7 ± 0.6, *n* = 100; podia with large endplates (205–215, *n* = 3).	Tables similar to skin but slightly smaller and with teeth on spire	8:2; 2 types of ossicles: finer oblong, curved, perforated plates with 2 larger central holes; and large robust curved rods with holes

1965, Vancouver Island, Saanich Inlet, Mill Bay, 48°38.8′N, 123°32.3′W, 18 m, sand.

Washington: 1 specimen, Station WP215N Rep A, collected by Alan Fukuyama, 7 Oct 1996, 66 m north of West Point outfall, Seattle, Puget Sound, 47°39.6′N, 122°26.8′W, 230 m. 1 specimen, AL172N Rep A, collected by Alan Fukuyama, 7 Oct 1996, 52.4 m north of Alki Point outfall, Seattle, Puget Sound, 47°34.2′N, 122°25.3′W, 143 m.

Description.—Total length 1.3—8.2 cm (measured along the outer curve of the body); mean length 3.3 cm for 16 specimens. Holotype 8 cm long (Fig. 4). Body curved with a blunt anterior end and tapering posterior end. Skin of interambulacral area soft with transverse wrinkles. Five bands of podia each with 4 irregular crowded rows more sparse distally. Podia cylindrical, non-retractile and bristling with ossicles.

In alcohol, small specimens white with yellowish podia; larger specimens off-white.

Ten dendritic tentacles including small ventral pair. Brown spots near base of tentacles and in entrance to mouth.

Madreporite in shape of a flattened hemisphere lies in the dorsal mesentery usually two-thirds of the distance from the anterior end of the calcareous ring. Narrow, convoluted stone canal attaches to the circular water ring at the posterior tips of the calcareous ring. One polian vesicle, usually on the ventral side. Two respiratory trees emerge from cloaca and immediately split into two branches, the dorsal branch longer than the ventral. Thin-walled cloaca about one-third of body length and attached to the body wall by numerous strands or muscles.

Retractor muscles fairly stout compared to *P. rigida*; attached to longitudinal muscles about ¼ of the distance from anterior end of body.

Two tufts of unbranched gonadal tubules attach to dorsal body wall about one-third of the way from anterior end of body, one tuft on each side of the dorsal mesentery.

Calcareous ring takes up a large proportion of internal body cavity and in severely contracted specimens may appear to span the length of the cavity. Posterior tails of radials long and thin; may be bent back on themselves at posterior end. Transverse thickenings indicate joints between mosaic of pieces. Ratio of interradial to radial length about 1:3 (Fig. 5F).

Ossicles of mid-skin small oval or squarish tables (diameter 70 μm ± 11 *SD*, *n* = 71) with a low spire consisting of two pillars (Fig. 5A). Pillars may be joined at the top and have one or two side branches, or appear as just two bumps. Most tables have four main holes around the spire with one to several secondary holes. Among oval tables are diamond-shaped tables (length 123 ± 21, *n* = 30) with a spire shaped like a low arch. Toward anterior and posterior ends and in the introvert, spires of tables have multiple spines at apex and tables slightly smaller on average (Fig. 5B). Supporting tables of podia curved rods (length 139 ± 18, $n = 100$) with a low central spire (height of spire 19 μm ± 8, $n = 100$) with two or three bumps, in side view (Fig. 5E). Podia have large end-plates (diameter 205–215, $n = 3$) (Fig. 5C). Five anal teeth surround anus.

Tentacles have two types of ossicles: large, elongate, curved perforated rods and more delicate elongate-oval or curved plates perforated with smaller holes and serrated around edges (Fig. 5D).

Etymology.—The species name, *pediparva,* is based on the Latin words *pedis* meaning foot and *parvus* meaning small or little, referring to the numerous, small podia.

Distribution and habitat.—P. pediparva is known from Fitz Hugh Sound, on the central British Columbia coast (51°38′N, 127°51′W), south to Eureka, California (41°10.7′N, 124°7.0′W) (Fig. 6). It ranges in depth from 8 to 120 m on the continental shelf. Usually dredged from firm substrata such as mud-gravel and sand-gravel.

Discussion

Table 1 compares the features of 14 species of *Pentamera* from the west coasts of North and South America, including the two new species described in this paper. New information, not included in original descriptions, has been added to complete the table.

Pentamera rigida is allied to *P. populifera* in the shape of the table ossicles, but those of *P. rigida* have a broad low spire and a more triangular rather than star-shaped plate. *P. rigida* seems to prefer a firm sand or gravel substratum while *P. populifera* is usually more common in mud. *P. rigida* also resembles *P. pseudopopulifera* in general appearance, but the tables are about one-half the diameter of *P. rigida* and the central spire is much smaller and more delicate.

In general appearance, *Pentamera pediparva* resembles *P. lissoplaca* with soft skin and fine podia in five rows, but the skin ossicles of the two species differ. *P. lissoplaca* has a few, tiny tables scattered among the dominant diamond-shaped plates without spires. *P. pediparva* has approximately equal proportions of oval tables and diamond-shaped tables of similar size. The curved supporting tables of *P. lissoplaca* have a moderately tall spire while those of *P. pediparva* have a low spire. *Pentamera constricta* (Ohshima 1915) from Japan has tables similar to *P. pediparva* but it also possesses large smooth plates and the skin is stiff and rough to the touch.

The known distributions of *P. rigida* and *P. pediparva* are within the Oregonian Province with a southern boundary near Point Conception, California. The northern boundary of this region is poorly defined and varies with the taxa being considered (see Lambert 1996) for discussion. The cluster of specimens in the British Columbia region is probably more indicative of collecting pressure than true abundance. I suspect that these two species may be mixed in with specimens of the three closely related species *P. populifera, P. pseudopopulifera* and *P. lissoplaca* in other museum collections. Also, a lack of collecting along the outer coasts of Washington and Oregon could explain the distribution gap for *P. pediparva.*

The two new species are included in the following key to the 14 species of *Pentamera* of the west coast of North and South America. This key is based primarily on ossicles. See Fig. 7 for explanation of dimensions of supporting tables used in the key. All measurements in μm.

Key to the *Pentamera* of the West Coast of North and South America

1(0) Mostly round to oval plates without spires, in skin; table ossicles rare or absent. 2

– Mostly large angular or star-shaped plates without a spire; occasional tables . . . . *Pentamera pseudocalcigera*

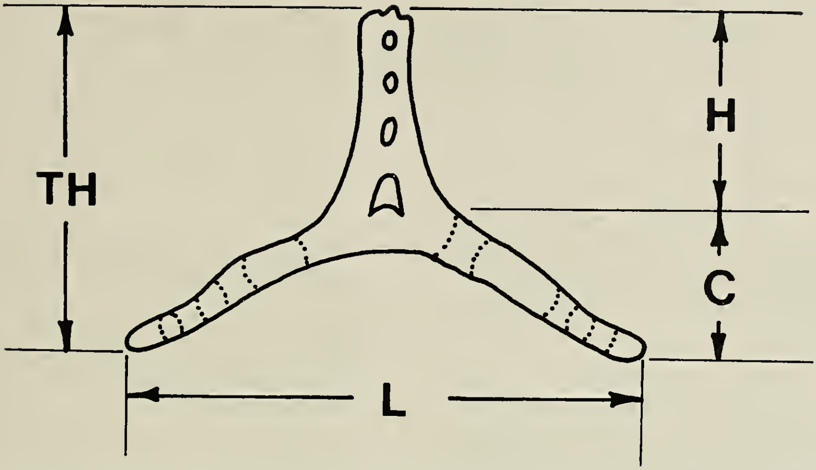

Fig. 7. Abbreviations for dimensions of supporting tables: TH, total height; H, height; C, height of curve; L, length.

– Mostly diamond-shaped plates; a few minute tables .... *Pentamera lissoplaca*
– Only table ossicles with spires in skin 3
2(1) Small oval plates with 2 central and up to 8 marginal knobs. Length of plates between 0 and 99 μm .... *Pentamera montereyensis*
– Thick, oval, knobbed, perforated plates; mean length 100 to 149 μm; diameter of podial end-plates 100 to 149 .... *Pentamera trachyplaca*
– Mostly oval plates; mean length between 150 and 199; diameter of podial end-plates 150 to 199 .... *Pentamera calcigera*
3(1) Supporting tables present in podia .. 4
– Supporting tables absent .... *Pentamera chierchia*
4(3) Spire of supporting table low, less than 24 μm 5
– Spire medium high, between 25 and 49 6
– Spire tall, between 50 and 74 8
5(4) Supporting tables with L:TH ratio of 1.5 to 1.9; mean length of tables 150 to 199; introvert with oval plates .... *Pentamera rigida*
– Supporting tables with L:TH ratio of 2 to 2.4; mean length of tables 100 to 149; introvert with rosettes .... *Pentamera pseudopopulifera*
– Supporting tables with L:TH ratio of 2.5 to 2.9; mean length of tables 50 to 99; introvert with tables .... *Pentamera pediparva*
6(4) Supporting tables with L:TH ratio of 1 to 1.4 7
– Supporting tables with L:TH ratio of 1.5 to 1.9 .... *Pentamera chiloensis*
7(6) Mean length of supporting tables 50 to 99; body U-shaped .... *Pentamera zacae*
– Mean length of supporting tables 100 to 149; body curved .... *Pentamera populifera*
8(4) Mean length of tables less than 50; width of spire at base less than 25 .... *Pentamera beebei*
– Mean length of tables 50 to 99; Width of spire at base 25 to 49 .... *Pentamera charlottae*

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The *Anacroneuria* of Costa Rica and Panama (Insecta: Plecoptera: Perlidae)

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Abstract.—Twenty seven *Anacroneuria* species are recorded for Costa Rica and Panama including 18 described as new species (*Anacroneuria alajuela, A. benedettoi, A. curiosa, A. exquisita, A. hacha, A. harperi, A. holzenthali, A. marca, A. marginata, A. maritza, A. perplexa, A. talamanca, A. tornada, A. uatsi, A. varilla, A. ventana, A. zapata, A. zarpa*). Redescriptions are given for nine species previously recorded from the area. Lectotypes are designated for *Anacroneuria expansa* Klapálek, *A. annulipalpis* Klapálek, *A. planicollis* Klapálek and *A. plutonis* (Banks); *A. expansa* Klapálek = *A. acutipennis* Klapálek, *A. chiapasa* Jewett = *A. planicollis* Klapálek, *A. dampfi* Jewett = *A. planicollis* Klapálek, and *A. tristani* (Navas) = *A. plutonis* (Banks) are placed in synonymy. A provisional key for males is provided.

The stonefly fauna of lower Mesoamerica includes only the speciose neotropical perlid genus *Anacroneuria*. Despite sporadic attempts (e.g., Needham & Broughton 1927, Jewett 1958, Harper 1992) this fauna remains virtually undocumented. Eleven of the twelve previously proposed Costa Rican and Panamanian species are known from obscure, scattered and undiagnostic original descriptions published early in this century. At that time the importance of internal male genitalic characters was unrecognized and similarities in size, coloration and subgenital plate structure led to the erroneous concept of *Anacroneuria* species with ranges extending from Mexico to Brazil (Needham & Broughton 1927). More recent studies (Zwick 1972, 1973; Stark 1995) suggest the male aedeagal structure is the most reliable structure for species recognition in this genus. Egg shape and size are useful in distinguishing some species but the chorionic surface lacks the detail found in other perlids.

In addition to the 12 species whose holotypes or lectotypes are based on Costa Rican or Panamanian material, Needham & Broughton (1927), Jewett (1958) and Harper (1992) include records of three earlier described species and records of three species based on paratypes. Needham & Broughton (1927) and Jewett (1958), for example, both record *A. cincta* (Pictet) and *A. nigrocincta* (Pictet) from the region but Zwick (1972, 1973) has shown neither of these can be considered valid records. Because the holotype of *A. cincta* is lost, that species is considered a nomen dubium, and the species identified as *A. nigrocincta* in these studies applies to another, presently unidentified species. Harper's (1992) record of *A. cincta* from Panama is based on Needham & Broughton's (1927) invalid definition of the species. Jewett (1958) included Panamanian specimens among the paratypes of *A. crenulata* Jewett and *A. flavominuta* Jewett. Harper's (1992) figures of the male aedeagi of these specimens indicate they are distinct from the respective allotypes. These specimens are assigned to two of the new species described in this study. Unfortunately the specimen listed by Harper (1992) as the putative male of *A. pallida* Jewett could not be located. *Anacroneuria sulana* Needham & Broughton (1927), recorded by Jewett (1958) from Panama, was placed as a synonym of *A. annulicauda* (Pictet) by Zwick (1972). Jewett's Panamanian specimens, presumably in the American Museum of Natural History, need to be reexamined before this identification is accepted.

During the late 1980's and early 1990's, R. W. Holzenthal and colleagues at the University of Minnesota and D. H. Funk, J. Jackson and colleagues at the Stroud Water Research Center made extensive light trap collections of Costa Rican stoneflies. This valuable material was made available for my study and has been supplemented with specimens from the museums listed below. Results from available material indicate a minimum of 27 species occur in Costa Rica and Panama. This includes nine of the earlier named species and 18 that are new to science. A relatively strong pattern of endemism emerges from this study with 21 species known only from Costa Rica-Panama. None of the species reported in Costa Rica or Panama are known to occur in South America and only two are currently reported from Mexico (Jewett 1958, Stark 1995). Males of thirteen species were taken in light traps from a single locality at Estacion Maritza in Guanacaste Province.

Materials and Methods

Aedeagai and female terminalia were prepared by clipping the abdomen and placing it in a small beaker of KOH. The solution was brought to a boil, then the terminalia were placed in dishes of distilled water and extraneous tissue removed with fine forceps. The aedeagus was also removed from the abdominal cavity with fine forceps and figures were prepared in dorsal, ventral and lateral aspects at 100×; figures of the male ninth sternum were drawn at 50× and the female terminalia at 25×. Figures of the adult head and pronota were drawn at 25× from specimens in alcohol.

Aedeagal preparations for scanning electron microscopy were made by crudely dissecting the structure from specimens in alcohol. The aedeagi were sonicated in acetone for one minute, air dried, placed on specimen stubs with double stick copper tape, sputter coated with gold-palladium, and the apex examined in ventral and lateral aspect with an AMRAY 1810D scanning electron microscope.

Holotype specimens of new species are placed in the United States National Museum (USNM); some specimens designated as holotypes are placed in the United States National Museum through the courtesy of Brigham Young University, Stroud Water Research Center, University of Minnesota and Utah State University. Paratypes and other specimens are deposited in the following collections as indicated:

Bill P. Stark, Clinton, Mississippi (BPS); Brigham Young University, Provo, Utah (BYU); C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado (CSU); Cornell University, Ithaca, New York (CU); Florida State Collection of Arthropods, Gainesville, Florida (FSCA); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (INBIO); Museum National d'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Natural History, Prague (NMP); Ohio State University, Columbus, Ohio (OSU); Stroud Water Research Center, Avondale, Pennsylvania (SWRC); University of Minnesota, Saint Paul, Minnesota (UMSP); Utah State University, Logan, Utah (USU).

Provisional Key to Regional Male *Anacroneuria*

1. Median pronotal band brown (Fig. 36) 2
– Median pronotal band yellow, or pronotum without distinct pigment bands 7
2. Hammer a low indistinct mound (Fig. 47) .... *hacha*
– Hammer well developed, thimble or nipple shaped (Figs. 7, 62) 3
3. Aedeagal apex projecting ventrally be-

tween hooks (Fig. 108); dorsal aedeagal keel absent .... *tornada*

– Aedeagal apex not projecting between hooks (Fig. 93); dorsal aedeagal keel well developed (Fig. 94) 4

4. Aedeagal apex with three subequal lobes (Fig. 95) .... *planicollis*

– Aedeagal apex simple or with minute lateral lobes (Figs. 65, 85) 5

5. Aedeagal apex beyond shoulders at least twice as long as wide (Fig. 84) .... *maritza*

– Aedeagal apex beyond shoulders about as long as wide (Fig. 64) 6

6. Lateral aspect of aedeagal apex wider than long at widest point (Fig. 38) *divisa*

– Lateral aspect of aedeagal apex longer than wide (Fig. 63). .... *lineata*

7. Hammer poorly developed or absent (Fig. 47) 8

– Hammer thimble shaped, well developed (Fig. 7) 12

8. Forewing length 7–11 mm 9

– Forewing length at least 14 mm 10

9. Aedeagal apex trilobed, lateral lobes small, hooks chelate (Fig. 90) . . . *perplexa*

– Aedeagal apex simple, hooks slender (Fig. 130) .... *varilla* in part

10. Hammer absent (Fig. 67); aedeagal apex simple, usually with a sharp transverse keel (Fig. 68) .... *magnirufa*

– Hammer a low obscure mound (Fig. 2); aedeagal apex trilobed, without keel (Fig. 4) 11

11. Mesal lobe of aedeagal apex deeply notched (Fig. 4); wing membrane without transparent circular spot near cord .... *acutipennis*

– Mesal lobe of aedeagal apex rounded (Fig. 44); wing membrane with transparent circular spot near cord . . *exquisita*

12. Head without brown pigment spot between or just anterior to ocelli (Fig. 11) 13

– Head with brown pigment between or just anterior to ocelli (Figs. 76, 96) . . 16

13. Aedeagal apex and hooks asymmetrical (Figs. 53–55) .... *harperi*

— Aedeagal apex and hooks symmetrical 14

14. Median yellow pronotal stripe less than a fourth of pronotal width (Fig. 131); aedeagal apex with clawlike dorsolateral lobes (Fig. 134) .... *zarpa*

– Median yellow pronotal stripe about half of pronotal width (Figs. 11, 31); aedeagal apex without clawlike dorsolateral lobes 15

15. Dorsal aedeagal apex acute and simple (Fig. 14) .... *annulipalpis*

– Dorsal aedeagal apex rounded and trilobed (Fig. 34) .... *curiosa*

16. Aedeagal apex massive with winglike shoulders (Figs. 20, 60) 17

– Aedeagal apex small and without winglike shoulders (Fig. 114) 18

17. Lateral aedeagal wings large and pointed (Fig. 60) .... *holzenthali*

– Lateral aedeagal wings small and rounded (Fig. 20) .... *benedettoi*

18. Forewing length at least 13 mm 19

– Forewing length no more than 10 mm 22

19. Aedeagal apex with small dorsolateral lobes, apex shoe shaped in lateral aspect (Figs. 128–129) .... *zapata*

– Aedeagal apex without dorsolateral lobes, lateral aspect not shoe shaped 20

20. Dorsal aedeagal keel well developed (Fig. 124); wing membrane usually with a circular transparent spot at cord .... *ventana*

– Dorsal aedeagal keel absent (Fig. 74); wing membrane without circular transparent spot 21

21. Aedeagal apex gradually narrowed to tip, bases of aedeagal hooks bulging (Fig. 100); M-line and lateral callosities on head distinct (Fig. 96) . . *plutonis*

– Aedeagal apex with almost parallel sides distal to shoulders, bases of hooks not enlarged (Fig. 75); head pattern with M-line and callosities indistinct (Fig. 71) .... *marca*

22. Ventral aedeagal apex with prominent pair of membranous lobes (Fig. 120) 23

– Ventral aedeagal apex without membranous lobes (Fig. 10) 24

23. Aedeagal apex offset from shoulders by lateral notches, tip acute (Fig. 24) .... *blanda*

– Aedeagal apex without lateral notches, tip truncate or emarginate (Fig. 119) .... *varilla* in part

24. Aedeagal apex projecting fingerlike from shoulders (Figs. 114–115) .... *uatsi*

– Aedeagal apex not fingerlike, lateral margins more or less convergent to tip (Figs. 10, 80) 25

25. Aedeagal apex with a U-shaped dorsal keel (Fig. 9) .... *alajuela*

– Aedeagal apex without U-shaped keel 26

26. Aedeagal apex gradually narrowed from bases of hooks to near tip (Fig. 104) .... *talamanca*

– Aedeagal apex not conspicuously narrowed beyond hooks (Figs. 29, 80) .. 27

27. Aedeagal apex with well developed dorsal keel (Fig. 79); area beyond hooks about as wide as long (Fig. 80) .... *marginata*

– Aedeagal apex with obscure dorsal keel (Fig. 29); area beyond hooks longer than wide (Fig. 30) .... *costana*

Anacroneuria acutipennis Klapálek
Figs. 1–5, 136, 159–160

Anacroneuria acutipennis Klapálek, 1923: 23. Holotype ♀, Volcan Chiriqui, Panama (NMP).

Anacroneuria expansa Klapálek, 1923:22. Lectotype ♀, Guatemala (NMP), new synonymy.

Anacroneuria sp. C: Harper, 1992:118.

Adult habitus.—Head yellow except for lappets and dark area forward of ocelli. Pale median pronotal stripe wide, midlateral dark stripes irregular (Fig. 1). Wing membrane transparent, veins pale brown; C and Sc pale.

Male.—Forewing length 16–17 mm. Hammer a low mound (Fig. 2). Aedeagal apex trilobed, mesal lobe deeply notched. Hooks stout, dorsal keel absent (Figs. 3–5, 159–160).

Female.—Forewing length 19–21 mm. Subgenital plate bilobed, lobes broad and usually emarginate; notch V-shaped. Transverse sclerite of sternum nine well developed; mesal sclerite T-shaped, lateral setae prominent (Fig. 136).

Nymph.—Unknown.

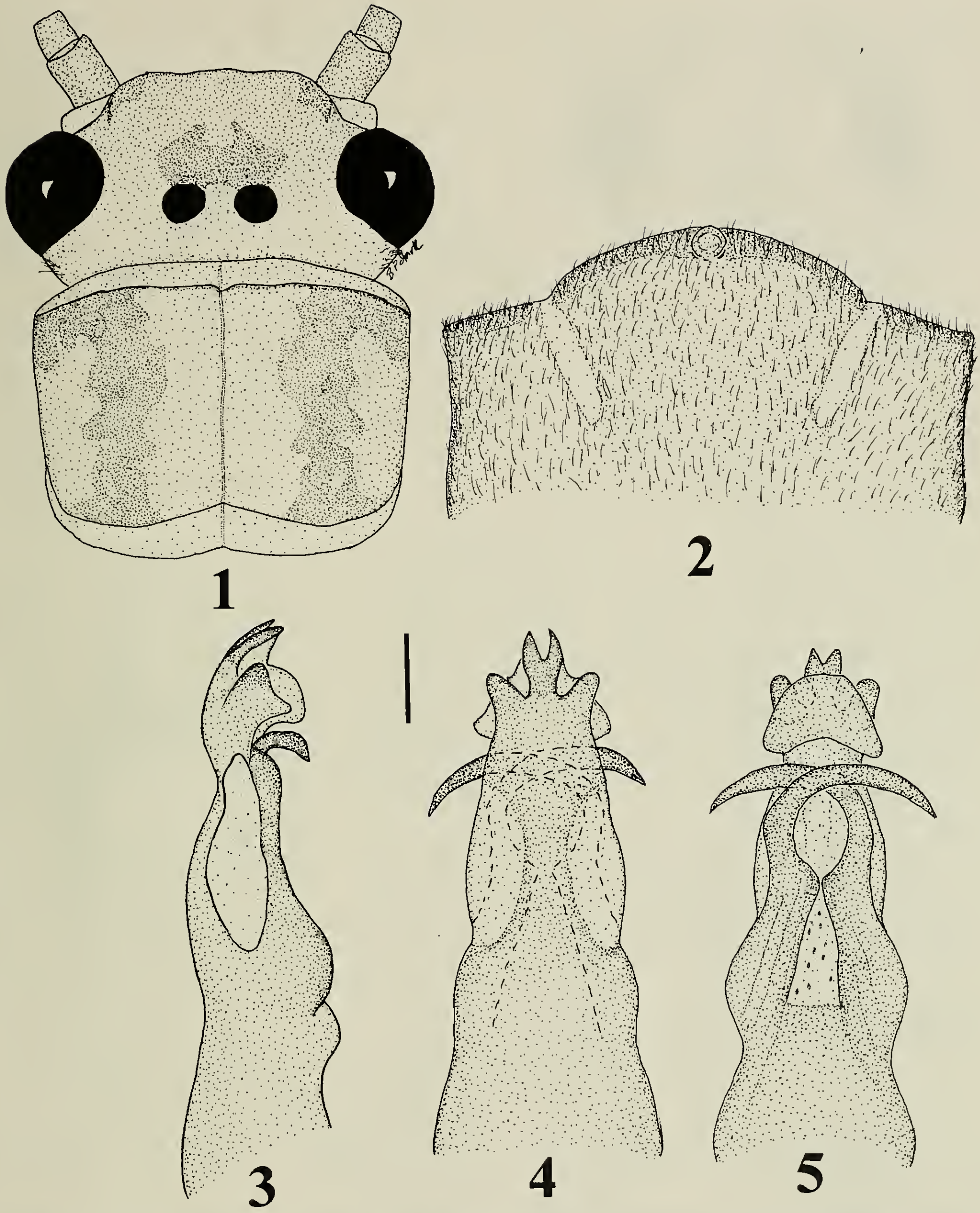
Material.—Costa Rica: Alajuela: Rio Peje, 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 1 ♂, 1 ♀ (UMSP). Cartago: Reserva Tapanti, Quebrada Palmitos, 1400 m, 2 Jun 1990, R. Holzenthal, R. Blahnik, F. Munoz, 1 ♂, 3 ♀ (BPS). Same location, 24 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♂ (INBIO). Same location, 1 Aug 1990, 3 ♀ (UMSP). Puntarenas: Rio Bellavista, ca. 1.5 mi NW Las Alturas, 1400 m, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (USNM). San Jose: Parque Nacional Braulio Carrillo, Rio Zurqui, 1650 m, 6 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (BPS). Guatemala: No locality data, *A. expansa* lectotype ♀ (NMP). Panama: Volcan Chiriqui, 1907, V. D. Whede, holotype ♀ (NMP). Same locality, 5500', 11 Jan 1964, S. L. Wood, 2 ♂ (BYU).

Comments.—A female specimen bearing label data "Anacroneuria expansa Klap. 1923, guat/de Selys 21" from the Natural History Museum, Prague, is selected as lectotype. Although the forewing length of this specimen is given as 28 mm (Klapálek 1923) it is similar in body size to other specimens of *A. acutipennis,* and it is indistinguishable from these specimens in subgenital plate shape and features of sternum nine and thus is placed as a synonym. The Panamanian material recorded as "*Anacroneuria* sp. C" by Harper (1992) is also assigned to this species.

Anacroneuria alajuela, new species
Figs. 6–10

Adult habitus.—Head with a large dark area over ocelli extending to M-line; lappets brown. Median pronotal stripe yellow, lateral stripes brown (Fig. 6). Wing membrane brown, veins brown.

Male.—Forewing length 9 mm. Hammer thimble shaped, height greater than basal diameter (Fig. 7). Aedeagal apex broad, scoop shaped and bearing a dorsal U-



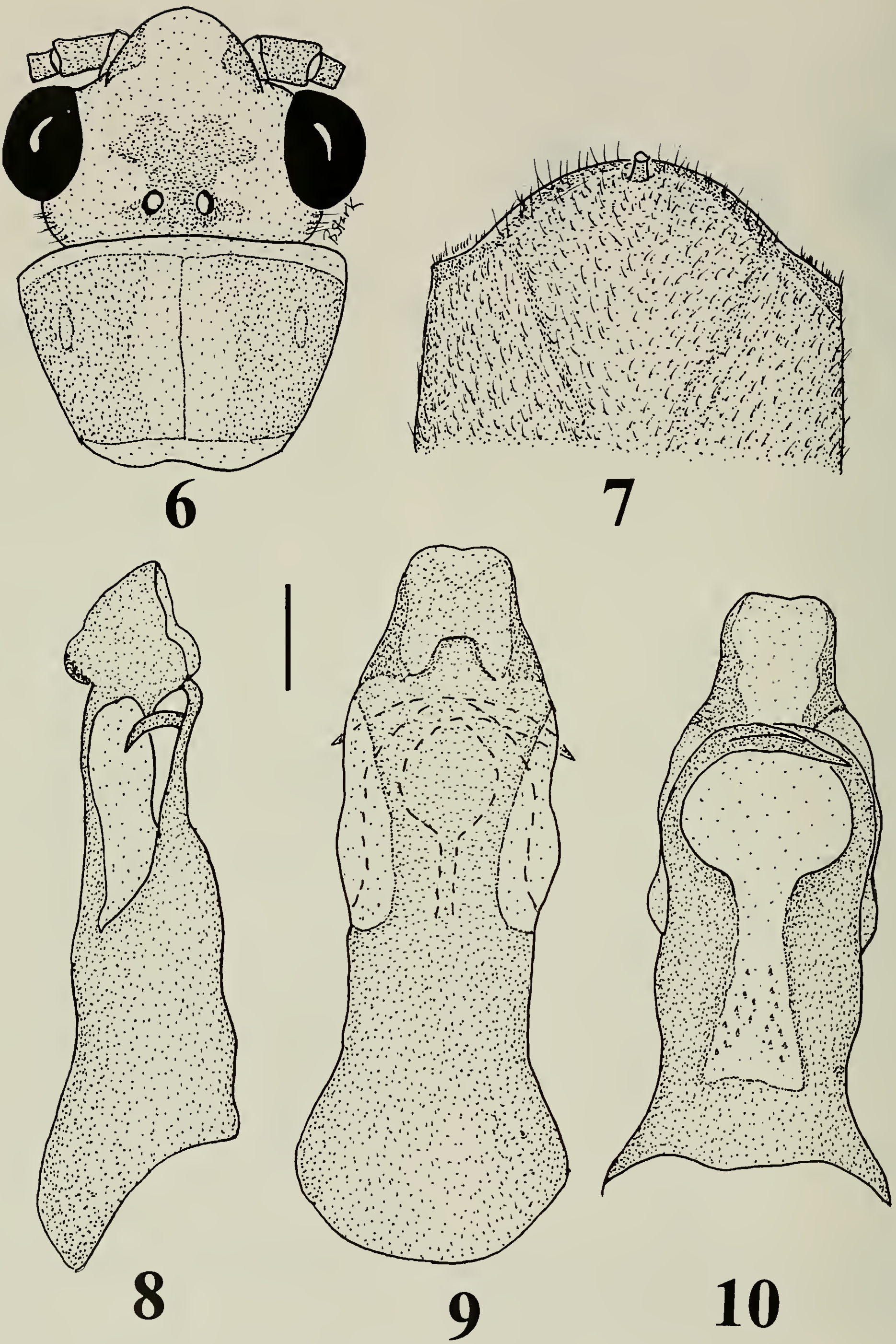
Figs. 1–5. *A. acutipennis* structures. 1. Head and pronotum. 2. Male sternum 9. 3. Aedeagus, lateral. 4. Aedeagus, dorsal. 5. Aedeagus, ventral. Scales: 0.6 mm (1), 0.3 mm (2), 0.15 mm (3–5).

shaped keel; hooks moderately thickened (Figs. 8–10).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The species name, based on the Costa Rican province in which the holotype was collected, is used as a noun in apposition.



Figs. 6–10. *A. alajuela* structures. 6. Head and pronotum. 7. Male sternum 9. 8. Aedeagus, lateral. 9. Aedeagus, dorsal. 10. Aedeagus, ventral. Scales: 0.6 mm (6), 0.3 mm (7), 0.15 mm (8–10).

Types.—Holotype ♂ from Costa Rica, Alajuela, 20 km S Upala, June 1990, F. D. Parker (USNM).

Diagnosis.—The broad aedeagal apex is similar to that of *A. divisa* (Figs. 38–40) and *A. lineata* (Figs. 63–65) but these species have dark mesal pronotal stripes, low moundlike hammers and narrow longitudinal aedeagal keels.

Anacroneuria annulipalpis Klapálek
Figs. 11–15, 137, 161–162

Anacroneuria annulipalpis Klapálek, 1922: 91. Lectotype ♀, Chiriqui, Panama (NMP).

Anacroneuria quadriloba Jewett: Harper, 1992:117.

Adult habitus.—Head yellow. Pronotum yellow except for irregular, dark lateral stripes (Fig. 11). Wing membrane pale amber, veins C, Sc pale, others brown.

Male.—Forewing length 12–16 mm. Hammer thimble shaped (Fig. 12). Aedeagal apex greatly narrowed into curved spine; ventral membranous processes present. Dorsal keel absent, hooks scooped at apex (Figs. 13–15, 161–162).

Female.—Forewing length 16–20 mm. Subgenital plate four lobed; outer lobes broad, but subequal in length to inner lobes. Transverse sclerite of sternum nine curved, mesal sclerite T-shaped and sparsely setose (Fig. 137).

Nymph.—Unknown.

Material.—Costa Rica: Alajuela: Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 30 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Same location, 1 May 1990, R. Holzenthal, R. Blahnik, 1 ♀ (UMSP). Guanacaste: Estacion Maritza, Rio Tempisquito, 5 May 1989, 7 ♂ (BPS). Same location, 11 May 1990, 1 ♂, 1 ♀ (SWRC). Same location, 30 May 1990, 2 ♂ (SWRC). Same location, 22 Oct 1990, 5 ♂ (INBIO). Puntarenas: Zona Protectora Las Tablas, Rio Coton, Sitio Coton, 1460 m, 15 Apr 1989, R. Holzenthal, R. Blahnik, 1 ♂, 1 ♀ (INBIO). Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 2 Aug 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂, 3 ♀ (UMSP). Rio Jaba, 1.4 km W Las Cruces, 1150 m, 14 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (BPS). San Vito de Java, 23 May 1960, C. F. Dowling, 1 ♂ (FSCA). San Jose: Parque Nacional Braulio Carrillo, Rio Zurqui, 1650 m, 6 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 2 ♂, 1 ♀ (UMSP). El Salvaje, Rio Tabarcia, 8 km E Palmichal, 1650 m, 19 Jan 1992, R. Holzenthal, K. Kjer, F. Quesada, 2 ♂ (INBIO). Panama: Chiriqui Province, 5 km NE El Hato del Volcan, 1 Oct 1975, D. Chandler, 1 ♂ (BYU). Volcan Chiriqui, 5500' 11 Jan 1964, S. L. Wood, 2 ♂ (BYU). Chiriqui, 2 ♀ syntypes (NMP).

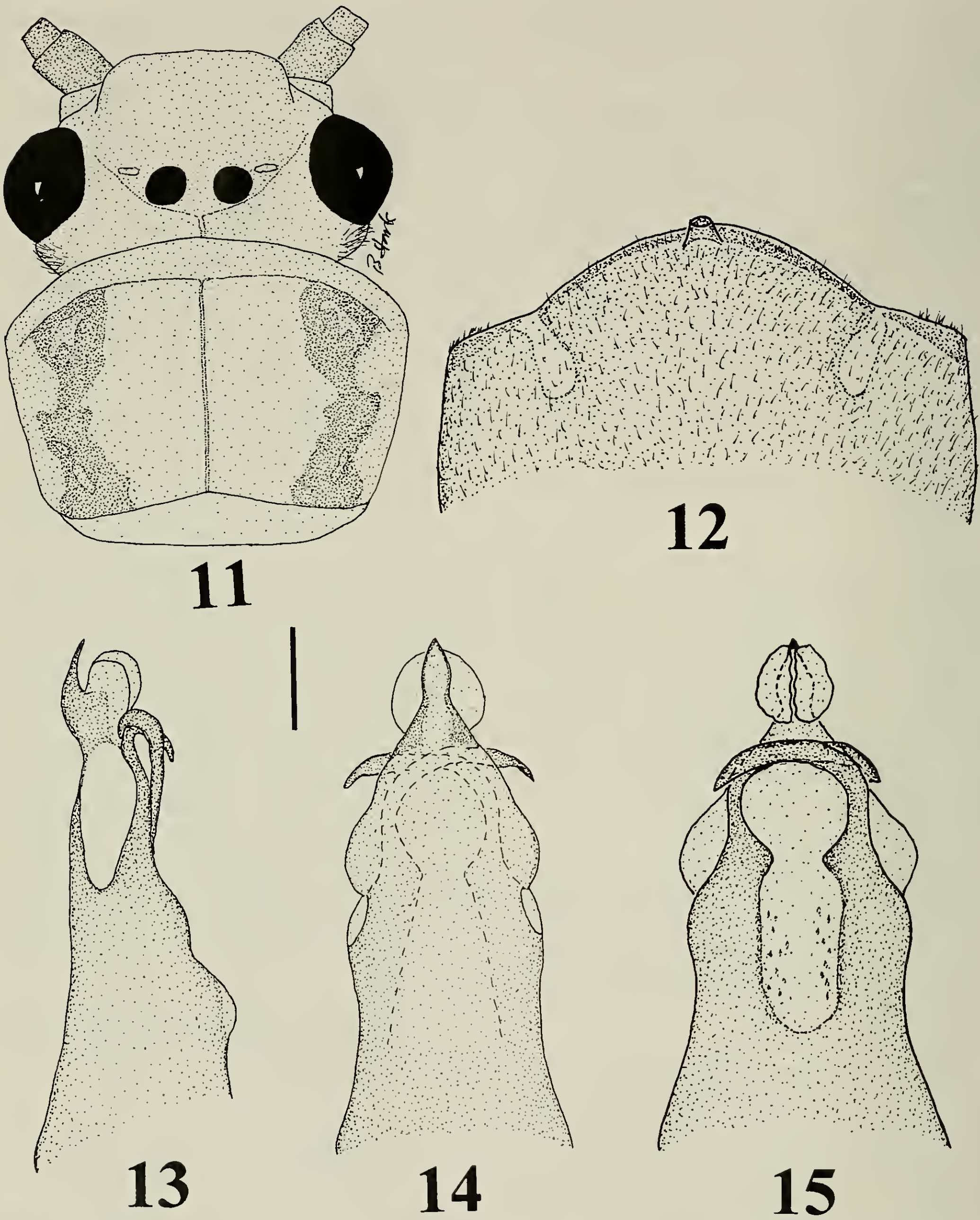
Comments.—Two female syntypes were located, each with damaged subgenital plates. One specimen is so severely damaged as to prevent diagnosis. The other has the left half of sternum eight and most of sternum nine intact and is chosen as lectotype. Both specimens are in the National Museum of Natural History, Prague and were studied while on loan to P. Zwick. Female *A. quadriloba* Jewett are indistinguishable from this species but the aedeagus of paratopotypes are more similar to those of *A. lineata* (Fig. 95). However, the Panamanian records listed for *A. quadriloba* by Harper (1992) are to be included with this species.

Costa Rican specimens show somewhat more size variation than has been noted for other *Anacroneuria*.

Anacroneuria benedettoi, new species
Figs. 16–20, 138, 163–164

Adult habitus.—Head mostly yellow brown with diffuse brown over ocelli and lappets. Median yellow pronotal stripe bordered by irregular, broad midlateral brown bands; anterolateral margins pale (Fig. 16). Wing membrane brown, veins brown.

Male.—Forewing length 10 mm. Hammer thimble shaped, height subequal to diameter (Fig. 17). Aedeagal apex trilobed,

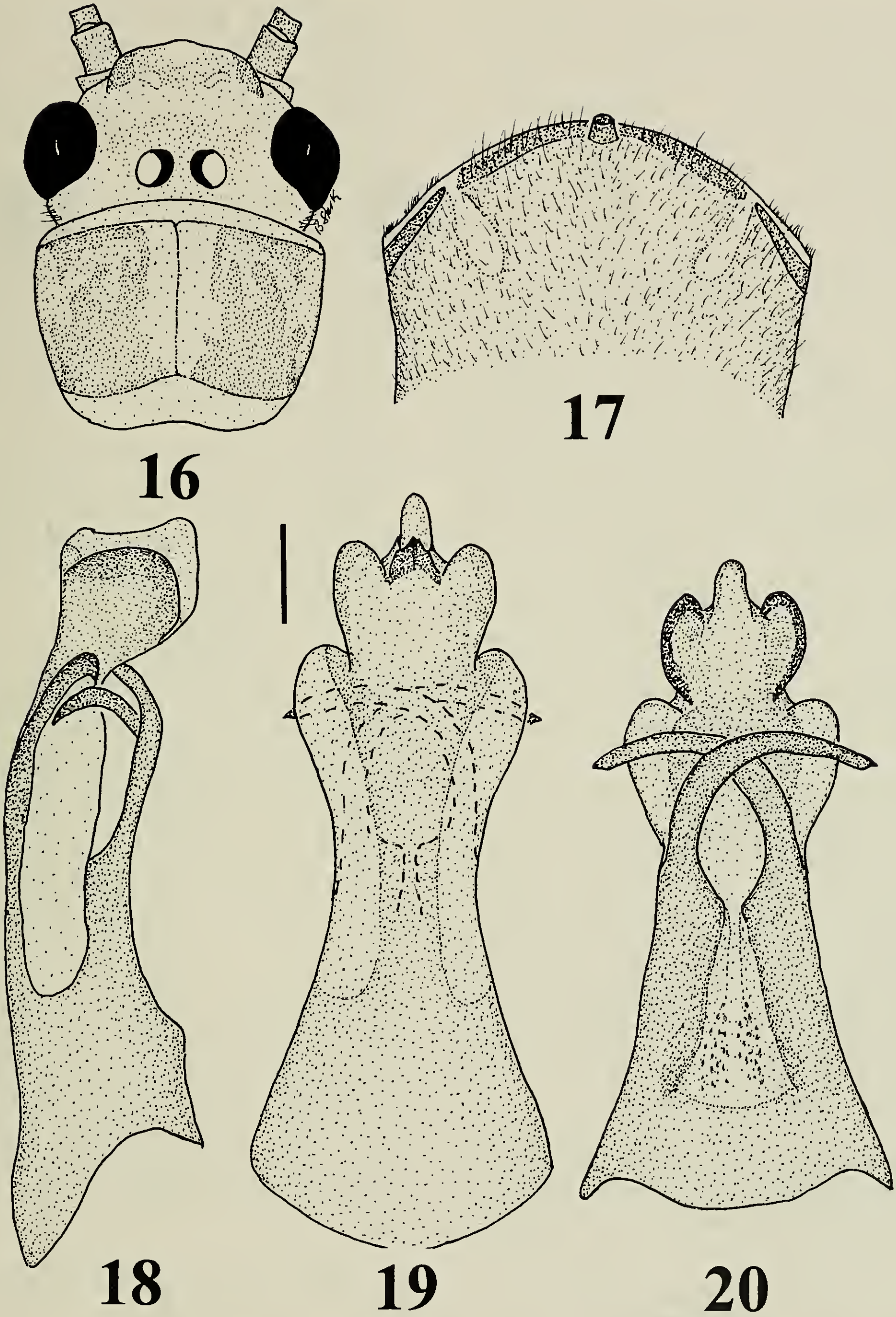


Figs. 11–15. *A. annulipalpis* structures. 11. Head and pronotum. 12. Male sternum 9. 13. Aedeagus, lateral. 14. Aedeagus, dorsal. 15. Aedeagus, ventral. Scales: 0.6 mm (11), 0.3 mm (12), 0.15 mm (13–15).

shoulders projecting laterally. Dorsal keel on mesal lobe, hooks slender (Figs. 18–20, 163–164).

Female.—Forewing length 12–13 mm. Subgenital plate four lobed. Lateral lobes longer than mesal lobes, mesal notch V-shaped. Transverse sclerite of sternum nine sinuate; T-shaped mesal sclerite setose, lateral setae prominent (Fig. 138).

Nymph.—Unknown.



Figs. 16–20. *A. benedettoi* structures. 16. Head and pronotum. 17. Male sternum 9. 18. Aedeagus, lateral. 19. Aedeagus, dorsal. 20. Aedeagus, ventral. Scales: 0.6 mm (16), 0.3 mm (17), 0.15 mm (18–20).

Etymology.—The patronym honors L. A. Benedetto for his generosity in sharing information on *Anacroneuria* type material.

Types.—Holotype ♂ from Costa Rica, Guanacaste, Rio Los Ahogados, 11.3 km ENE Quebrada Grande, 470 m, 7 Mar 1986, R. Holzenthal, W. Fasth (USNM). Paratypes: Costa Rica: Alajuela: Laguna Rio Cuarto, 2.8 km N Rio Cuarto, 400 m, 13 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 2 ♂ (UMSP). Guanacaste: Rio Gongora, 4 km NE Quebrada Grande, 590 m, 21 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 6 ♂ (INBIO, UMSP). Rio Aguacate, 0.5 km E Aguacate, 590 m, 16 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 1 ♂ (UMSP). Rio Orosi, Estacion Pitilla, 700 m, 22 May 1990, R. Holzenthal, R. Blahnik, 2 ♂ (BPS). Parque Nacional Guanacaste, El Hacha, Quebrada Alcornoque, 250 m, 26 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 9 ♂ (BPS). Estacion Maritza, Rio Tempisquito, 28 May 1989, 1 ♂ (SWRC). Limon: Rio Banano, 16 km WSW Bomba, 150 m, 26 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 8 ♂ (UMSP). Puntarenas: Reserva Biologica Carara, Quebrada Bonita, 35 m, 18–20 May 1990, R. Holzenthal, R. Blahnik, 1 ♂ (UMSP). 2 mi SW San Vito de Java, 22–24 Jun 1964, R. Woodruff, 2 ♂ (FSCA). San Jose: Reserva Biologica Carara, Rio Carara, Carara, 280 m, 14 Feb 1991, R. Holzenthal, F. Munoz, J. Huisman, 2 ♂, 1 ♀ (UMSP). Panama: Bocas del Toro Province: Miramar, 3 Apr 1979, H. Wolda, 1 ♂ (BYU).

Diagnosis.—This species is similar to *A. holzenthali* but has smaller and apically rounded aedeagal wings rather than long and pointed wings typical of *A. holzenthali.*

Anacroneuria blanda Needham & Broughton
Figs. 21–25, 139

Anacroneuria blanda Needham & Broughton, 1927:117. Holotype ♀, Barro Colorado Island, Panama (CU).
Anacroneuria blanda: Harper, 1992:117.

Adult habitus.—Head yellow except for lappets and dark area covering ocelli and extending forward and laterally to M-line. Median pronotal stripe yellow, lateral stripes brown, anterolateral margins pale (Fig. 21).

Male.—Forewing length 9 mm. Hammer cylindrical, height greater than diameter (Fig. 22). Triangular aedeagal apex offset from shoulders by transverse dorsolateral grooves; ventral aspect with a pair of membranous lobes, lateral aspect sinuate. Dorsal keel absent, hooks somewhat scoop shaped at the tips (Figs. 23–25).

Female.—Forewing length 13–14 mm. Subgenital plate bilobed, margins rounded or truncate, notch V-shaped. Transverse sclerite of sternum nine absent, posterior margin concave; mesal sclerite triangular and sparsely setose (Fig. 139).

Nymph.—Unknown.

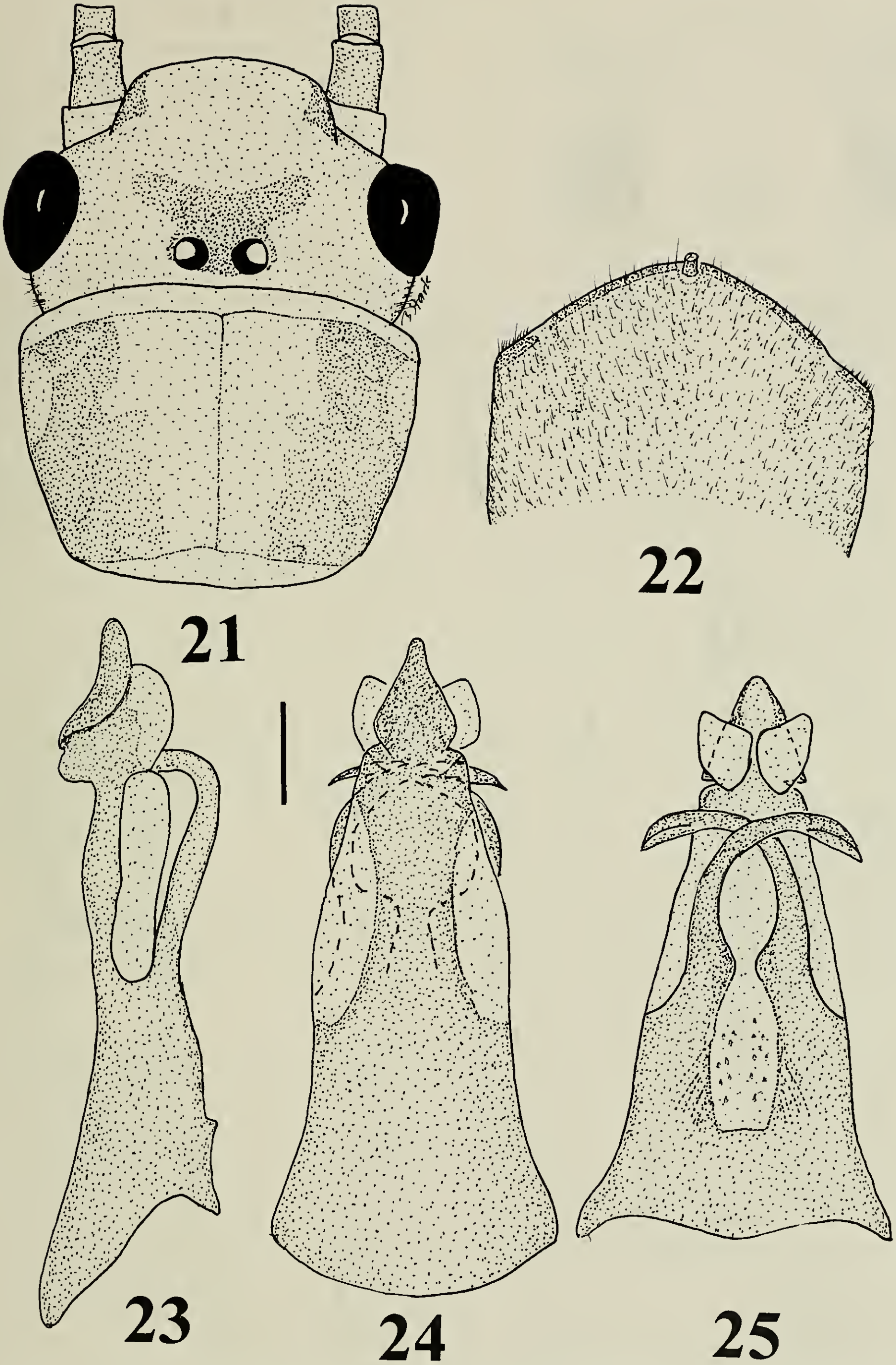
Material.—Costa Rica: Alajuela: 20 km S Upala, 5–10 Mar 1991, F. Parker, 2 ♂ (BYU, USU). Puntarenas: 2.8 mi E Golfito, 3–4 Jul 1967, O. S. Flint, Ortiz, 1 ♂ (USNM). Panama: Rio Agua Salud, Pipeline Road, 8–12 Jul 1967, O. S. Flint, Ortiz, 1 ♂ (USNM). Cerro Campana, 11–14 Jul 1967, O. S. Flint, 2 ♀ (USNM). Barro Colorado Island, W. C. Allee, Holotype ♀ (CU).

Comments.—*Anacroneuria blanda* was known from the holotype female until Harper (1992) assigned the additional Panamanian specimens listed above to this species. Although these specimens have a larger area of dark pigment on the head than the holotype, they are indistinguishable in other features and I concur with this placement.

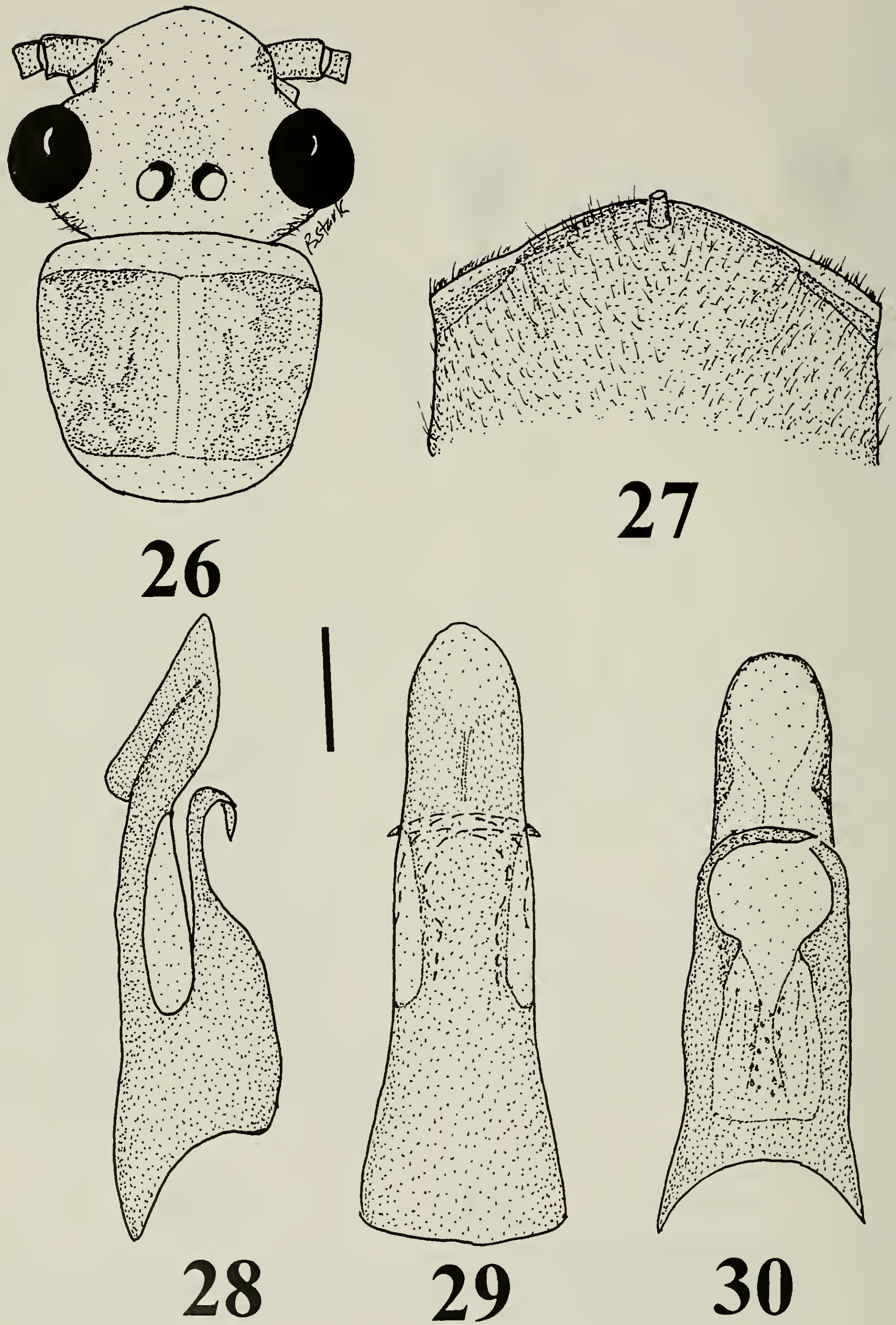
Anacroneuria costana (Navas)
Figs. 26–30

Neoperla costana Navas, 1924:72. Holotype ♂, Costa Rica (MNHN).

Adult habitus.—Head yellow with diffuse yellow brown over ocelli; lappets brown. Median pronotal stripe pale, irreg-



Figs. 21–25. *A. blanda* structures. 21. Head and pronotum. 22. Male sternum 9. 23. Aedeagus, lateral. 24. Aedeagus, dorsal. 25. Aedeagus, ventral. Scales: 0.6 mm (21), 0.3 mm (22), 0.15 mm (23–25).



Figs. 26–30. *A. costana* structures. 26. Head and pronotum. 27. Male sternum 9. 28. Aedeagus, lateral. 29. Aedeagus, dorsal. 30. Aedeagus, ventral. Scales: 0.6 mm (26), 0.3 mm (27), 0.15 mm (28–30).

ular midlateral stripes brown, margins pale (Fig. 26). Wings transparent, veins brown.

Male.—Forewing length 8.5 mm. Hammer thimble shaped, height greater than diameter (Fig. 27). Aedeagal apex simple, scoop shaped; dorsal keel weak, hooks slender (Figs. 28–30).

Female.—Unknown.

Nymph.—Unknown.

Material.—Costa Rica: Puntarenas: Rio Guineal, ca. 1 km E Finca Helechales, 840 m, 22 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♂ (BPS). Rio Singri, ca. 2 km S Finca Helechales, 22 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 2 ♂ (UMSP, INBIO).

Comments.—*Anacroneuria costana* is a member of a large and difficult species complex found throughout Central and South America. Among Costa Rican species, *A. costana* most closely resembles *A. marginata,* new species, but that species has a shorter and more robust aedeagal apex. The aedeagus of these Puntarenas males closely resembles the figures of the holotype provided by L. Benedetto (L. Benedetto, pers. comm.).

Anacroneuria curiosa, new species
Figs. 31–35, 165–166

Anacroneuria flavominuta: Harper, 1992: 116.

Adult habitus.—Head yellow except for lappets. Pronotum with irregular dark lateral bands and a wide mesal yellow band (Fig. 31). Femora yellow with narrow black apical band. Wing membrane and most veins brown; R vein dark brown, C pale.

Male.—Forewing length 8–9 mm. Hammer thimble shaped, height greater than diameter (Fig. 32). Dorsal aspect of aedeagal apex trilobed; mesal lobe longer than lateral lobes and weakly keeled basally (Figs. 33–35, 165–166). Apex offset from dorsal sclerite by prominent transverse fold (Fig. 165).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The species name, meaning inquisitive or curious, alludes to the peculiar transverse dorsal fold on the aedeagal apex whose function will require even greater curiosity to discern.

Types.—Holotype ♂ and 15 ♂ paratypes from Costa Rica, Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal (USNM). Additional Paratypes: Costa Rica: Alajuela: Rio Bochinche tributary, Cerro Campana, 6 km NW Dos Rios, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 3 ♂ (UMSP). Guanacaste: Quebrada Garcia, 470 m, 8 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (BPS). Parque Nacional Guanacaste, Estacion Pitilla, Rio Orosi, 700 m, 19 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 2 ♂ (USNM). Parque Nacional Guanacaste, Estacion Maritza, Rio Tempisquito, 550 m, 30 Aug 1990, J. Huisman, R. Blahnik, F. Quesada, 1 ♂ (UMSP). Estacion Maritza, Rio Tempisquito, 25 May 1990, 1 ♂ (SWRC). Same location, 30 May 1990, 1 ♂ (INBIO). Nicaragua: Pte. Quinama, E Villa Somoza, 29 Jul 1967, O. S. Flint, 1 ♂ (USNM).

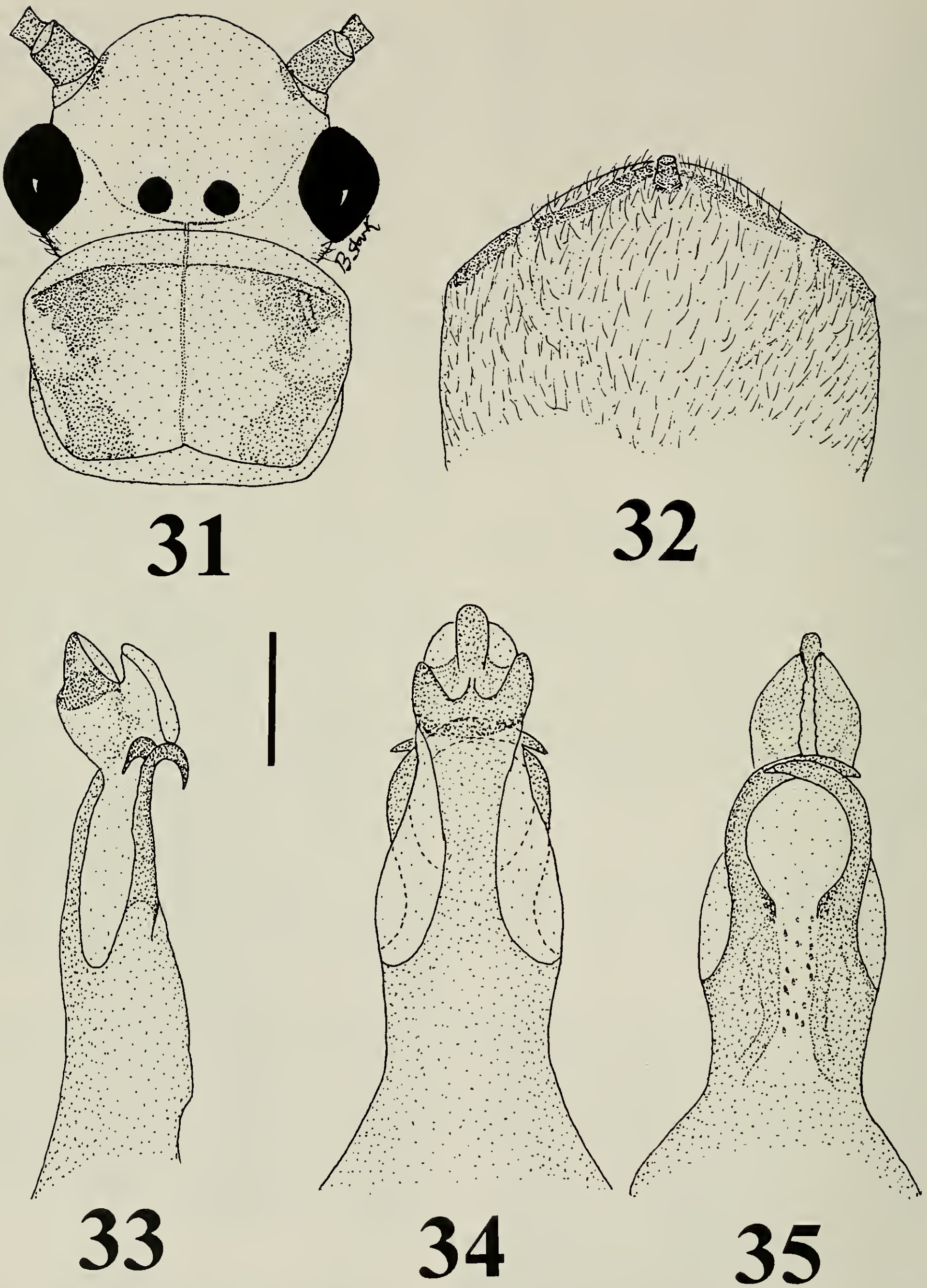
Diagnosis.—This species resembles *A. uatsi* in size and general coloration but the two are quite distinct in aedeagal features. In dorsal aspect *A. curiosa* has a complete transverse fold (Fig. 34) whereas *A. uatsi* has only a minute keel (Fig. 114).

Comments.—This small species ranges at least from Panama to Nicaragua but may be uncommon. Harper's (1992) figure of the aedeagus of an *A. flavominuta* paratype from Panama is typical of this species and distinct from the allotype male of *A. flavominuta* from Mexico.

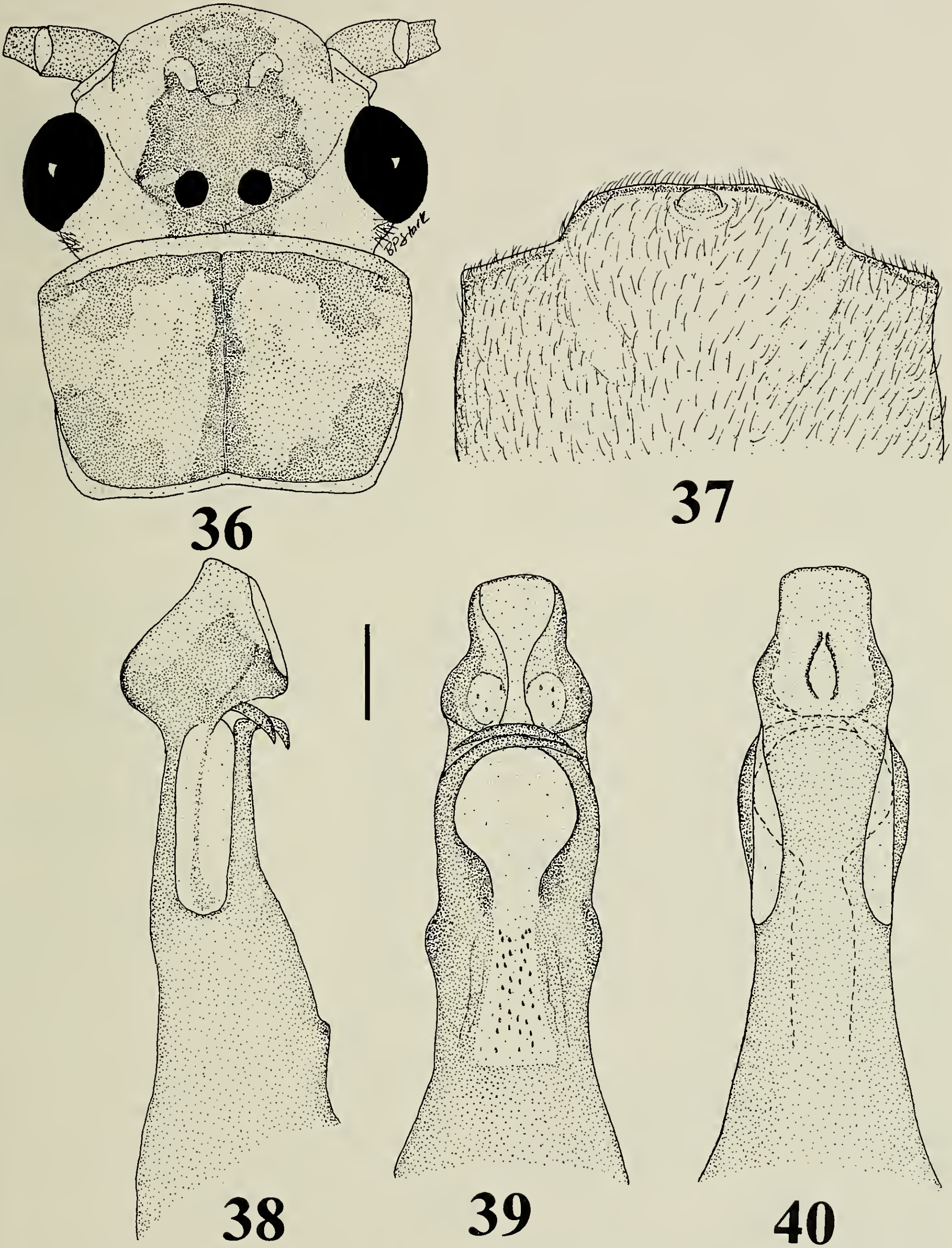
Anacroneuria divisa (Navas)
Figs. 36–40, 141, 167–168

Forquilla divisa Navas 1924:74. Syntype ♀, Costa Rica (NMNH).

Adult habitus.—Head with dark pattern over ocelli extending onto clypeus, but interrupted by pale M-line; pale oval areas



Figs. 31–35. *A. curiosa* structures. 31. Head and pronotum. 32. Male sternum 9. 33. Aedeagus, lateral. 34. Aedeagus, dorsal. 35. Aedeagus, ventral. Scales: 0.6 mm (31), 0.3 mm (32), 0.15 mm (33–35).



Figs. 36–40. *A. divisa* structures. 36. Head and pronotum. 37. Male sternum 9. 38. Aedeagus, lateral. 39. Aedeagus, ventral. 40. Aedeagus, dorsal. Scales: 0.6 mm (36), 0.3 mm (37), 0.15 mm (38–40).

lateral to ocelli and minute spots anterolateral to ocelli, lappets diffuse brown. Median pronotal stripe brown; anterior and posterior margins brown, disc and anterolateral margins pale (Fig. 36). Wing membrane brown, veins C, Sc and R pale, other veins brown.

Male.—Forewing length 13–15 mm. Hammer low, nipple shaped (Fig. 37). Aedeagal apex simple, scoop shaped with broad, rounded shoulders. Lateral aspect expanded through dorsal keel; hooks slender (Figs. 38–40, 167–168).

Female.—Forewing length 17–19 mm. Subgenital plate four lobed; lateral lobes larger than median lobes. Transverse sclerite of sternum nine with median notch; median sclerite T-shaped, lateral setae prominent (Fig. 141).

Nymph.—Unknown.

Material.—Costa Rica: Alajuela: Cerro Campana, Rio Bochinche tributary, 6 km NW Dos Rios, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen 12 ♂, 3 ♀ (UMSP, INBIO). Rio Peje, 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 4 ♀ (INBIO). Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 30 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Guanacaste: Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 12 ♂ (BPS, INBIO, UMSP). Estacion Maritza, Rio Tempisquito, 11 Feb 1990, 2 ♂ (SWRC). Same location, 17 Mar 1989, 1 ♂, 1 ♀ (BPS). Same location, 11 Apr 1990, 10 ♂ (SWRC). Same location, 28 May 1989, 4 ♂, 1 ♀ (INBIO). Same location, 22 Oct 1990, 6 ♂, 1 ♀ (SWRC). Same location, 11 Nov 1989, 1 ♂, 1 ♀ (BPS). Parque Nacional Guanacaste, Rio San Josecito, Estacion Mengo, 960 m, 28 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 2 ♂ (UMSP). Parque Nacional Guanacaste, Rio Orosi, Estacion Pitilla, 700 m, 22 May 1990, R. Holzenthal, R. Blahnik, 14 ♂, 5 ♀ (BPS, UMSP). Parque Nacional Guanacaste, El Hacha, Quebrada Alcornoque, 250 m, 26 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂ (UMSP). Parque Nacional Rincon de la Vieja, Quebrada Zapilote, 785 m, 3 Mar 1986, R. Holzenthal, 1 ♂ (BPS). Quebrada Garcia, 470 m, 8 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (BPS).

Comments.—The male syntype is missing but L. Benedetto provided notes on the female syntype.

Anacroneuria exquisita, new species
Figs. 41–45

Adult habitus.—Head yellow. Median pronotal stripe broad and pale; irregular lateral stripes brown, margins pale (Fig. 41). Wings pale amber, transparent circular window beyond cord; veins C, Sc and R pale, others brown.

Male.—Forewing length 14 mm. Hammer a low membranous disc (Fig. 42). Aedeagal apex trilobed, lateral lobes small and covered ventrally by membranous processes. Dorsal keel inconspicuous, hooks slender (Figs. 43–45).

Female.—Unknown.

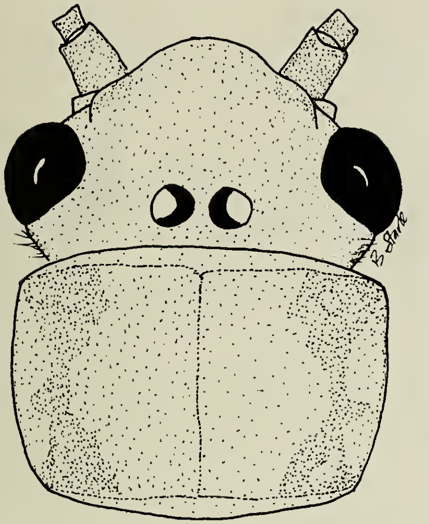
Nymph.—Unknown.

Etymology.—The species name, meaning excellent or admirable, refers to the distinctive adult color pattern.

Types.—Holotype ♂ (USNM) and four ♂ paratypes (BPS, UMSP) from Costa Rica, San Jose, Parque Nacional Braulio Carrillo, Rio Zurqui, 1650 m, 6 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage.

Diagnosis.—*A. exquisita* is similar in aedeagal features to *A. perplexa* (Figs. 88–90) but that species is smaller and darker (Fig. 86). *A. ventana* has a similar wing pattern but differs in aedeagal structure (Figs. 124–125), hammer shape (Fig. 122) and head pattern (Fig. 121).

A series of female specimens from Estacion Maritza are similar in color pattern but they are smaller, have a dark ocellar patch and the dark pronotal stripes are larger and convergent posteriorly. Thus these specimens remain unassociated and the female of *A. exquisita,* unknown.



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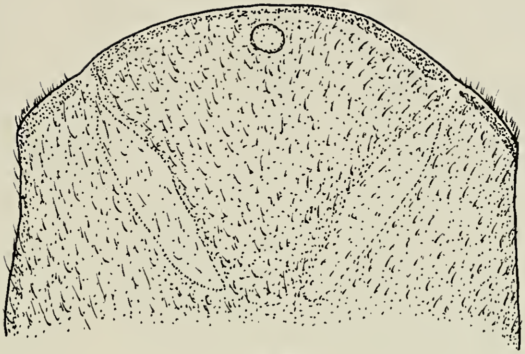

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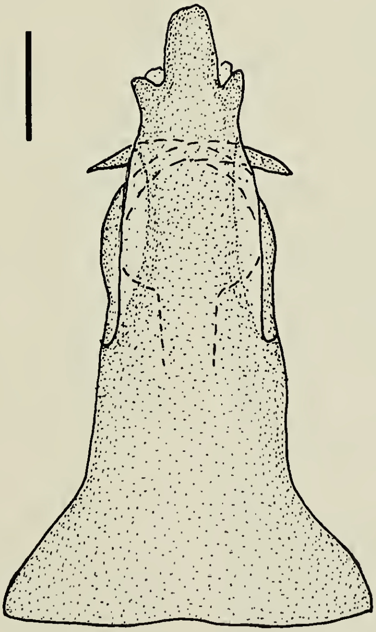

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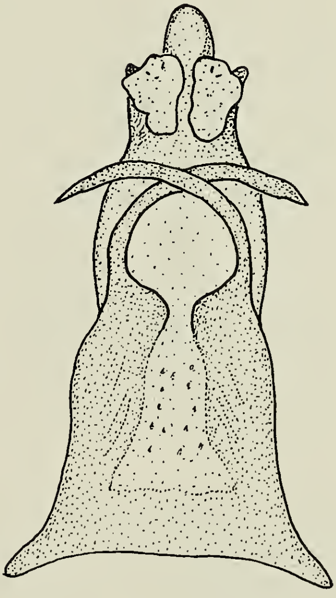

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Figs. 41–45. *A. exquisita* structures. 41. Head and pronotum. 42. Male sternum 9. 43. Aedeagus, lateral. 44. Aedeagus, dorsal. 45. Aedeagus, ventral. Scales: 0.6 mm (41), 0.3 mm (42), 0.15 mm (43–45).

Anacroneuria hacha, new species
Figs. 48–50, 169–170

Adult habitus.—Dark head pattern covers ocelli and extends to anterior margin; pattern diffuse and almost interrupted at M-line. Median pronotal stripe diffuse brown, bordered by yellow; irregular midlateral stripes brown, margins pale (Fig. 46). Wing membrane brown, veins brown.

Male.—Forewing length 10–11 mm. Hammer a low indistinct mound (Fig. 47). Aedeagal apex simple, dorsal margin truncate or emarginate, keel well developed. Lateral aspect somewhat hatchet shaped; hooks slender (Fig. 48–50, 169–170).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—Hacha, Spanish for axe, refering to the hatchet shaped aedeagal apex, is used as a noun in apposition.

Types.—Holotype ♂ (USNM) and 1 ♂ paratype (SWRC) from Costa Rica, Guanacaste, Estacion Maritza, Rio Tempisquito, 27 Apr 1989. Additional Paratypes: Costa Roca: Type locality, 11 May 1990, 2 ♂ (SWRC). Same location, 21 May 1990, 1 ♂ (SWRC). Same location, 30 May 1990, 6 ♂ (BPS). Same location, 10 Oct 1989, 1 ♂ (SWRC). Same location, 22 Oct 1990, 4 ♂ (INBIO). Parque Nacional Guanacaste Maritza, Rio Tempisquito, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 6 ♂ (UMSP). Same location, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 10 ♂ (USNM).

Diagnosis.—*A. hacha* is similar to *A. divisa* in color pattern (Fig. 36) and general aedeagal shape (Figs. 38–40), but the two are distinguished on the basis of the hammer (Figs. 37, 47) and aedeagal keel (Figs. 40, 49).

Anacroneuria harperi, new species
Figs. 51–55, 142

Anacroneuria sp. B: Harper, 1992:118.

Adult habitus.—Head yellow with diffuse brown area forward of ocelli; lappets brown. Median pronotal stripe yellow; most of disc pale brown, anterolateral margins pale (Fig. 51). Wing membrane brown, veins brown.

Male.—Forewing length 7 mm. Hammer thimble shaped, height greater than diameter (Fig. 52). Aedeagal body asymmetrical, apex twisted in a slight sinistral direction. Hooks twisted and asymmetrical; apex of right hook recurved. Dorsal keel absent (Figs. 53–55).

Female.—Forewing length 9 mm. Subgenital plate four lobed; inner lobes smaller than outer lobes. Transverse sclerite of sternum nine narrow; mesal area of sclerite densely setose. Mesal sclerite T-shaped, lateral setae prominent (Fig. 142).

Nymph.—Unknown.

Etymology.—The patronym honors P. Harper for his recognition of this interesting species.

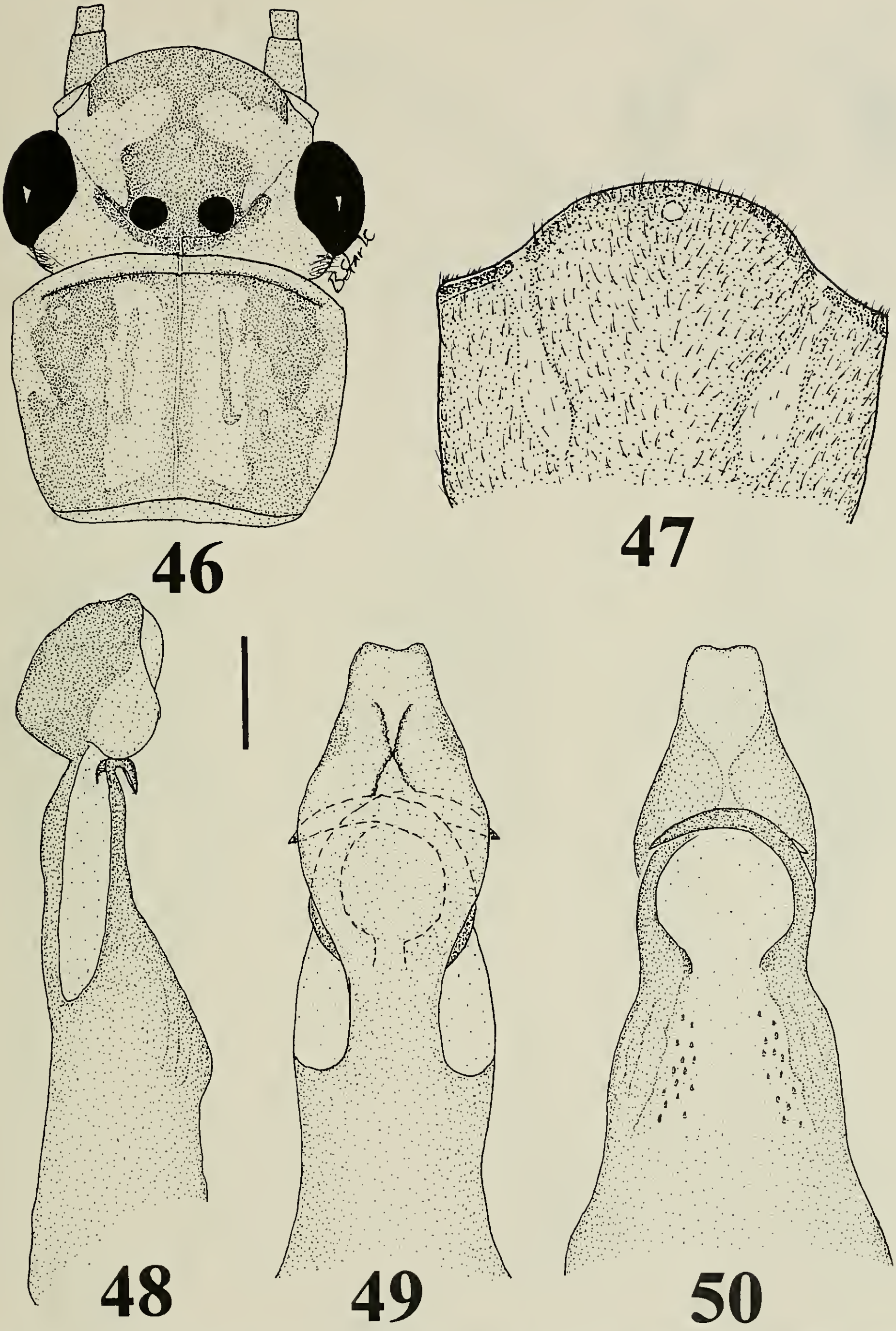
Types.—Holotype ♂ from Panama, Alajuela, 17 Apr 1911, A. Busck (USNM). Paratypes: Panama: Alajuela: 6 Apr 1911, A. Busck, 1 ♂, 1 ♀ (USNM). Same location, 16 Apr 1911, A. Busck, 1 ♂ (USNM). Same location, 8 Mar 1912, A. Busck, 1 ♀ (USNM). Darien Province: Santa Fe, 28 May 1967, D. M. Delong, C. A. Triplehorn, 1 ♂ (OSU).

Diagnosis.—In size and general coloration this species is similar to *A. curiosa* and *A. uatsi* but the twisted aedeagal apex (Figs. 53–55) is unique to this species.

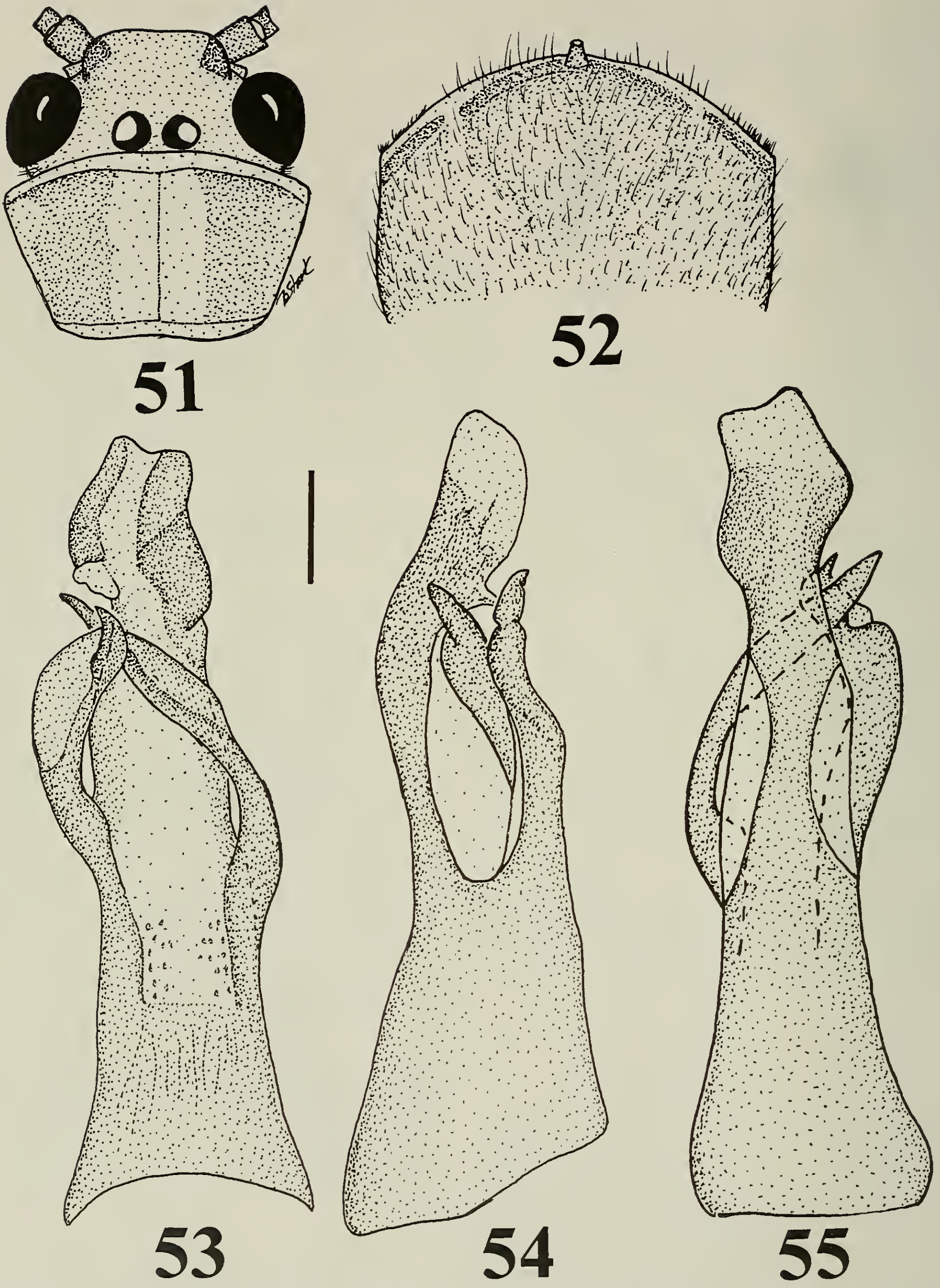
Anacroneuria holzenthali, new species
Figs. 56–60, 143, 171–172

Adult habitus.—Dark pattern covers ocelli and extends forward to midpoint of lappets; pattern interrupted by a pair of minute pore sized unpigmented spots and a larger mesal spot. Pronotum dark except for slender mesal stripe and anterolateral marginal spots (Fig. 56). Wing membrane brown, veins brown.

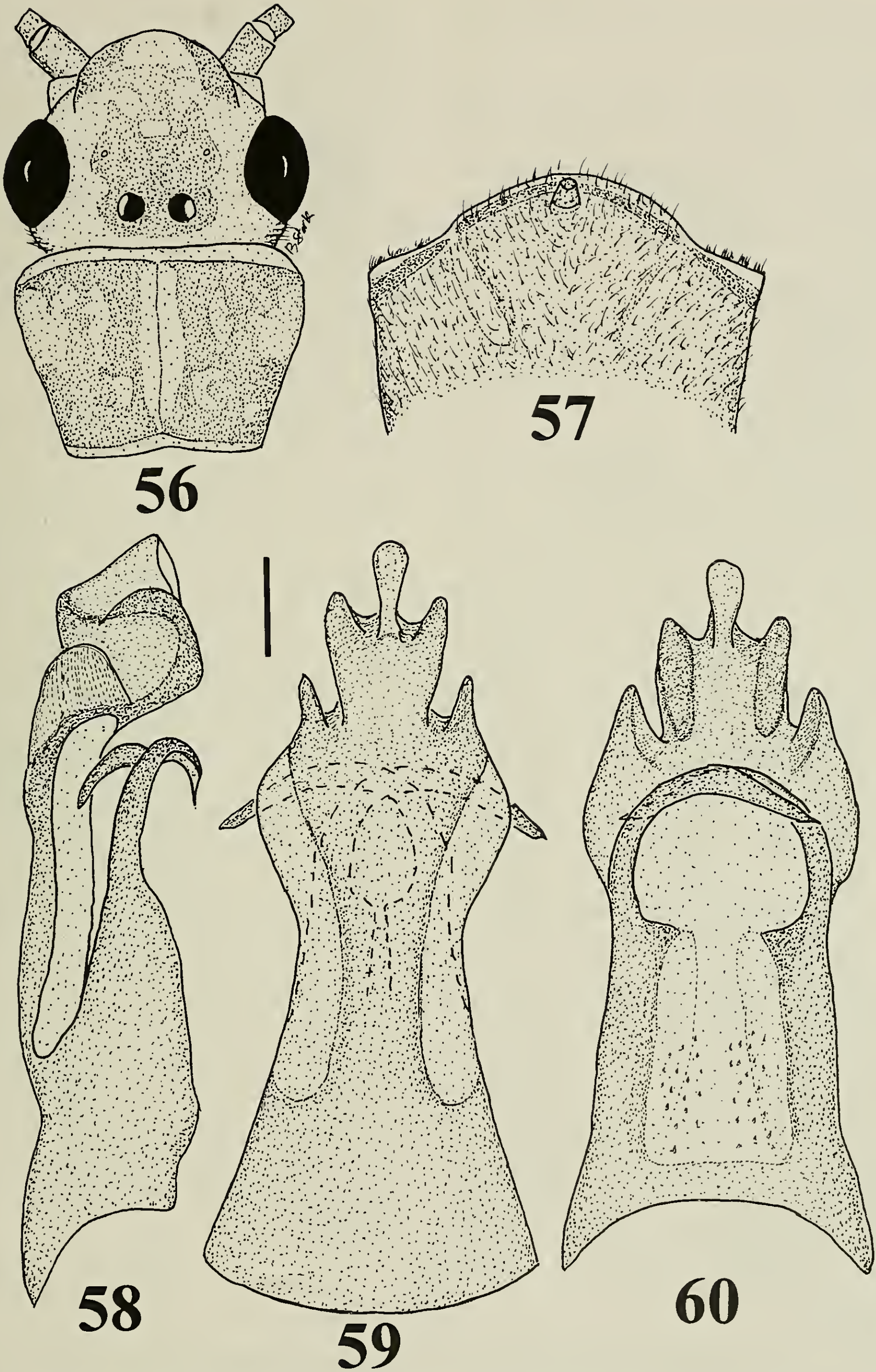
Male.—Forewing length 10–12 mm. Hammer thimble shaped (Fig. 57). Aedeagal apex multilobed, shoulders winged.



Figs. 46–50. *A. hacha* structures. 46. Head and pronotum. 47. Male sternum 9. 48. Aedeagus, lateral. 49. Aedeagus, dorsal. 50. Aedeagus, ventral. Scales: 0.6 mm (46), 0.3 mm (47), 0.15 mm (48–50).



Figs. 51–55. *A. harperi* structures. 51. Head and pronotum. 52. Male sternum 9. 53. Aedeagus, ventral. 54. Aedeagus, lateral. 55. Aedeagus, dorsal. Scales: 0.6 mm (51), 0.3 mm (52), 0.15 mm (53–55).



Figs. 56–60. *A. holzenthali* structures. 56. Head and pronotum. 57. Male sternum 9. 58. Aedeagus, lateral. 59. Aedeagus, dorsal. 60. Aedeagus, ventral. Scales: 0.6 mm (56), 0.3 mm (57), 0.15 mm (58–60).

Dorsal keel transverse, hooks slender (Figs. 58–60, 171–172).

Female.—Forewing length 14–15 mm. Subgenital plate four lobed; mesal notch deep, V-shaped, lateral notches shallow. Transverse sclerite of sternum nine sinuate, mesal sclerite T-shaped and setose. Setae on sclerite stalk minute, lateral setae prominent (Fig. 143).

Nymph.—Unknown.

Etymology.—The patronym honors R. W. Holzenthal for his outstanding contributions to our understanding of the Costa Rican aquatic insect fauna.

Types.—Holotype ♂ from Costa Rica, Guanacaste, Parque Nacional Rincon de la Vieja, Quebrada Zapilote, 785 m, 3 Mar 1986, R. Holzenthal (USNM). Paratypes: Costa Rica: Alajuela, Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 6–10 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 6 ♂, 11 ♀ (INBIO, UMSP). Guanacaste: Quebrada Garcia, 10.6 km ENE Quebrada Grande, 470 m, 8 Mar 1986, R. Holzenthal, W. Fasth, 3 ♂ (UMSP). Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 4 ♂, 1 ♀ (USNM). Same location, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 2 ♂ (UMSP). Parque Nacional Guanacaste, Rio Tempisquito Sur, Maritza, 600 m, 30 Aug 1990, J. Huisman, F. Quesada, 1 ♂, 1 ♀ (BPS). Estacion Maritza, Rio Tempisquito, 11 May 1990, 2 ♂ (SWRC). Same location, 17 Mar 1989, 1 ♂, 1 ♀ mating (SWRC). Same location, 28 Apr 1989, 1 ♂, 1 ♀ (SWRC). Heredia: Quebrada Chiquiza, Rava Avis Biological Station, 550 m, 31 Mar 1989, R. Blahnik, Solis 1 ♂ (UMSP). Nicaragua: Chontales, Santo Domingo, Nov 1985, J. M. Maes, 1 ♂ (USNM).

Diagnosis.—See under *A. benedettoi.*

Anacroneuria lineata (Navas)
Figs. 61–65

Neoperla lineata Navas, 1924:73. Holotype ♂, Costa Rica (MNHN).

Adult habitus.—Head with dark pattern over ocelli extending to M-line; lappets and small triangular patch forward of M-line dark. Median pronotal stripe diffuse brown, bordered by yellow; margins dark (Fig. 61). Wing membrane transparent, veins brown.

Male.—Forewing length 12 mm. Hammer nipple shaped (Fig. 62). Aedeagal apex broad, scoop shaped with a pair of small lateral projections at shoulder. Dorsal keel prominent, hooks slender (Figs. 63–65).

Female.—Unknown.

Nymph.—Unknown.

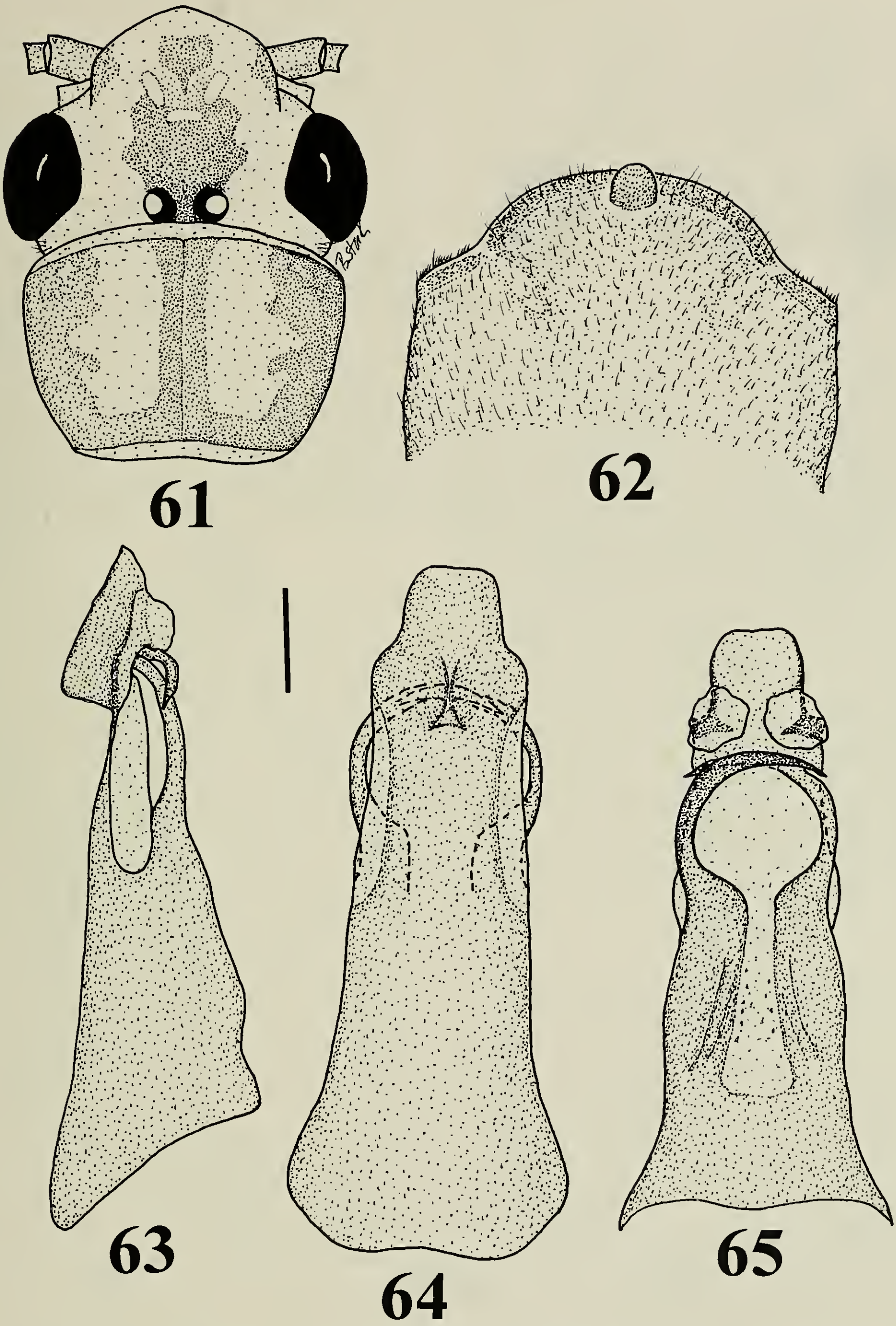
Material.—Costa Rica: Alajuela: Rio Pizote, ca. 5 km N Dos Rios, 470 m, 9 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Parque nacional Rincon de la Vieja, Quebrada Provision, 810 m, 4 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Guanacaste: Rio Mena, 4.2 km W Santa Cecilia, 11 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 3 ♂ (USNM). Estacion Maritza, Rio Tempisquito, 10 Oct 1989, 1 ♂ (SWRC). Same location, 11 Apr 1990, 1 ♂ (SWRC). Same location, 11 May 1990, 2 ♂ (INBIO). Rio Gongora, 4 km NE Quebrada Grande, 590 m, 21 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 10 ♂ (UMSP, BPS). San Jose: Palmital de Guarco, Cerro de la Muerte, km 37 Pan American Highway, 7 May 1995, R. W. Baumann, B. Houseman, 1 ♂ (BYU). MEXICO: Chiapas: 10 mi N Palenque, 14 June 1971, J. Zimmerman, 6 ♂, 5 ♀ (BPS).

Comments.—Figures of the holotype aedeagus provided by L. Benedetto seem to match this species.

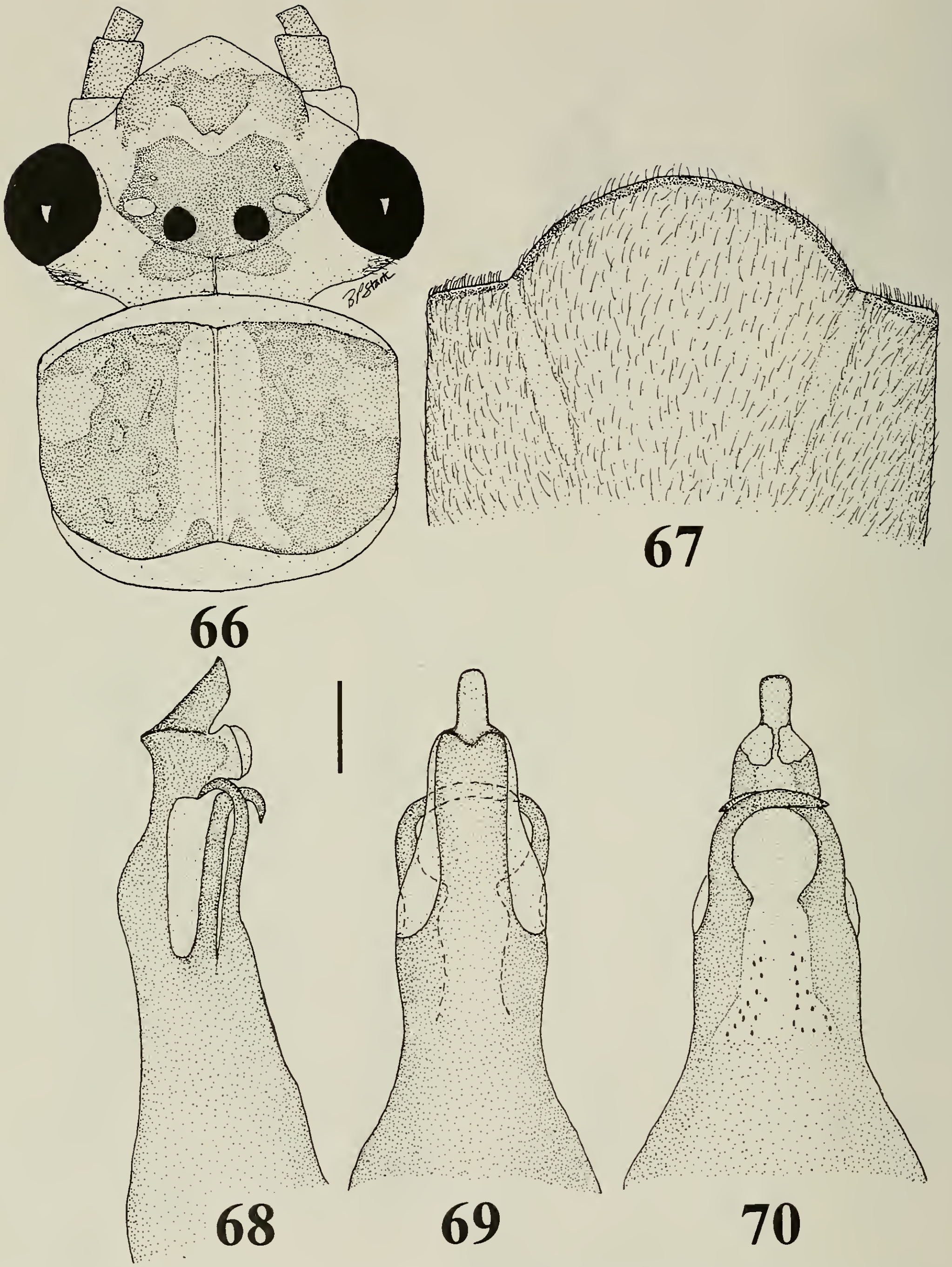
Anacroneuria magnirufa Jewett
Figs. 66–70, 144, 155, 173–174

Anacroneuria magnirufa Jewett, 1958:162. Holotype ♀, El Volcan, Chiriqui, Panama (AMNH).

Adult habitus.—Dark brown pigment extends from behind ocelli to M-line; lateral



Figs. 61–65. *A. lineata* structures. 61. Head and pronotum. 62. Male sternum 9. 63. Aedeagus, lateral. 64. Aedeagus, dorsal. 65. Aedeagus, ventral. Scales: 0.6 mm (61), 0.3 mm (62), 0.15 mm (63–65).



Figs. 66–70. *A. magnirufa* structures. 66. Head and pronotum. 67. Male sternum 9. 68. Aedeagus, lateral. 69. Aedeagus, dorsal. 70. Aedeagus, ventral. Scales: 0.6 mm (66), 0.3 mm (67), 0.15 mm (68–70).

callosities prominent; lappets and mesal field forward of M-line dark brown. Pronotum brown except for scattered pale rugosities and a narrow pale mesal band (Fig. 66). Wing membrane and veins dark brown.

Male.—Forewing length 17–20 mm. Hammer absent (Fig. 67). Aedeagal apex narrow and scoop shaped, ventral aspect with a pair of small membranous processes. Dorsal keel a thin transverse ridge, hooks slender (Figs. 68–70, 173–174).

Female.—Forewing length 23–26 mm. Subgenital plate bilobed, margins truncate or slightly rounded. Mesal notch shallow, small longitudinal tubercle forward of notch. Transverse sclerite absent from sternum nine, mesal sclerite sparsely setose (Fig. 144).

Nymph.—Unknown.

Material.—Costa Rica: Alajuela: Rio Peje, 1 km SE San Vicente, 1450 m, 15 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 26 ♂, 15 ♀ (BPS, INBIO, UMSP). Rio Pizote, 5 km S Brasilia, 390 m, 12 Mar 1986, R. Holzenthal, W. Fasth, 2 ♂ (UMSP). Rio Bochinche, Cerro Campana, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂ (UMSP). Rio San Lorencito, Reserva Forestal San Ramon, 980 m, 1 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂, 2 ♀. Same location, 6–10 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♂ (BPS). Guanacaste: Rio Los Ahogados, 11.3 km ENE Quebrada Grande, 470 m, 7 Mar 1986, R. Holzenthal, W. Fasth, 2 ♂, 1 ♀ (UMSP). Rio Gongora, 590 m, 21 Aug 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂, 1 ♀ (UMSP). Estacion Maritza, Rio Tempisquito, 14 Jan 1990, 1 ♂ (SWRC). Same location, 11 Feb 1990, 1 ♂ (SWRC). Same location, 11 Apr 1990, 1 ♂ (SWRC). Same location, 28 Apr 1989, 1 ♂, 3 ♀ (SWRC). Same location, 11 May 1990, 1 ♂ (SWRC). Same location, 30 May 1990, 1 ♂ (SWRC). Same location, 5 Jul 1989, 1 ♀ (SWRC). Same location, 19 Aug 1989, 2 ♂, 2 ♀ (SWRC). Same location, 10 Oct 1989, 2 ♂, 1 ♀ (SWRC). Same location, 11 Nov 1989, 1 ♂ (SWRC). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 10 Aug 1990, R. Holzenthal, R. Blahnik, F. Munoz, 2 ♂ (UMSP). Same location, 16 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♂ (BPS). Panama: Chiriqui, Guadalupe Arriba, 11–17 Sep 1985, H. Wolda, 2 ♂ (BYU). Same location, 10–16 Jul 1985, H. Wolda, 2 ♂ (BYU). Same location, 24–30 Jul 1985, H. Wolda, 1 ♂ (BYU).

Comments.—Collections of *A. magnirufa* in Costa Rica are known from throughout the year, and the known species range is from Panama to Honduras. Few specimens are available from Panama and these are larger and have a slightly wider aedeagal apex and less conspicuous dorsal keel than Costa Rican specimens. No specimens are known from Nicaragua and only two paratype males are known from Honduras. All Costa Rican female specimens have a mesal tubercle near the subgenital plate notch. This conspicuous feature was not mentioned by Jewett (1958) and is not shown in figures of the holotype made by Benedetto (L. Benedetto, pers. comm.). This variation in both male and female specimens from Chiriqui suggests the possibility that two closely related species are involved.

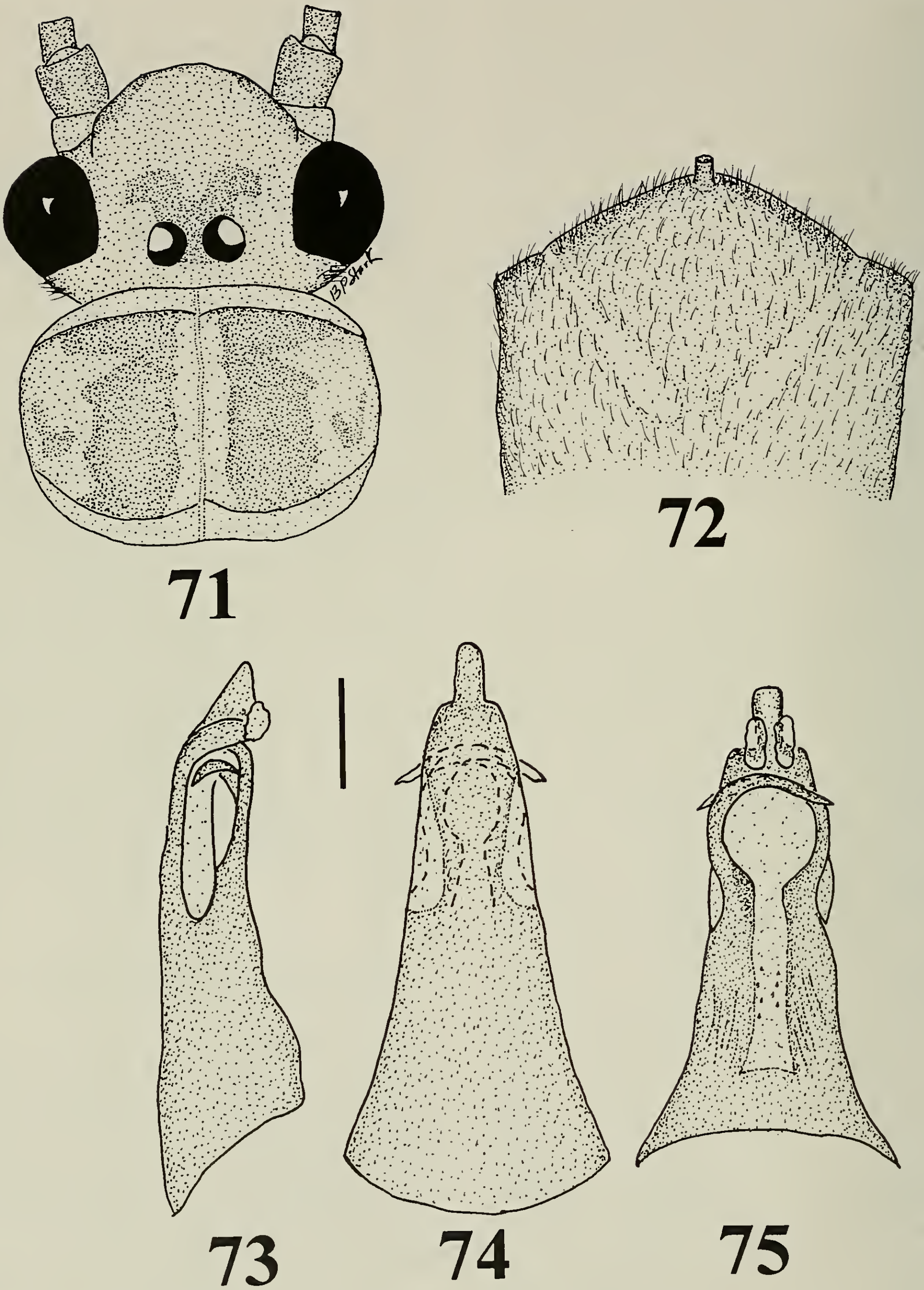
Anacroneuria marca, new species

Figs. 71–75, 145, 175–176

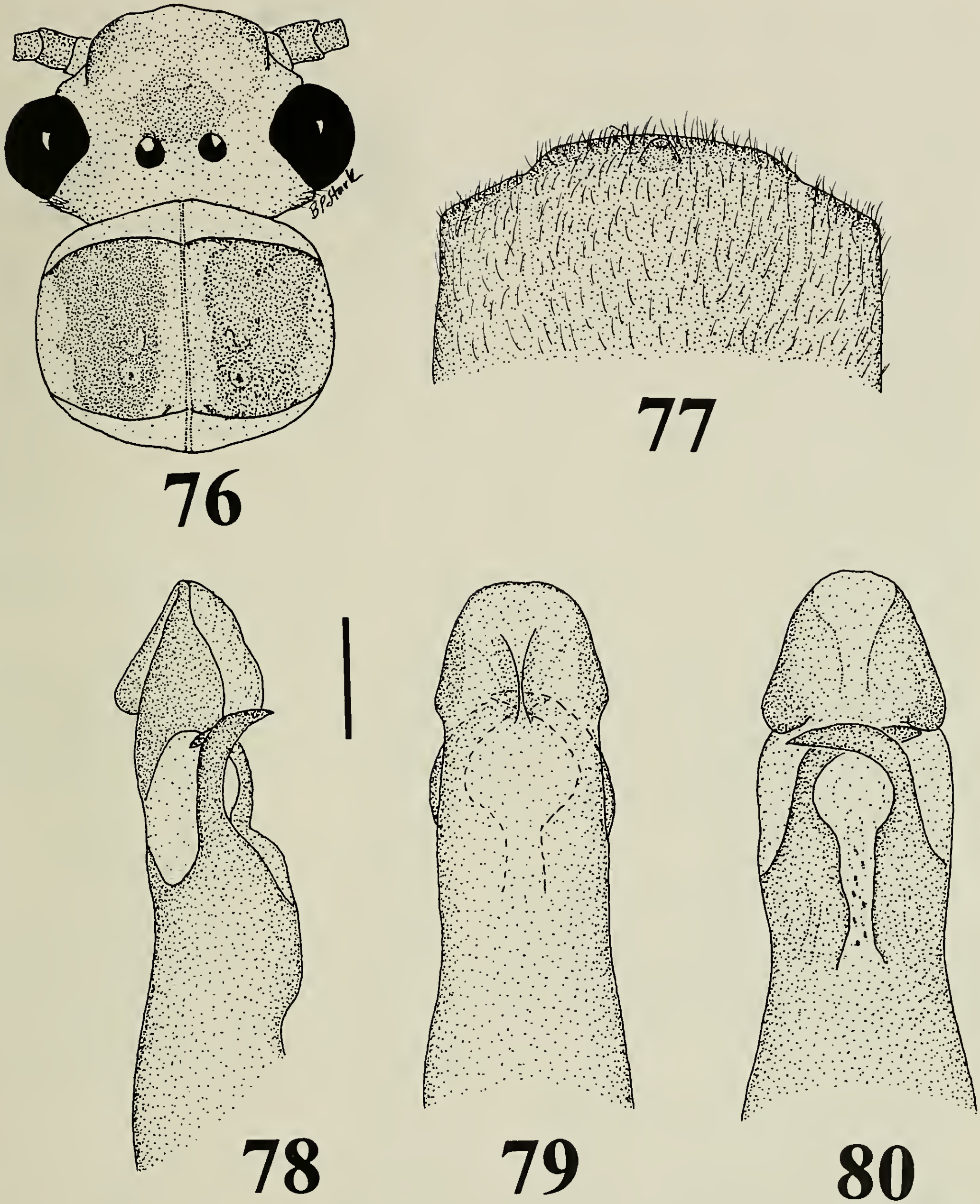
Adult habitus.—Head with a pair of brown L-shaped marks extending from ocelli but sometimes fused between ocelli; lappets brown. Pronotum with a narrow median yellow band; lateral area brown but with scattered pale rugosities and pale anterolateral margin (Fig. 71). Wing membrane transparent, veins brown.

Male.—Forewing length 16 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 72). Aedeagal apex simple, abruptly narrowed from shoulders to a slender scoop. Hooks slender, dorsal keel absent (Figs. 73–75, 175–176).

Female.—Forewing length 20 mm.



Figs. 71–75. *A. marca* structures. 71. Head and pronotum. 72. Male sternum 9. 73. Aedeagus, lateral. 74. Aedeagus, dorsal. 75. Aedeagus, ventral. Scales: 0.6 mm (71), 0.3 mm (72), 0.15 mm (73–75).



Figs. 76–80. *A. marginata* structures. 76. Head and pronotum. 77. Male sternum 9. 78. Aedeagus, lateral. 79. Aedeagus, dorsal. 80. Aedeagus, ventral. Scales: 0.6 mm (76), 0.3 mm (77), 0.15 mm (78–80).

Subgenital plate bilobed; notch V-shaped, lobes truncate to emarginate. Transverse sclerite of sternum nine wide; intersegmental membrane covered with microtrichia; setal patch of mesal sclerite interrupted into a median stalk and lateral setal areas (Fig. 145).

Nymph.—Unknown.

Etymology.—Marca, Spanish for brand, refers to the L-shaped marks on the head, and is used as a noun in apposition.

Types.—Holotype ♂ from Costa Rica, Heredia, Parque Nacional Braulio Carrillo, Rio Peje, 480 m, 29 May 1990, R. Holzenthal, R. Blahnik, F. Munoz (USNM). Paratypes: Costa Rica: Alajuela: Rio Peje, ca. 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 3 ♂ (UMSP). Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 30 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 9 ♀ (UMSP). Same location, 6 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♀ (INBIO). Cartago: Reserva Tapanti, Rio Grande de Orosi, 1650 m, 8 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 3 ♂, 3 ♀ (BPS). Puntarenas: Rio Coton, Las Alturas, 1360 m, 18 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 1 ♂, 1 ♀ (INBIO). Same location, 16 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♂ (BPS). Zona Protectora Las Tablas, Rio Coton, Sitio Coton, 1460 m, 15 Apr 1989, R. Holzenthal, R. Blahnik, 1 ♂, 1 ♀ (USNM). San Jose: Rio Chirripo Pacifica, 9.5 km NE Rivas, 1370 m, 23 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♀ (UMSP).

Diagnosis.—The color pattern of *A. marca* is similar to that of *A. ventana* (Fig. 121) but hammer shape (Fig. 122) and the aedeagal keel (Fig. 124) distinguish these species. *A. zapata* is also similar but has a trilobed aedeagal apex (Fig. 130).

Anacroneuria marginata, new species
Figs. 76–80, 177–178

Adult habitus.—Diffuse brown pattern extends from ocelli to M-line and laterally to lappets. Pronotum with narrow pale median and marginal stripes; dark midlateral stripes rugose (Fig. 76). Wing membrane amber, veins brown.

Male.—Forewing length 8 mm. Hammer thimble shaped, height less than basal diameter (Fig. 77). Aedeagal apex simple, broad and rounded at tip. Dorsal keel moderately developed, hooks short (Figs. 78–80, 177–178).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The species name, meaning bordered, refers to the pale marginal bands on the pronotum.

Types.—Holotype ♂ from Costa Rica, Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal (USNM). Paratypes: Costa Rica: Guanacaste: Parque Nacional Guanacaste, Maritza, Rio Tempisquito Sur, 30 Aug 1990, 600 m, J. Huisman, F. Quesada, 1 ♂ (UMSP). Estacion Maritza, Rio Tempisquito, 14 Jan 1990, 1 ♂ (SWRC). Same location, 17 Mar 1989, 1 ♂ (SWRC). Same location, 27 Apr 1989, 2 ♂ (BPS). Same location, 28 May 1989, 1 ♂ (SWRC). Same location 30 May 1990, 1 ♂ (INBIO). Same location, 22 Oct 1990, 1 ♂ (INBIO).

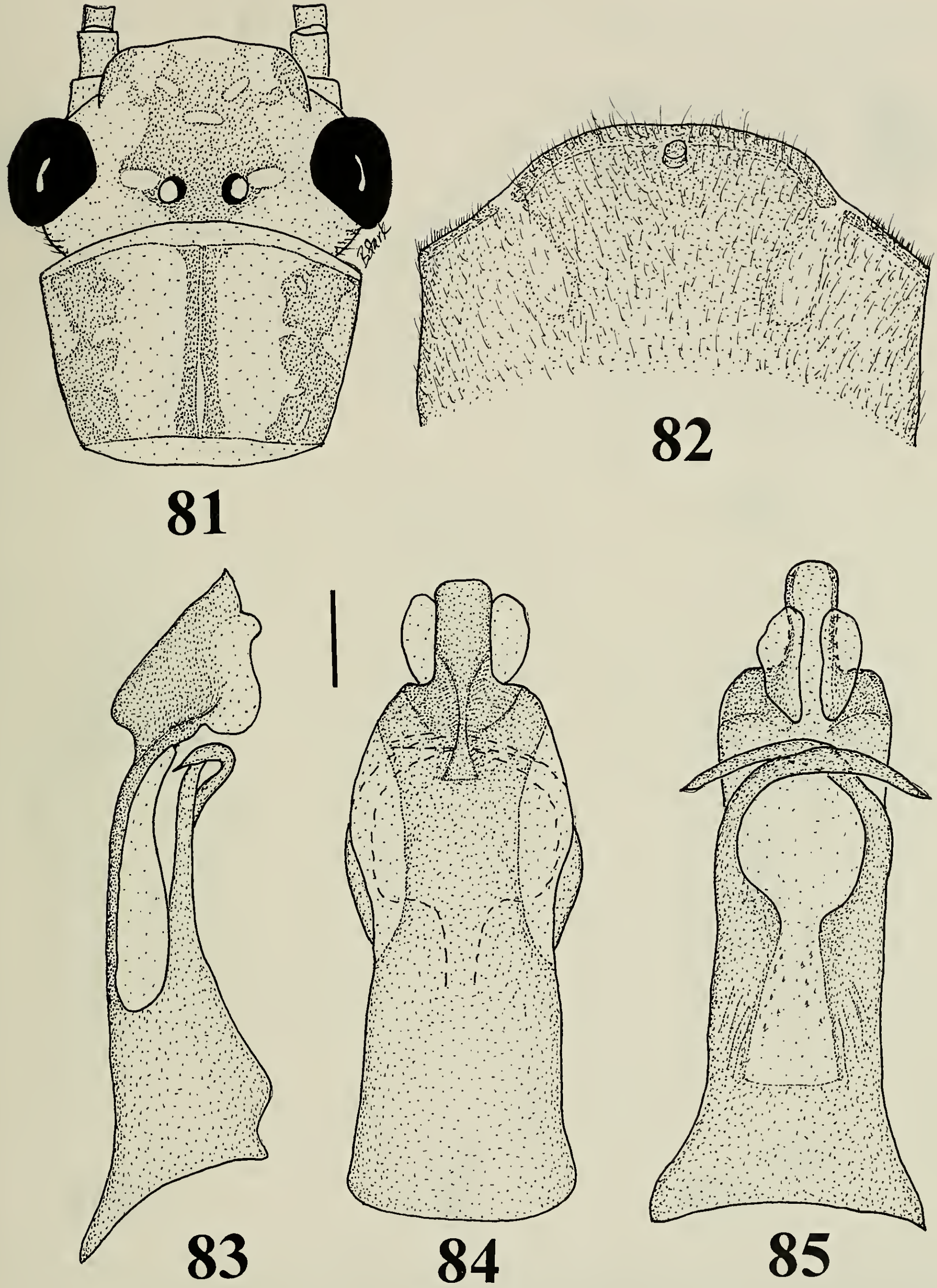
Diagnosis.—The aedeagus of this species is similar to that of *A. costana* (Figs. 28–30) but the apex is shorter and wider and the keel more pronounced in *A. marginata.*

Anacroneuria maritza, new species
Figs. 81–85, 146, 151–152

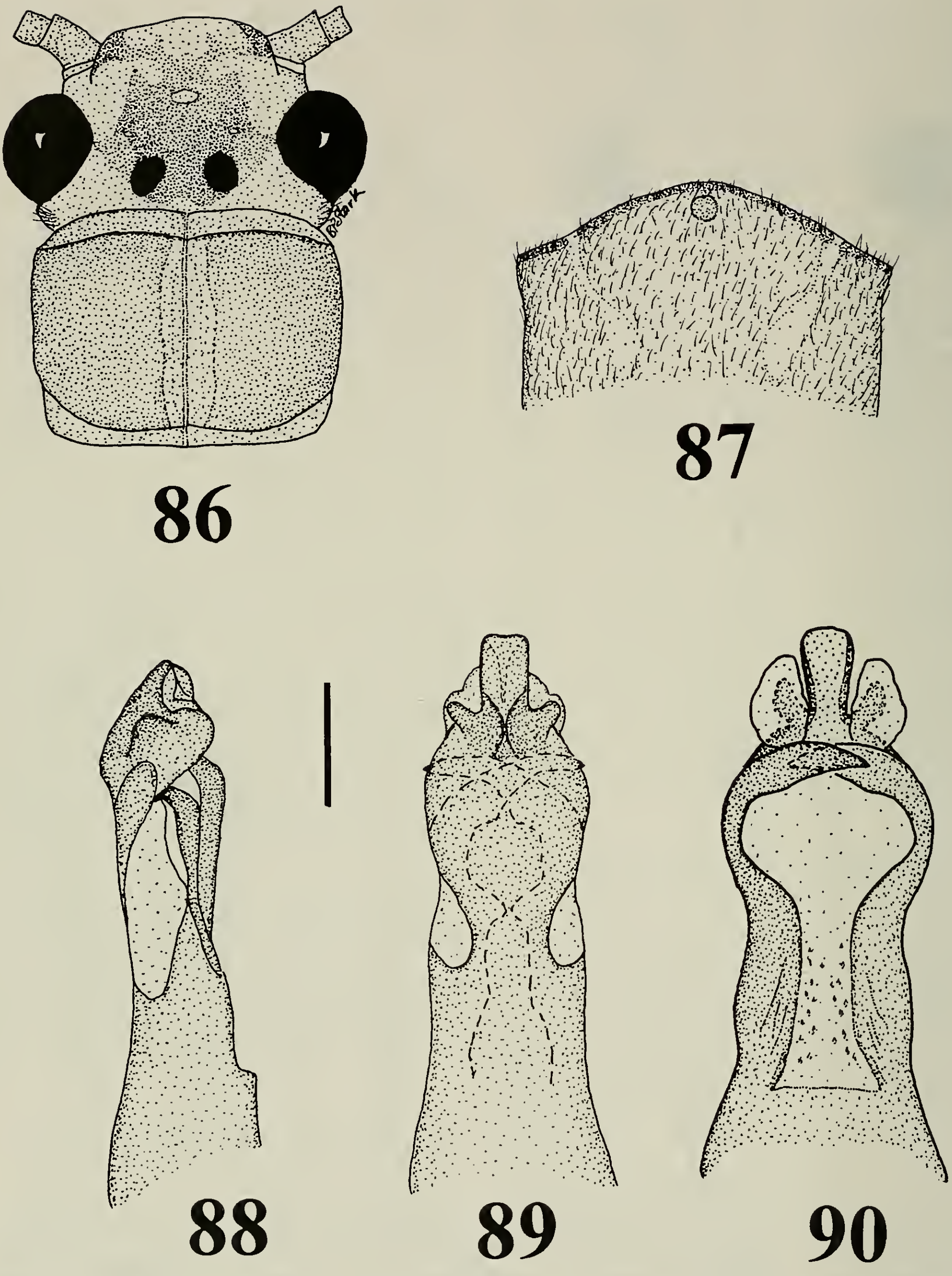
Adult habitus.—Dark brown covers ocelli and extends forward to M-line; lappets and a small mesal spot forward of M-line brown. Median brown pronotal stripe bordered by yellow; irregular midlateral stripes brown, margins pale (Fig. 81). Wing membrane brown, veins brown except pale C and Sc.

Male.—Forewing length 12–13 mm. Hammer thimble shaped, height less than basal diameter (Fig. 82). Aedeagal apex scoop shaped, tip with parallel margins and well developed dorsal keel. Ventral aspect covered with large membranous lobes; hooks slender (Figs. 83–85).

Female.—Forewing length 15–16 mm. Subgenital plate bilobed, notch broadly V-shaped. Transverse sclerite of sternum nine absent; mesal sclerite V-shaped and sparse-



Figs. 81–85. *A. maritza* structures. 81. Head and pronotum. 82. Male sternum 9. 83. Aedeagus, lateral. 84. Aedeagus, dorsal. 85. Aedeagus, ventral. Scales: 0.6 mm (81), 0.3 mm (82), 0.15 mm (83–85).

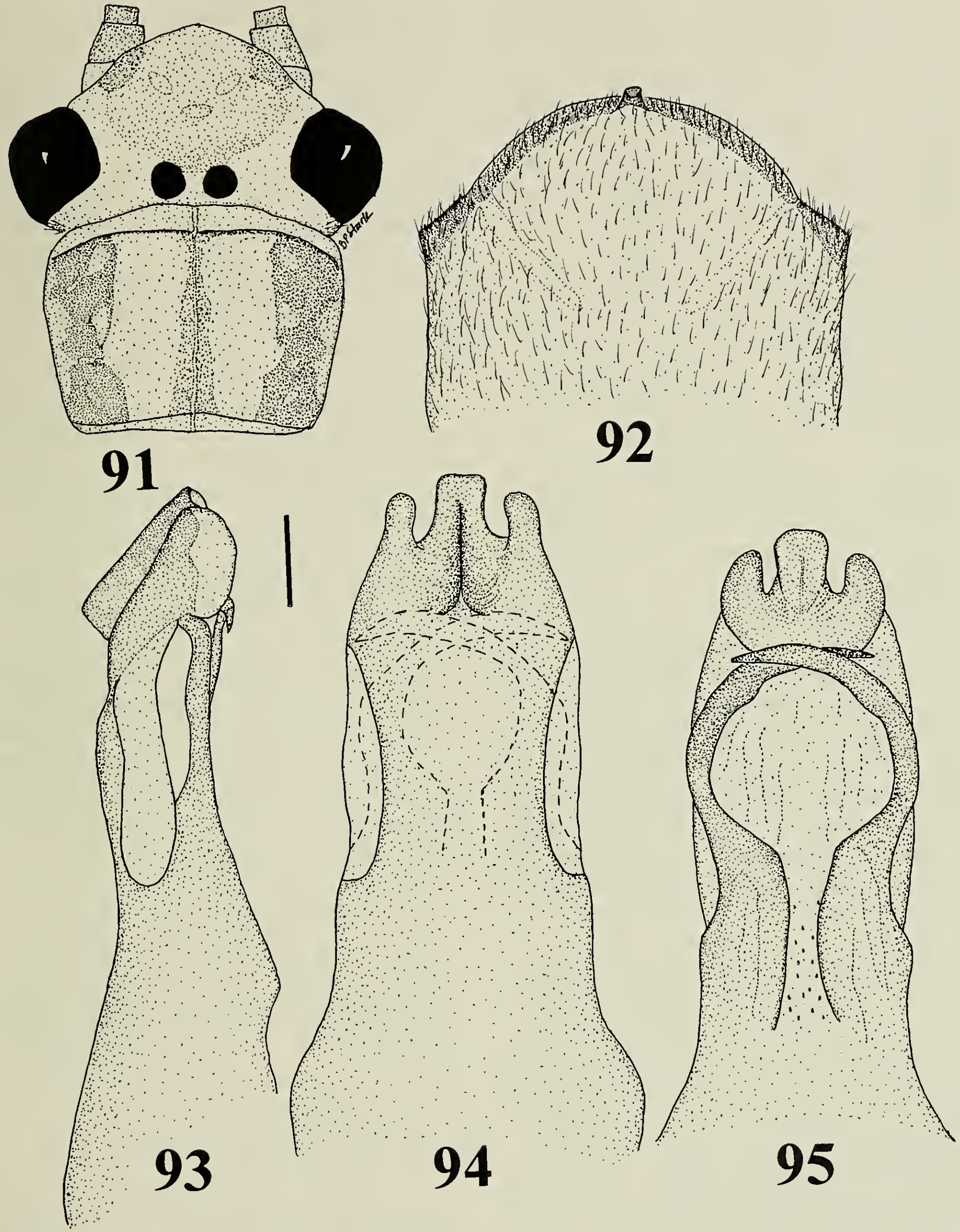


Figs. 86–90. *A. perplexa* structures. 86. Head and pronotum. 87. Male sternum 9. 88. Aedeagus, lateral. 89. Aedeagus, dorsal. 90. Aedeagus, ventral. Scales: 0.6 mm (86), 0.3 mm (87), 0.15 mm (88–90).

ly setose. Patch of long red-brown setae at base of lateral bar (Fig. 146).

Nymph.—Body length 14–17 mm. Head pattern brown except for pale M-line and oval areas anterolateral to ocelli. Pronotum brown with scattered pale rugosities (Fig. 151).

Etymology.—The species name, based on



Figs. 91–95. *A. planicollis* structures. 91. Head and pronotum. 92. Male sternum 9. 93. Aedeagus, lateral. 94. Aedeagus, dorsal. 95. Aedeagus, ventral. Scales: 0.6 mm (91), 0.3 mm (92), 0.15 mm (93–95).

the type locality, is used as a noun in apposition.

Types.—Holotype ♂ from Costa Rica, Guanacaste, Estacion Maritza, Rio Tempisquito, 11 Feb 1989 (USNM). Paratypes: Costa Rica: Same location, 16 Mar 1989, 1 ♂ (BPS). Same location 17 Mar 1989, 1 ♂ (INBIO). Same location, 7 Apr 1989, 3 ♂, 2 ♀ (SWRC, BPS). Same location, 11 Apr 1990, 1 ♂ (INBIO). Same location, 27 Apr 1989, 1 ♂ (SWRC). Same location, 24 May 1989, 3 ♂ (BPS, SWRC). Same location, 28 May 1989, 1 ♀ (USNM). Same location, 22 Oct 1990, 1 ♂ (SWRC). Same location, 11 Nov 1989, 1 ♂ (INBIO). Same location, reared from eggs, 2 ♂, 2 ♀ (SWRC). Same location, 30 Aug 1990, J. Huisman, R. Blahnik, F. Quesada, 1 ♂ (UMSP). Guanacaste: Rio Los Ahogados, 470 m, 7 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Hacienda la Pacifica, 75 m, 8 Jun 1973, G. Ekis, 1 ♂ (BYU). Monteverde, 22 Jun 1986, W. Hanson, 7 ♂ (USU).

Diagnosis.—The color pattern is similar to several species including *A. divisa* (Fig. 36) and *A. planicollis* (Fig. 91) but aedeagal features (Figs. 39, 85, 95) easily distinguish these species.

Comments.—Scientists at the Stroud Water Research Center reared two males and two females of this species from eggs collected at Estacion Maritza (J. Jackson, pers. comm.). The first egg mass collected 26 Aug 1992 produced a female on 18 Feb 1993 and a male on 11 Mar 1993. The second egg mass from 29 Nov 1992 produced a male on 14 May 1994 and a female on 3 Jun 1994. The nymphal description is based on exuviae from these specimens.

Anacroneuria perplexa, new species
Figs. 86–90, 179–180

Adult habitus.—Dark head pattern covers ocelli and extends anterolaterally to lappets; small pale spot located in center of head. Pronotum mostly brown but with inconspicuous mesal yellow band (Fig. 86). Wing membrane brown, veins brown.

Male.—Forewing length 8 mm. Hammer absent or reduced to obscure membranous spot (Fig. 87). Aedeagal apex trilobed, lateral lobes small and ear shaped. Dorsal keel well developed, hooks enlarged and somewhat chelate (Figs. 88–90, 179–180).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The species name, meaning tangled or confused, refers to the initial difficulty experienced in separating this species from other small, dark forms with poorly developed hammers.

Types.—Holotype ♂ (USNM) and 2 ♂ paratypes (UMSP) from Costa Rica, Limon, Rio Barbilla, ca. 8 km W B-line, 30 m, 31 Jan 1986, R. Holzenthal, J. Morse, W. Fasth. Additional paratypes: Costa Rica: Limon: Reserva Biol. Hitoy-Cerere, Rio Cerere, 90 m, 23 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 8 ♂ (UMSP, BPS). Rio Banano, 16 km WSW Bomba, 150 m, 26 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, (UMSP). Puntarenas: Rio Jaba, 1.4 km W Las Cruces, 1150 m, 14 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (INBIO). Villa Neilly, 21 Jun 1964, R. Woodruff, 1 ♂ (FSCA). San Jose: Escazu, 7–10 Apr 1988, F. D. Parker, 1 ♂ (USU).

Diagnosis.—A male paratype of *A. crenulata* from Temescaltepec, Mexico, is very similar to this species and distinct from the allotype of *A. crenulata.* The Mexican specimen differs from Costa Rican specimens most conspicuously in having long slender aedeagal hooks. Additional comments are given under *A. exquisita.*

Anacroneuria planicollis Klapálek
Figs. 91–95, 147

Anacroneuria planicollis Klapálek, 1923: 22. Lectotype ♂, Sierra du Naya, Mexico (NMP).

Anacroneuria dampfi Jewett, 1958:165. New synonymy.

Anacroneuria chiapasa Jewett, 1958:166. New synonymy.

Adult habitus.—Head pattern usually with brown ocellar spot, shading to diffuse brown forward of ocelli; lappets brown. Median pronotal stripe brown, bordered by yellow; lateral brown stripes interrupted by scattered pale areas on disc and along margins (Fig. 91). Wing membrane transparent, veins brown except C and Sc pale.

Male.—Forewing length 14–15 mm.

Hammer thimble shaped, height subequal to basal diameter (Fig. 92). Aedeagal apex trilobed, mesal lobe slightly larger. Hooks slender, dorsal keel well developed (Figs. 93–95).

Female.—Forewing length 16–17 mm. Subgenital plate bilobed, lobes truncate to emarginate. Mesal sclerite of sternum nine T-shaped; lateral arms with long setae, stalk with fine short setae (Fig. 147).

Nymph.—Unknown.

Material.—Costa Rica; Monteverde, 22 Jun 1986, W. J. Hanson, 2 ♂ (USU). Alajuela: 20 km S Upala, 12 Feb–5 Mar 1991, F. Parker, 2 ♂ (USU). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 15 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (UMSP). Same location, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂, 2 ♀ (INBIO). Mexico: Sierra du Naya, L. Diguet, 1898, lectotype ♂, paralectotype ♀ (NMP). Nicaragua: Nuevosegovia, Dipilto, Dec 1986, J. Maes, 1 ♂ (USNM). Panama: Chiriqui, Cerro Punta, 3 mi N on Pan American Highway, 4 Apr 1954, G. Field, 1 ♂ (USNM).

Comments.—The type series included four male and three female specimens from Mexico and a female from Costa Rica (Klapálek 1923). Of these, a syntype male and female were found in the Natural History Museum, Prague and studied while on loan to P. Zwick. the male is designated as lectotype. Synonymy of the two Jewett (1958) species is based on study of the holotypes and male allotypes.

Anacroneuria plutonis (Banks)
Figs. 96–100, 148, 157, 181–182

Neoperla plutonis Banks, 1914:610. Lectotype ♀, La Trinidad, Costa Rica (MCZ).

Forquilla tristani Navas, 1932:29. New synonymy.

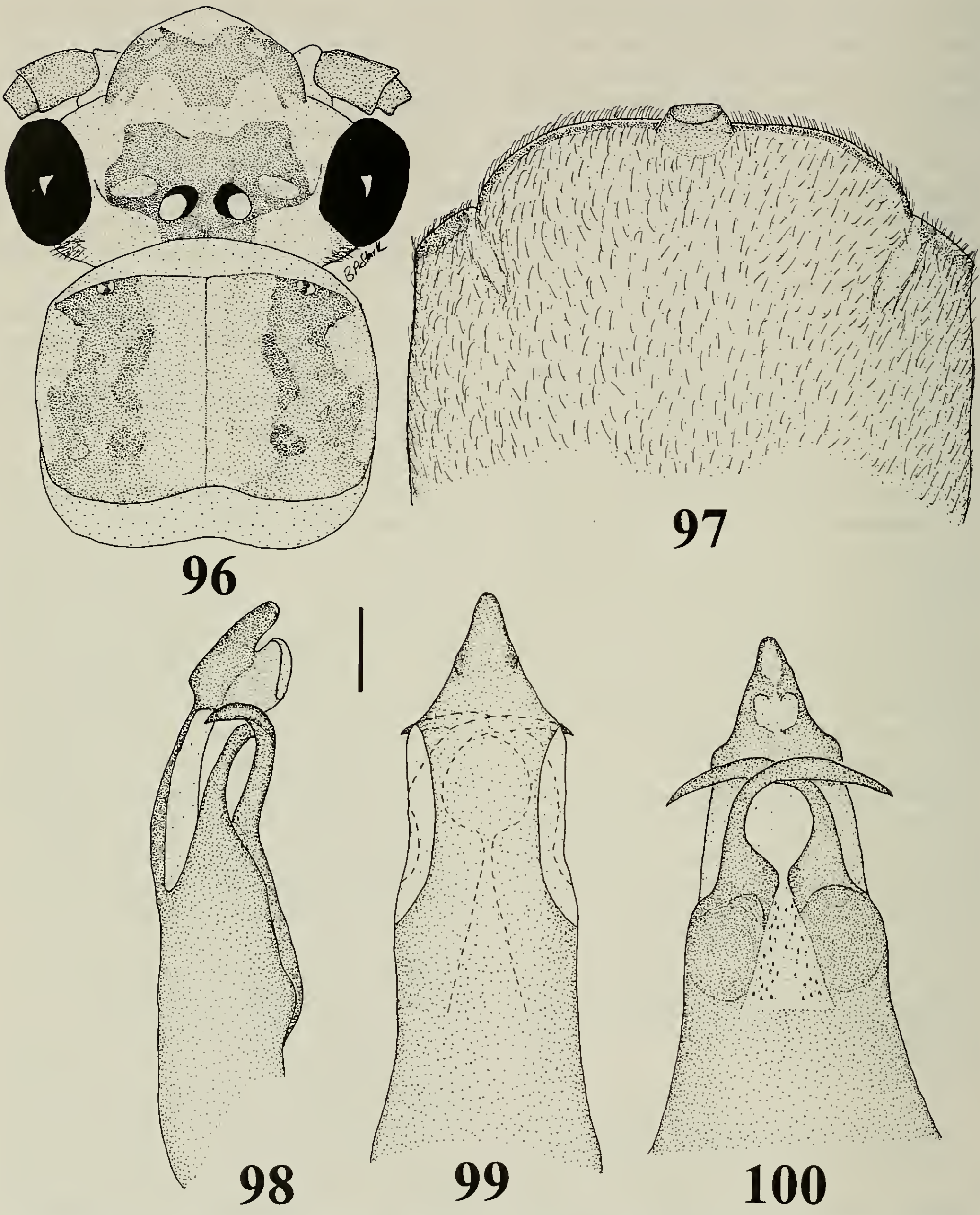
Adult habitus.—Head pattern dark brown from ocellar area to M-line except for pale oval spots lateral to ocelli; lappets connected by a diffuse brown band along anterior margins of M-line. Pronotum diffuse brown to dark brown but without distinct bands (Fig. 96). Wing membrane brown, veins brown.

Male.—Forewing length 19–21 mm. Hammer thimble shaped, height less than basal diameter (Fig. 97). Aedeagal apex simple, gradually tapered to a narrow tip. Hooks slender, dorsal keel absent (Figs. 98–100, 157, 181–182).

Female.—Forewing length 25–28 mm. Subgenital plate bilobed; lobes truncate, notch shallow and U-shaped. Transverse sclerite absent, mesal sclerite T-shaped, sparsely setose (Fig. 148).

Nymph.—Unknown.

Material.—Costa Rica: Alajuela: Rio Sarapiqui, ca. 2 km SE Cariblanco, 710 m, 22 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂, 1 ♀ (BPS). Quebrada Latas, 8.9 km NE Bajos del Toro, 1030 m, 6 Sep 1990, R. Holzenthal, R. Blahnik, J. Huisman, 2 ♂ (UMSP). Reserva Forestal San Ramon, Rio San Lorencito, 6–10 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 4 ♂ (UMSP, INBIO). Cartago: Reserva Tapanti, Quebrada Palmitos, 1400 m, 24 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 1 ♀ (UMSP). Same location, 2 Jun 1990, R. Holzenthal, R. Blahnik, F. Munoz, 7 ♂ (BPS, INBIO). Guanacaste: Estacion Maritza, Rio Tempisquito, 14 May 1989, 1 ♂ (SWRC). Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂ (UMSP). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Rio Coton, Las Alturas, 1360 m, 16 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♂ (UMSP). Same location, 18 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 1 ♂ (BPS). San Jose: El Salvaje, Rio Tabarcia, 8 km E Palmichal, 1650 m, 19 Jan 1992, R. Holzenthal, K. Kjer, F. Quesada, 11 ♂, 3 ♀ (BPS, UMSP, INBIO). Rio Parrita Chiquita, 1990 m, 18 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂, 1 ♀ (USNM).



Figs. 96–100. *A. plutonis* structures. 96. Head and pronotum. 97. Male sternum 9. 98. Aedeagus, lateral. 99. Aedeagus, dorsal. 100. Aedeagus, ventral. Scales: 0.6 mm (96), 0.3 mm (97), 0.15 mm (98–100).

Comments.—*Anacroneuria plutonis* and *A. tristani* are both large dark species described from Costa Rican specimens. Navas (1932) reports the forewing length of *A. tristani* females is 18.5 mm but the type specimen is actually larger than the *A. plutonis* lectotype from La Trinidad (L. Benedetto, pers. comm.). I have not seen the specimens identified by Jewett (1958) as *A. tristani* but the four lobed female subgenital plate mentioned in Jewett's description clearly indicates this material was misidentified.

Anacroneuria talamanca, new species
Figs. 101–105, 149

Adult habitus.—Ocellar area covered by a small brown quadrangle; lateral margins of frons diffuse brown, lappets brown. Median pronotal stripe yellow, lateral stripes brown (Fig. 101). Wing membrane transparent veins brown.

Male.—Forewing length 7–8 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 102). Aedeagal apex simple, slender with small dorsal keel. Hooks enlarged and ventrally keeled (Figs. 103–105).

Female.—Forewing length 9–10 mm. Subgenital plate bilobed; lobes truncate, median notch shallow and V-shaped. Transverse sclerite of sternum nine poorly developed, mesal sclerite with long stem, lateral arms poorly developed and sparsely setose (Fig. 149).

Nymph.—Unknown.

Etymology.—The species name, based on the Cordillera Talamanca, is used as a noun in apposition.

Types.—Holotype ♂ from Costa Rica, San Jose, Reserva Biol. Carara, Rio Carara, Carara, 200 m, 14 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman (USNM). Paratypes: Costa Rica: Heredia: Estacion Biol. La Selva, Rio Puerto Viejo, 30 m, 10 Feb 1986, R. Holzenthal, 1 ♂ (UMSP). La Selva, 14 Jun 1986, W. J. Hanson, 1 ♂ (USU). Panama: Bocas del Toro: Miramar, 1 May 1979, H. Wolda, 1 ♂, 2 ♀ (BYU). Same location, 22 May 1979, H. Wolda, 1 ♀ (BYU).

Diagnosis.—The aedeagus of this species is similar to that of the allotype of *A. crenulata* Jewett and to the holotype of *A. litura* (Pictet) (Zwick 1972). *A. talamanca* differs from these in having the apical aedeagal section beyond the hooks about as long as wide; in *A. crenulata* and *A. litura* this section is distinctly longer than wide and has a dorsal keel more than twice the length of the keel of *A. talamanca.* In addition, the female holotype of *A. crenulata* has a four lobed subgenital plate whereas the subgenital plate of *A. talamanca* is bilobed.

Anacroneuria tornada, new species
Figs. 106–110

Adult habitus.—Diffuse brown area forward of ocelli, lappets brown. Narrow brown median pronotal stripe bordered by narrow yellow stripes; midlateral stripes brown, margins pale (Fig. 106). Wing membrane transparent, veins brown.

Male.—Forewing length 16 mm. Hammer a low disc (Fig. 107). Aedeagal apex multilobed, curved abruptly ventrad between hook tips. Apex in dorsal aspect somewhat truncate, keel absent. Hooks stout, enlarged apically (Figs. 109–110).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—Tornada, Spanish for renegade, refers to the unusual aedeagal apex of this species and is used as a noun in apposition.

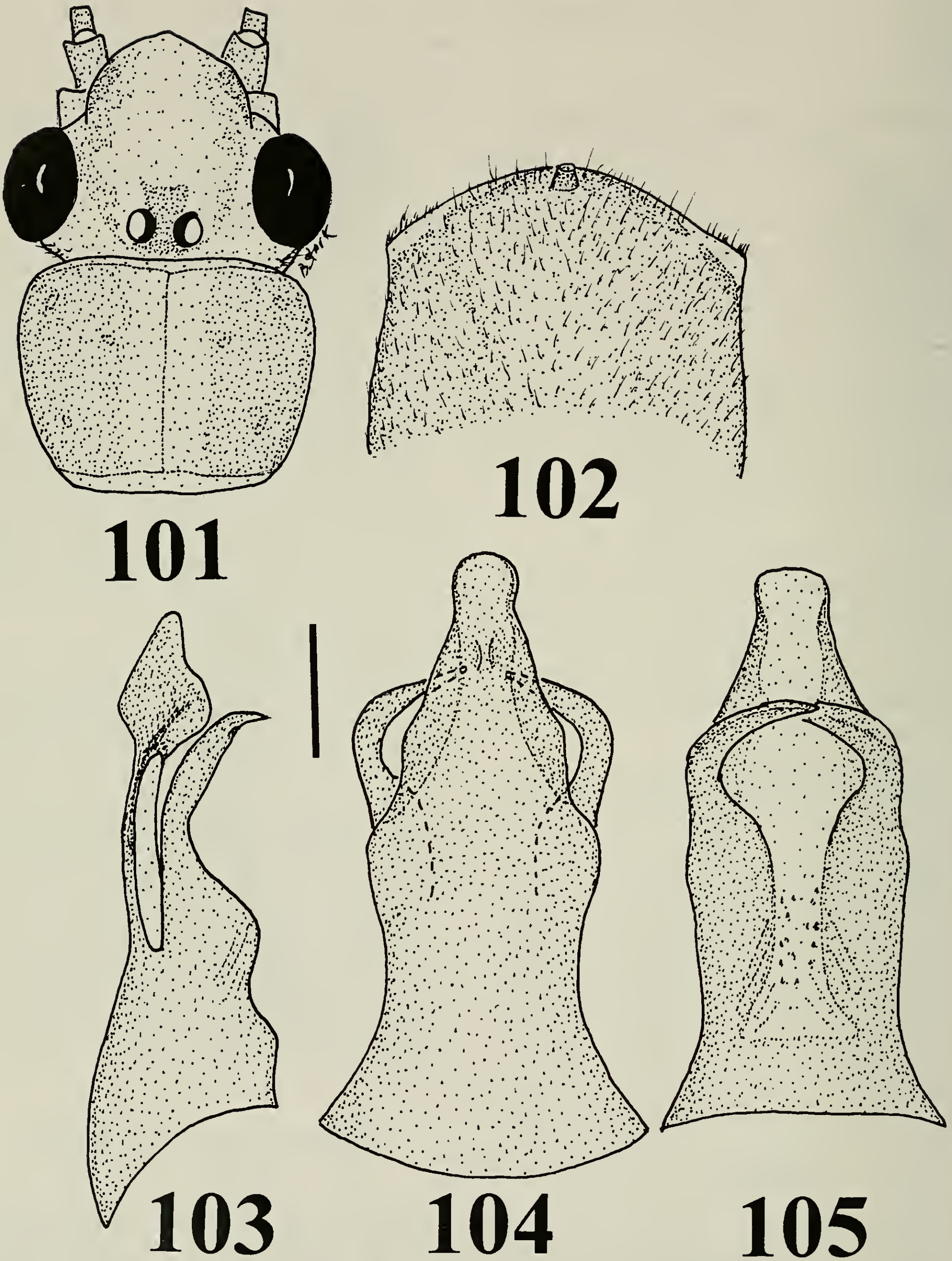
Types.—Holotype ♂ from Costa Rica, Cartago, Reserva Tapanti, Quebrada Palmitos, 1400 m, 2 Jun 1990, R. Holzenthal, R. Blahnik, F. Munoz (USNM).

Diagnosis.—The color pattern of *A. tornado* is similar to that of *A. maritza* (Fig. 81), *A. divisa* (Fig. 36) and *A. planicollis* (Fig. 51) but the aedeagal apex clearly distinguishes these species (Figs. 39, 85, 95, 110).

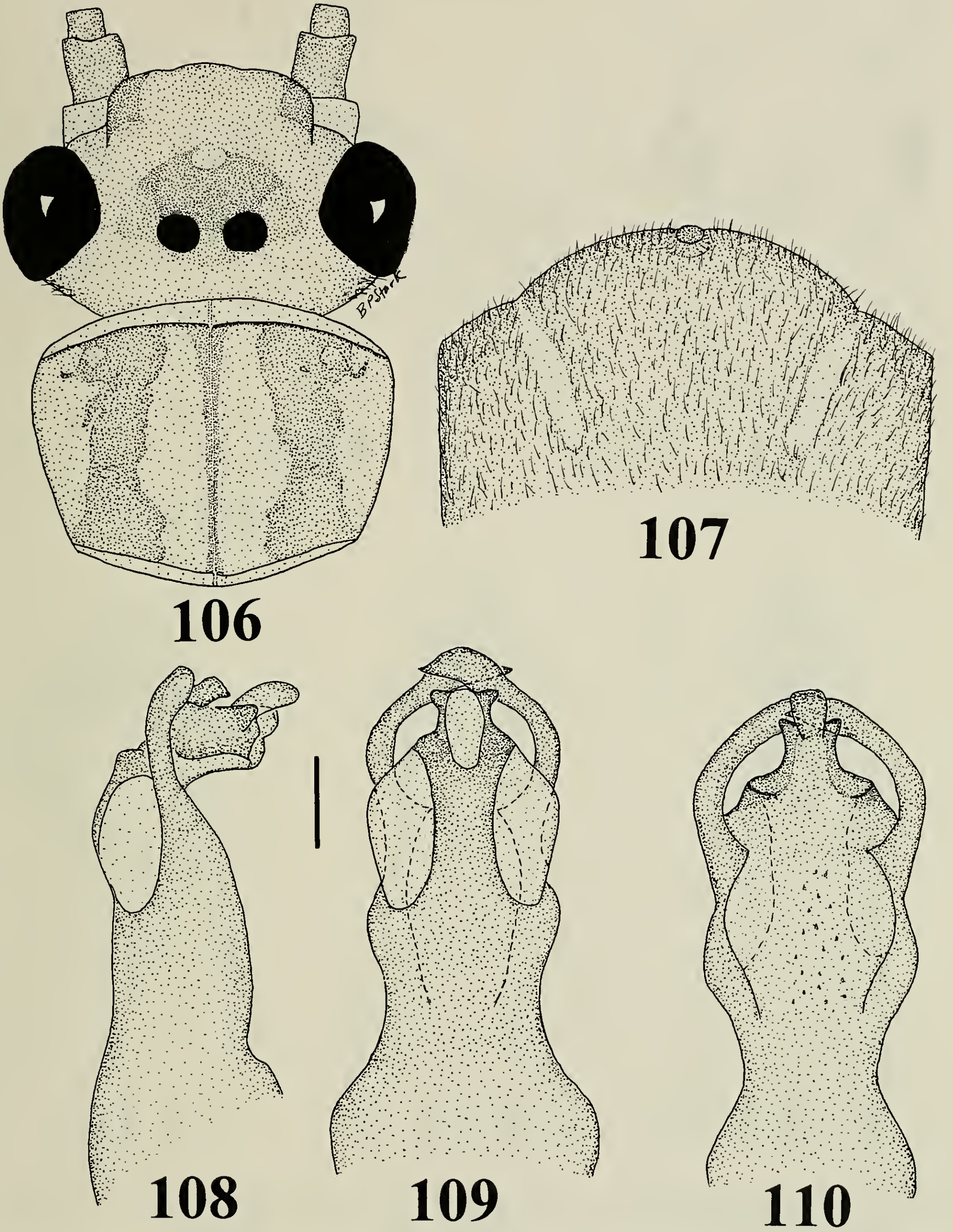
Anacroneuria uatsi, new species
Figs. 111–115, 150, 153–154

Adult habitus.—Head yellow except dark areas on lappets and over ocelli. Median third of pronotum pale, lateral margins brown (Fig. 111). Wing membrane transparent, veins brown except pale C and Sc.

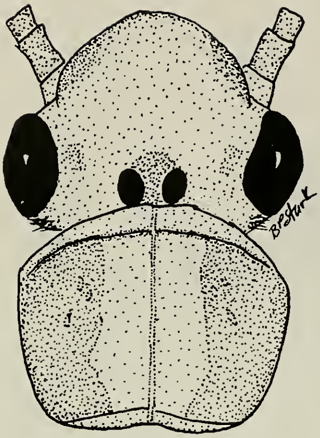
Male.—Forewing length 9 mm. Hammer thimble shaped, length greater than basal diameter (Fig. 112). Aedeagal apex a slender, finger shaped structure arising from a



Figs. 101–105. *A. talamanca* structures. 101. Head and pronotum. 102. Male sternum 9. 103. Aedeagus, lateral. 104. Aedeagus, dorsal. 105. Aedeagus, ventral. Scales: 0.6 mm (101), 0.3 mm (102), 0.15 mm (103–105).



Figs. 106–110. *A. tornada* structures. 106. Head and pronotum. 107. Male sternum 9. 108. Aedeagus, lateral. 109. Aedeagus, dorsal. 110. Aedeagus, ventral. Scales: 0.6 mm (106), 0.3 mm (107), 0.15 mm (108–110).



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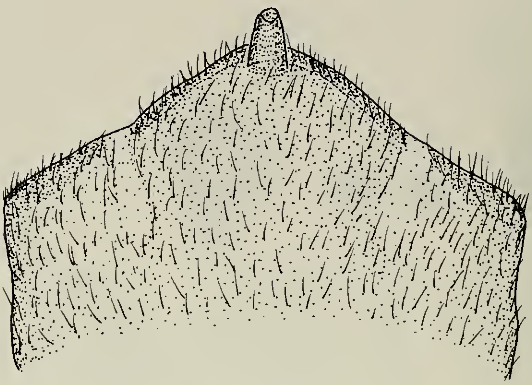

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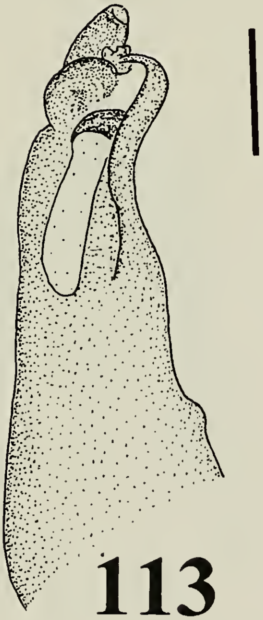

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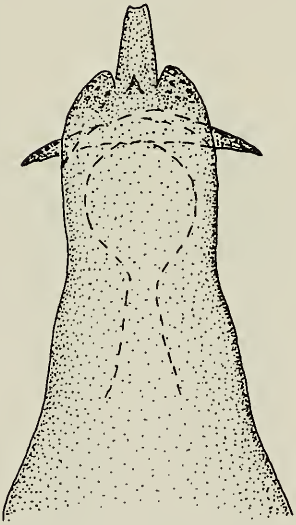

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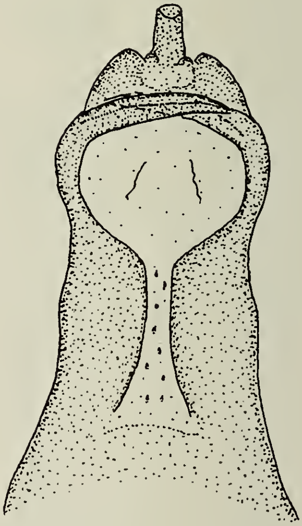

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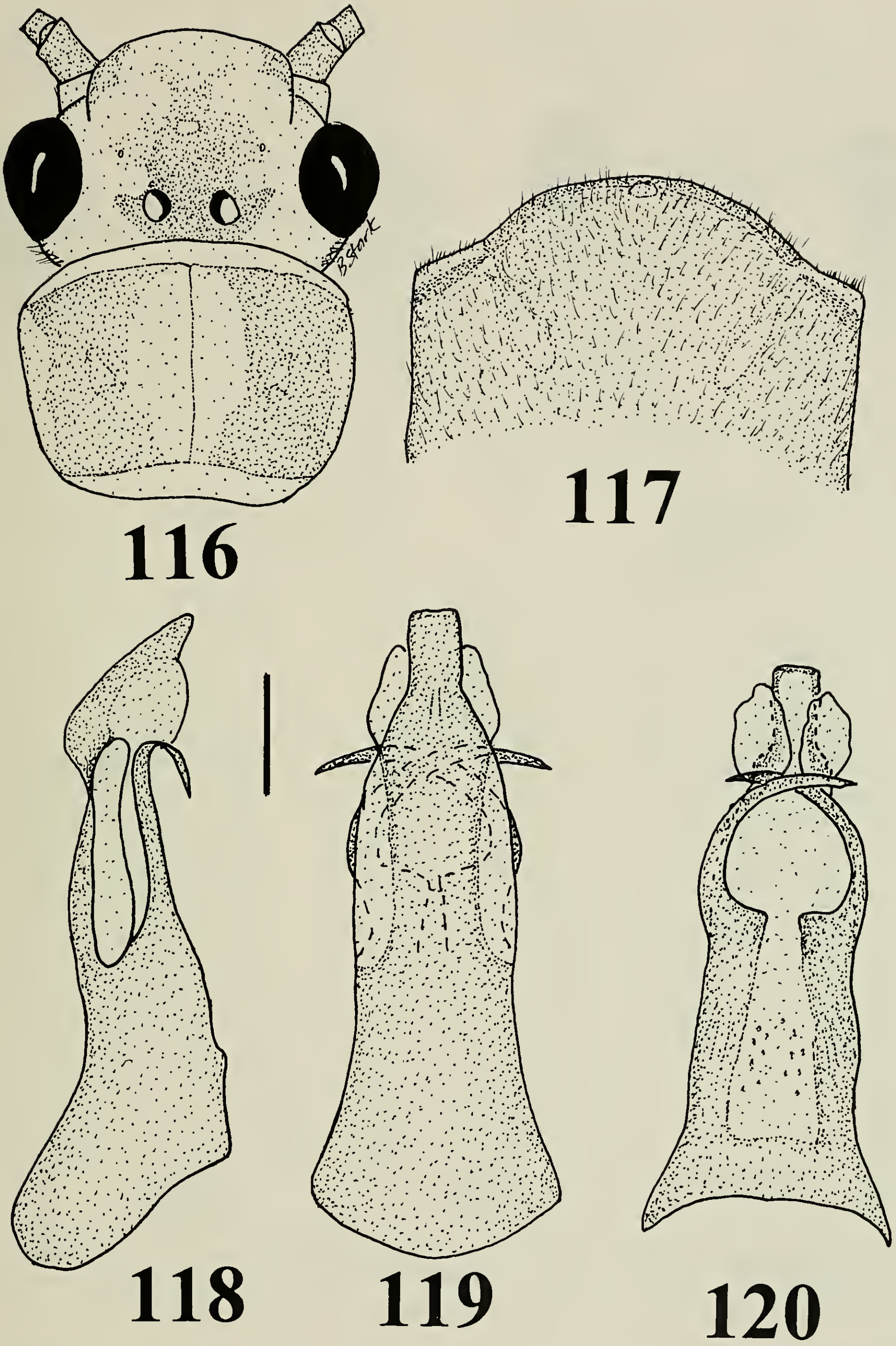
Figs. 111–115. *A. uatsi* structures. 111. Head and pronotum. 112. Male sternum 9. 113. Aedeagus, lateral. 114. Aedeagus, dorsal. 115. Aedeagus, ventral. Scales: 0.6 mm (111), 0.3 mm (112), 0.15 mm (113–115).

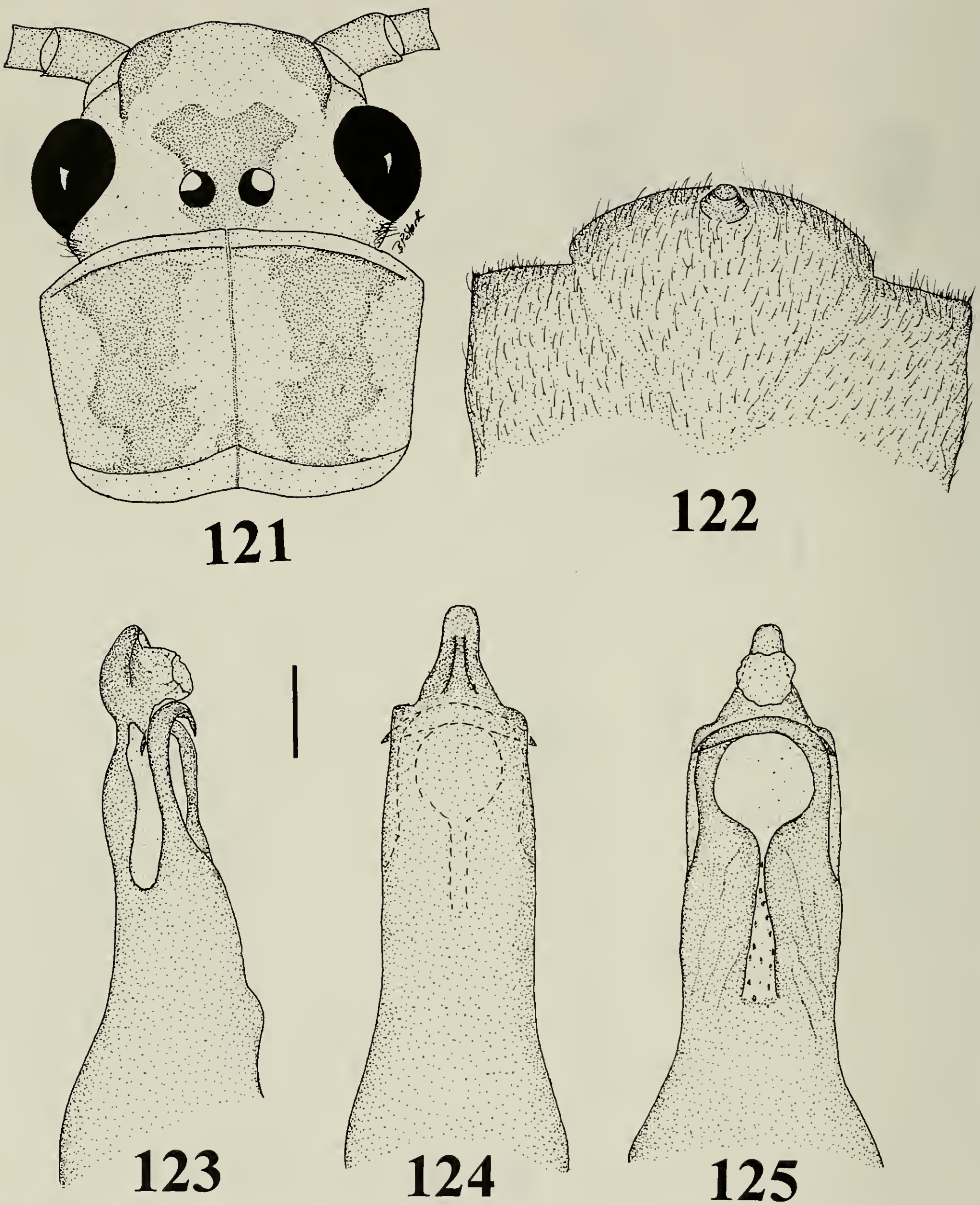
broad base with rounded, slightly projecting shoulders. Dorsomesal keel minute, triangular, hooks slender (Figs. 113–115).

Female.—Forewing length 10 mm. Subgenital plate with four subequal lobes. Transverse sclerite of sternum nine narrow; mesal T-shaped sclerite setose (Fig. 150).

Nymph.—Body length 9–11 mm. Head forward of ocelli dark brown except for incomplete M-line and anterior margin. Pro-



Figs. 116–120. *A. varilla* structures. 116. Head and pronotum. 117. Male sternum 9. 118. Aedeagus, lateral. 119. Aedeagus, dorsal. 120. Aedeagus, ventral. Scales: 0.6 mm (116), 0.3 mm (117), 0.15 mm (118–120).

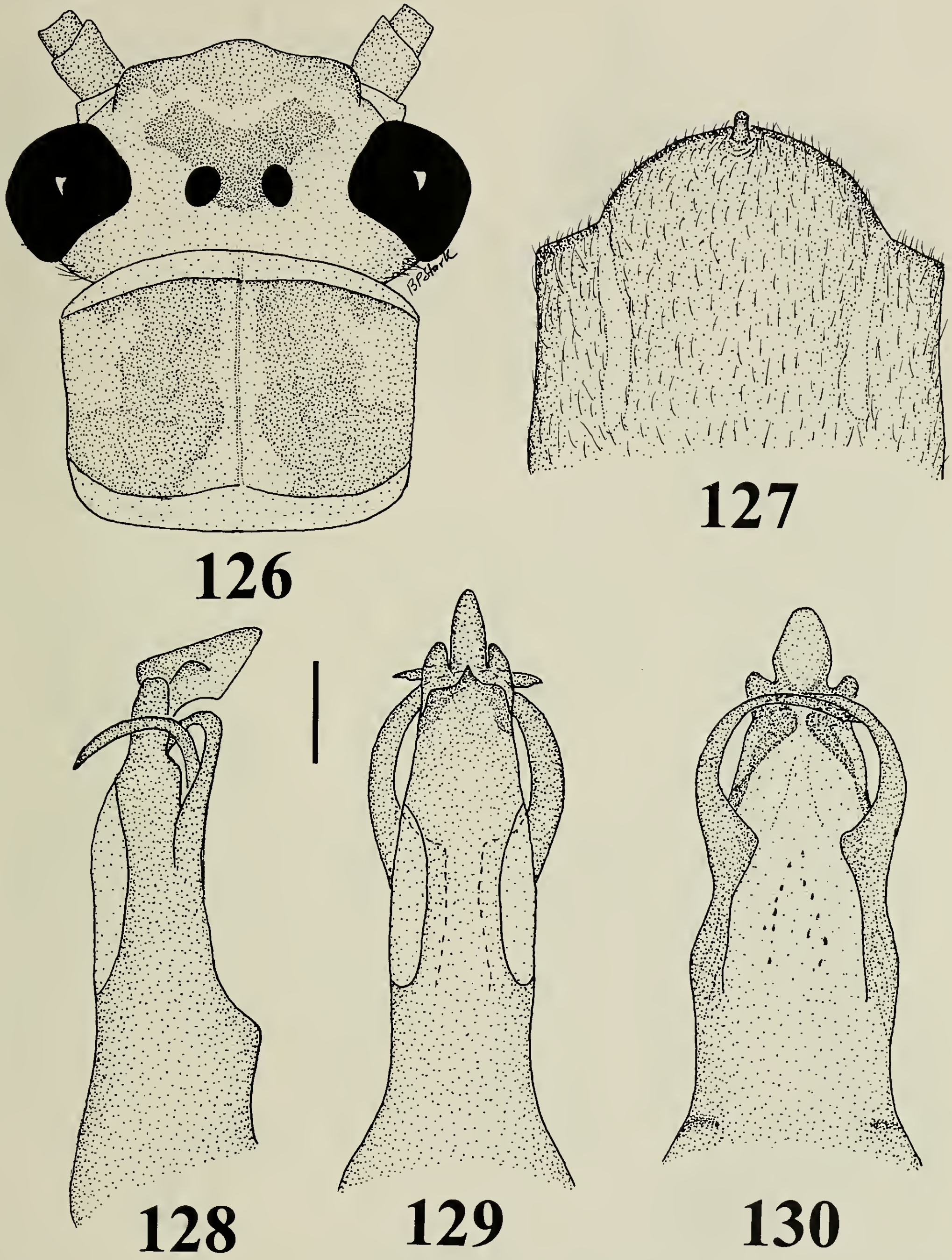


Figs. 121–125. *A. ventana* structures. 121. Head and pronotum. 122. Male sternum 9. 123. Aedeagus, lateral. 124. Aedeagus, dorsal. 125. Aedeagus, ventral. Scales: 0.6 mm (121), 0.3 mm (122), 0.15 mm (123–125).

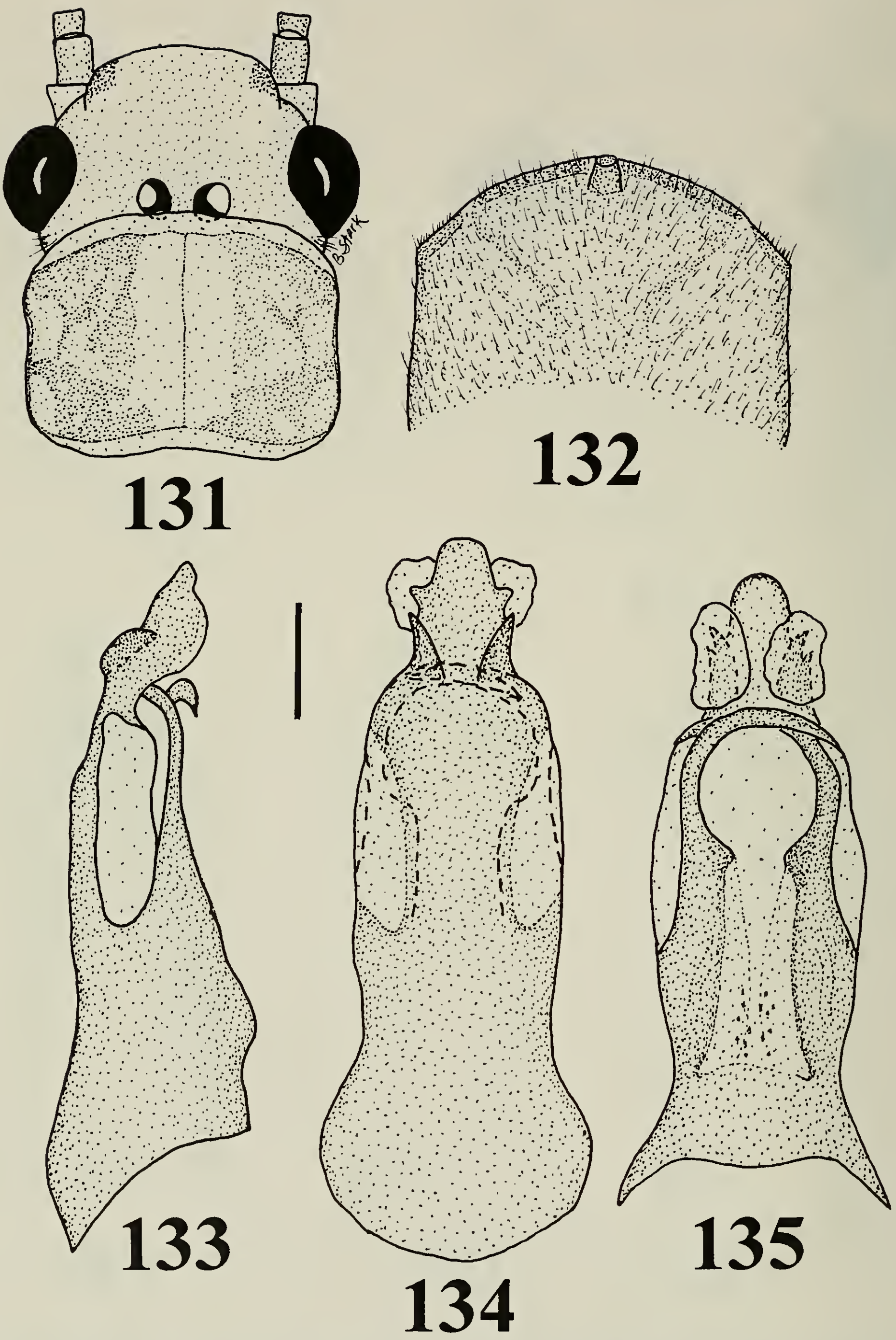
notum predominantly brown (Fig. 153). Anterodorsal femoral bristles grouped in irregular basal and apical patches and a median transverse row (Fig. 154).

Etymology.—The species name, based on the type locality, is used as a noun in apposition.

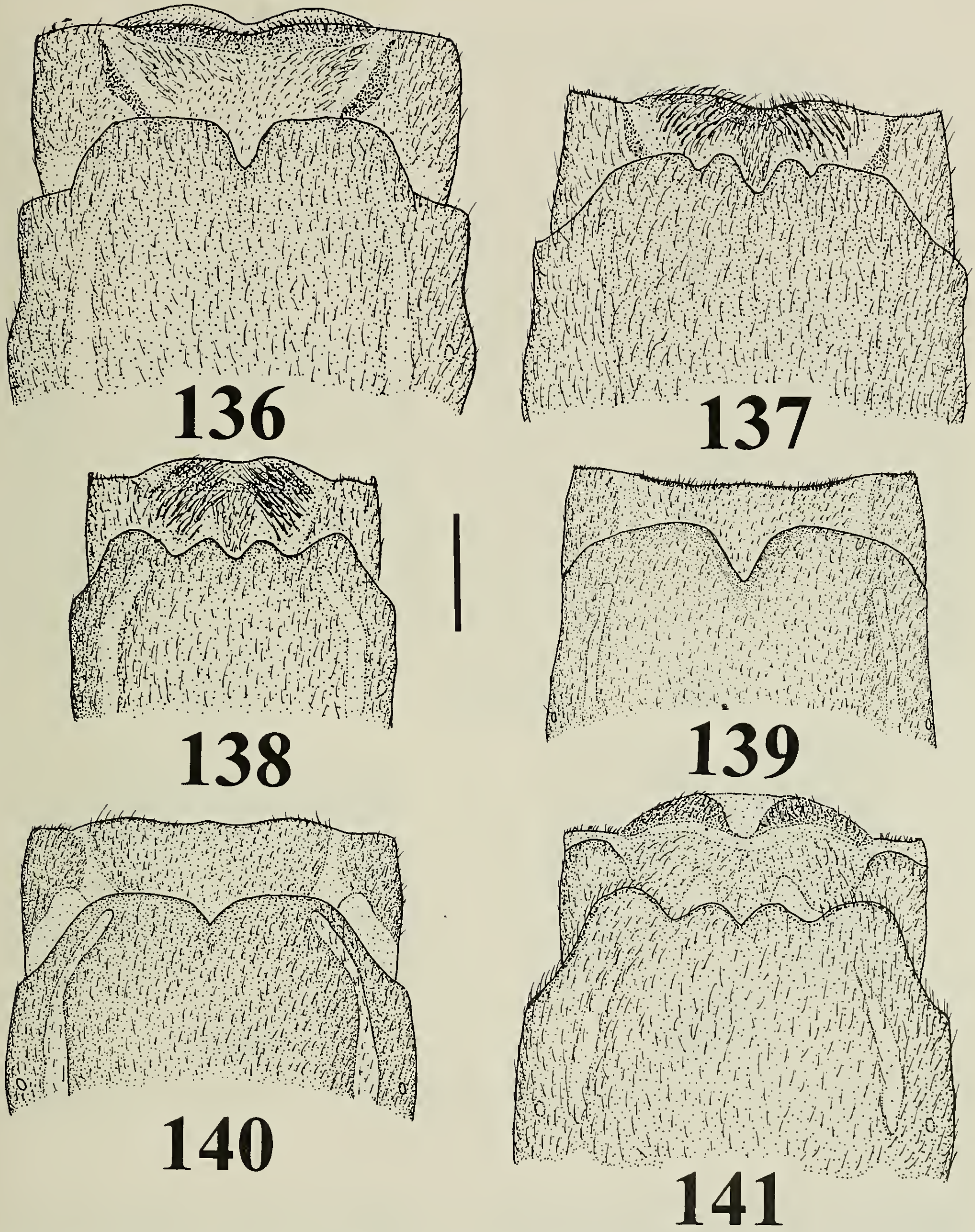
Types.—Holotype ♂ and ♂ paratype from Costa Rica, Limon, Rio Uatsi, 8 km W Bribri, 60 m, 25 Mar 1987, R. Holzen-



Figs. 126–130. *A. zapata* structures. 126. Head and pronotum. 127. Male sternum 9. 128. Aedeagus, lateral. 129. Aedeagus, dorsal. 130. Aedeagus, ventral. Scales: 0.6 mm (126), 0.3 mm (127), 0.15 mm (128–130).

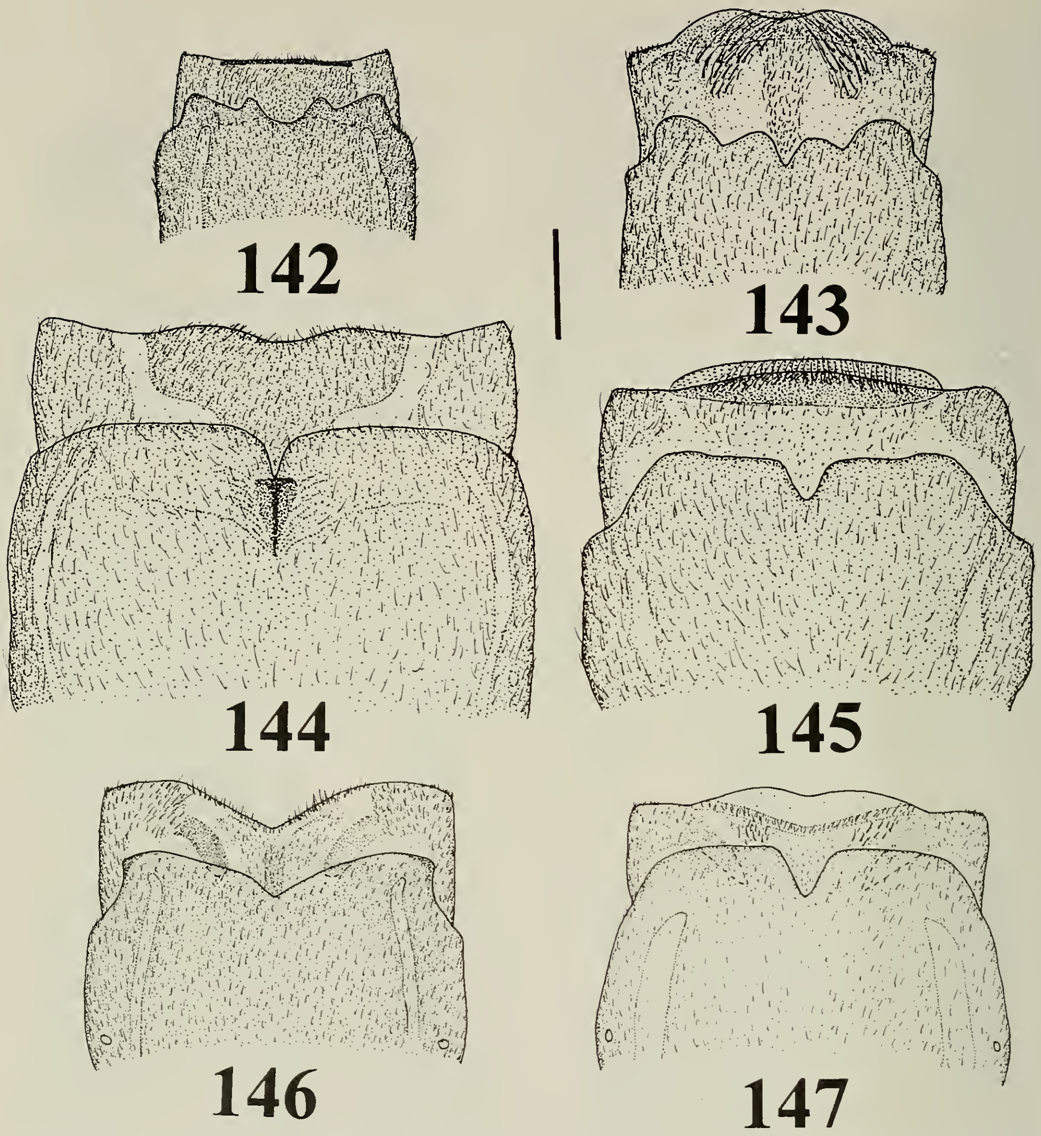


Figs. 131–135. *A. zarpa* structures. 131. Head and pronotum. 132. Male sternum 9. 133. Aedeagus, lateral. 134. Aedeagus, dorsal. 135. Aedeagus, ventral. Scales: 0.6 mm (131), 0.3 mm (132), 0.15 mm (133–135).



Figs. 136–141. *Anacroneuria* female sterna 8 and 9. 136. *A. acutipennis*. 137. *A. annulipalpis*. 138. *A. benedettoi*. 139. *A. blanda*. 140. *A. varilla*. 141. *A. divisa*. Scale = 0.6 mm.

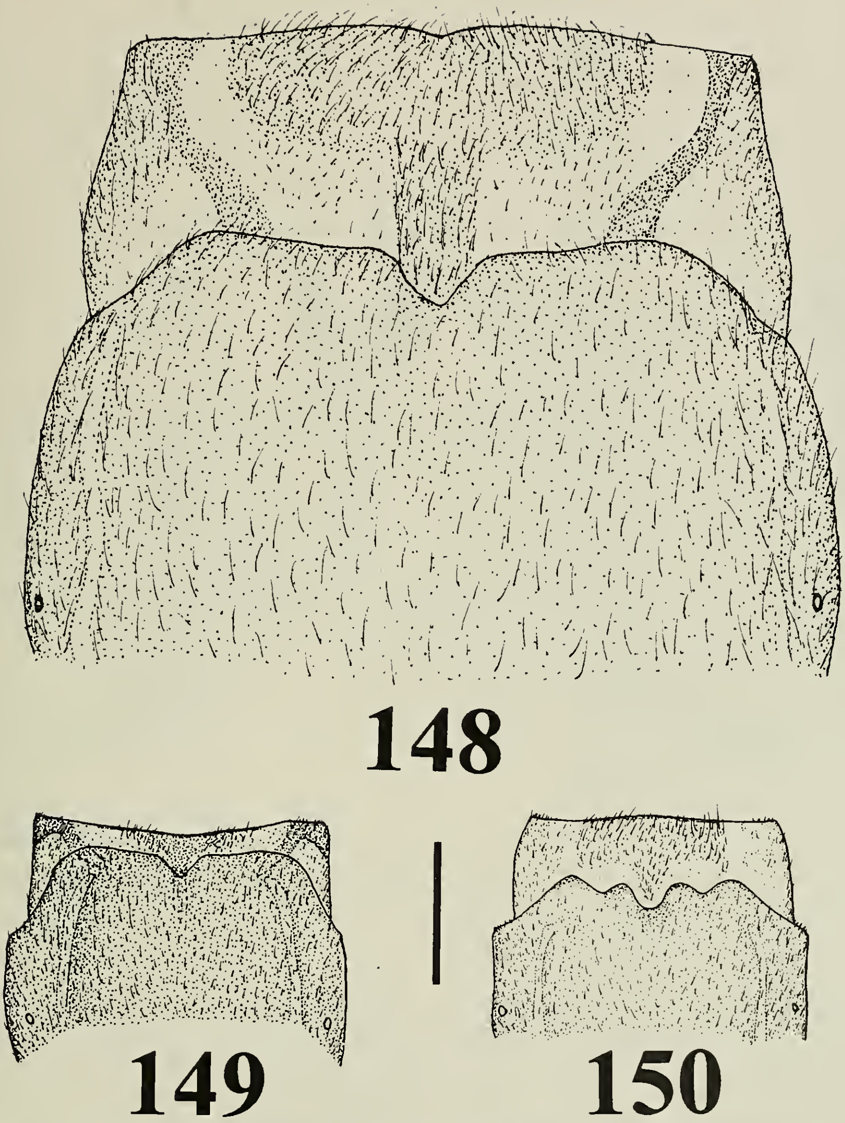
thal, S. Hamilton, M. Heyn (USNM). Additional paratypes: Costa Rica: Guanacaste: Rio Tempisquito, 3 km S route 1, 75 m, 6 Mar 1986, R. Holzenthal, W. Fasth, 2 ♂ (UMSP). Las Canas, Rio Carabici, 26 Jul 1967, O. S. Flint, 1 ♂ (USNM). Limon: E.A.R.T.H., Rio Destierra, Pozo Azul, 15 m, 5 Feb 1992, R. Holzenthal, F. Munoz,



Figs. 142–147. *Anacroneuria* female sterna 8 and 9. 142. *A. harperi.* 143. *A. holzenthali.* 144. *A. magnirufa.* 145. *A. marca.* 146. *A. maritza.* 147. *A. planicollis.* Scale = 0.6 mm.

K. Kjer, 1 ♂, 1 ♂ (BPS). Reserva Biol. Hitoy-Cerere, Rio Cerere, 90 m, 23 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Rio Uatsi, W Uatsi, 50 m, 2 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 2 nymphs (UMSP). Puntarenas: 2.8 mi E Golfito, 18 Jul 1967, O. S. Flint, 1 ♂ (USNM). Rio Rincon, 6.5 km S Rincon, 20 m, 7 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (INBIO). Quebrada Pita, 3 km W Golfito, 15 m, 15 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 22 ♀ (UMSP, INBIO). Quebrada Portera, N Grande Portera, 5 Jul 1992, T. Shepard, 1 ♂ (CSU).

Diagnosis.—See under *A. curiosa.* The nymphs were associated by dissection of male genitalia from a pre-emergent individual.



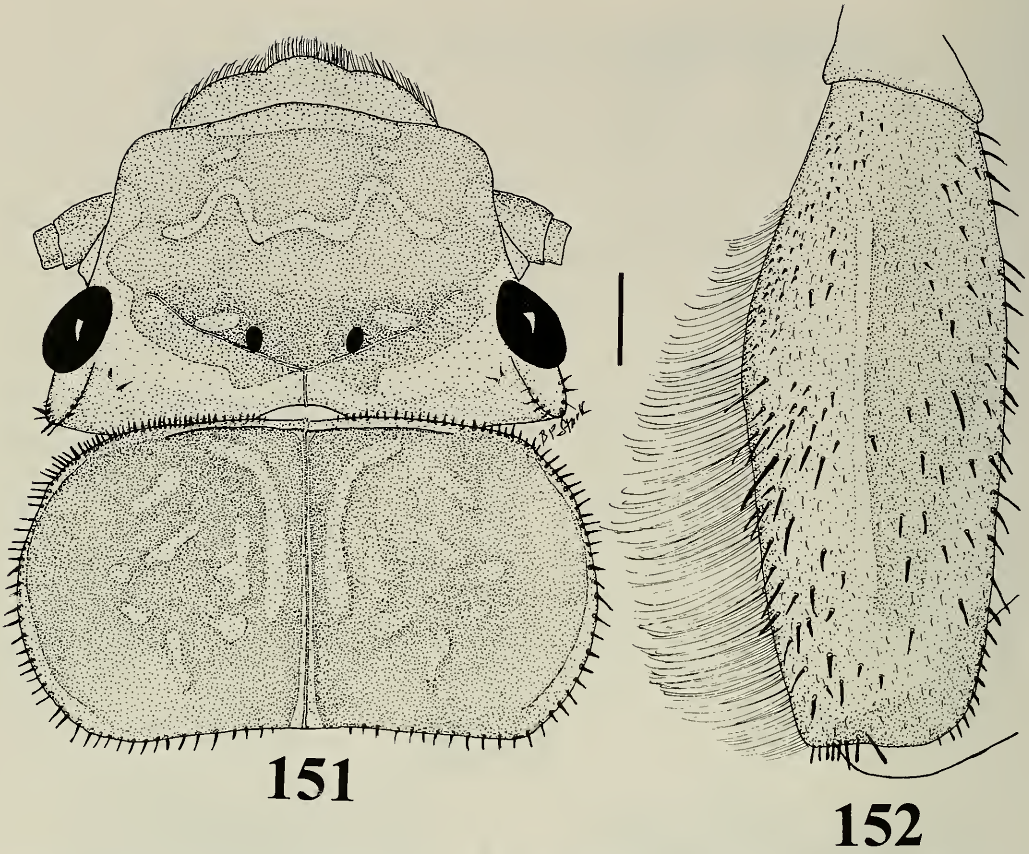
Figs. 148–150. *Anacroneuria* female sterna 8 and 9. 148. *A. plutonis.* 149. *A. talamanca.* 150. *A. uatsi.* Scale = 0.6 mm.

Anacroneuria varilla, new species
Figs. 116–120, 140, 183–184

Adult habitus.—Head yellow except for lappets and diffuse quadrangular brown spot over ocelli. Pronotum with irregular midlateral dark bands and a pale mesal band (Fig. 116). Wing membrane transparent, veins brown.

Male.—Forewing length 9–10 mm. Hammer reduced to a low membranous mound or short thimble (Fig. 117). Aedeagal apex a simple slender scoop with a pair of large ventral membranous processes; inconspicuous lateral notches occur at base of tip. Hooks very slender, dorsal keel inconspicuous (Figs. 118–120, 183–184).

Female (putative).—Forewing length 13 mm. Subgenital plate bilobed, notch shal-



Figs. 151–152. *A. maritza* nymphal structures. 151. Head and pronotum. 152. Fore femur. Scales: 0.6 mm (151), 0.3 mm (152).

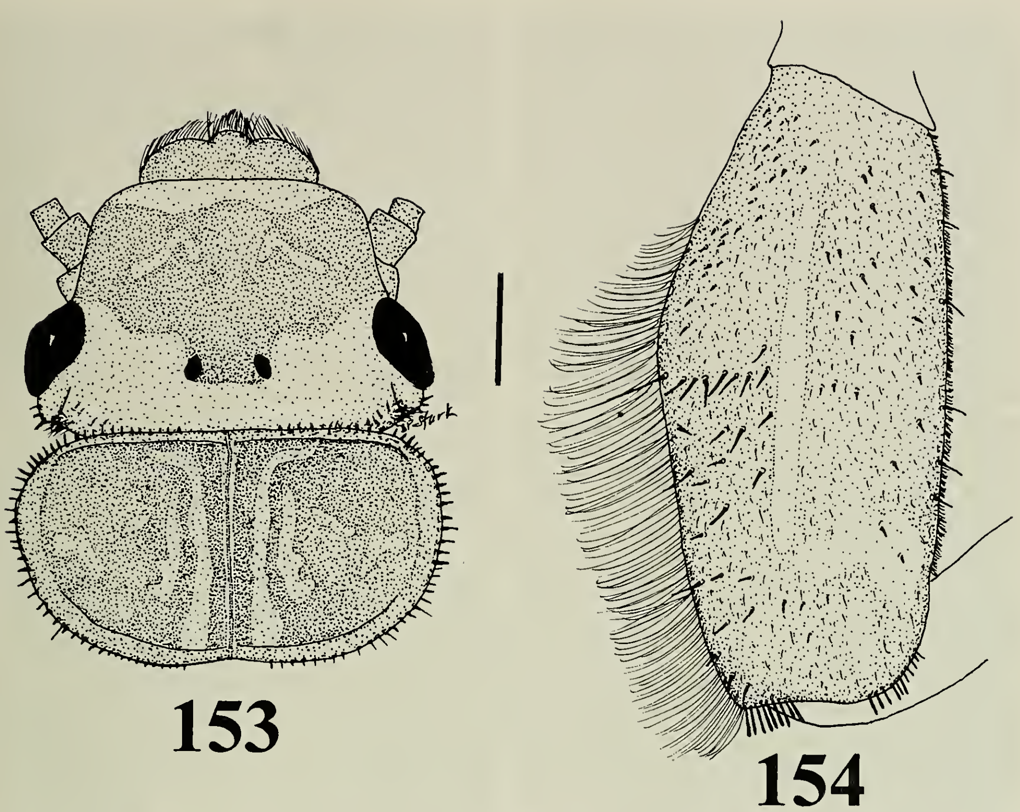
low. Transverse sclerite of sternum nine indistinct, mesal sclerite with sparse scattered setae (Fig. 140).

Nymph.—Unknown.

Etymology.—The species name, Spanish for small rod, refers to the thin aedeagal hooks and is used as a noun in apposition.

Types.—Holotype ♂ (USNM) and 6 ♂ paratypes (UMSP) from Costa Rica, Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen. Additional paratypes: Costa Rica: Guanacaste: Parque Nacional Guanacaste, Rio Orosi, 700 m, 22 May 1990, R. Holzenthal, R. Blahnik, 1 ♂ (BPS). Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 3 ♂ (USNM). Estacion Maritza, Rio Tempisquito, 8 Feb 1989, 2 ♂ (SWRC). Same location, 17 Mar 1989, 3 ♀ (INBIO). Same location, 27 Apr 1989, 3 ♂, 2 ♀ (BPS, INBIO, SWRC). Same location, 22 Oct 1990, 1 ♂ (SWRC). Same location, 11 May 1990, 12 ♂ (SWRC, INBIO). Panama: Chiriqui Province: Cuenca Fortuna, Quebrada Arena 3500′, 23 May 1985, R. W. Flowers, 1 ♂ (BPS).

Diagnosis.—The hammer shape and general coloration of this species are similar to *A. perplexa,* however the aedeagal hooks of that species are stout (Fig. 90) and the apex is trilobed (Figs. 89–90). These features easily distinguish *A. varilla* which has slender hooks and a simple apex (Figs. 119–120).



Figs. 153–154. *A. uatsi* nymphal structures. 153. Head and pronotum. 154. Fore femur. Scales: 0.6 mm (153), 0.3 mm (154).

Anacroneuria ventana, new species

Figs. 121–125

Adult habitus.—Dark Y-shaped spot covers ocelli and extends to M-line; lappets dark brown. Broad median pronotal band pale, irregular midlateral bands brown, marginal areas pale (Fig. 121). Wing membrane brown except for transparent window beyond cord, veins brown.

Male.—Forewing length 15 mm. Hammer thimble shaped, height less than basal diameter (Fig. 122). Aedeagal apex simple, tapered to a small rounded tip with a membranous ventral process. Hooks slender, dorsal keel moderately developed (Figs. 123–125).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The species name, Spanish for window, refers to the transparent apical area in the wing membrane and is used as a noun in apposition.

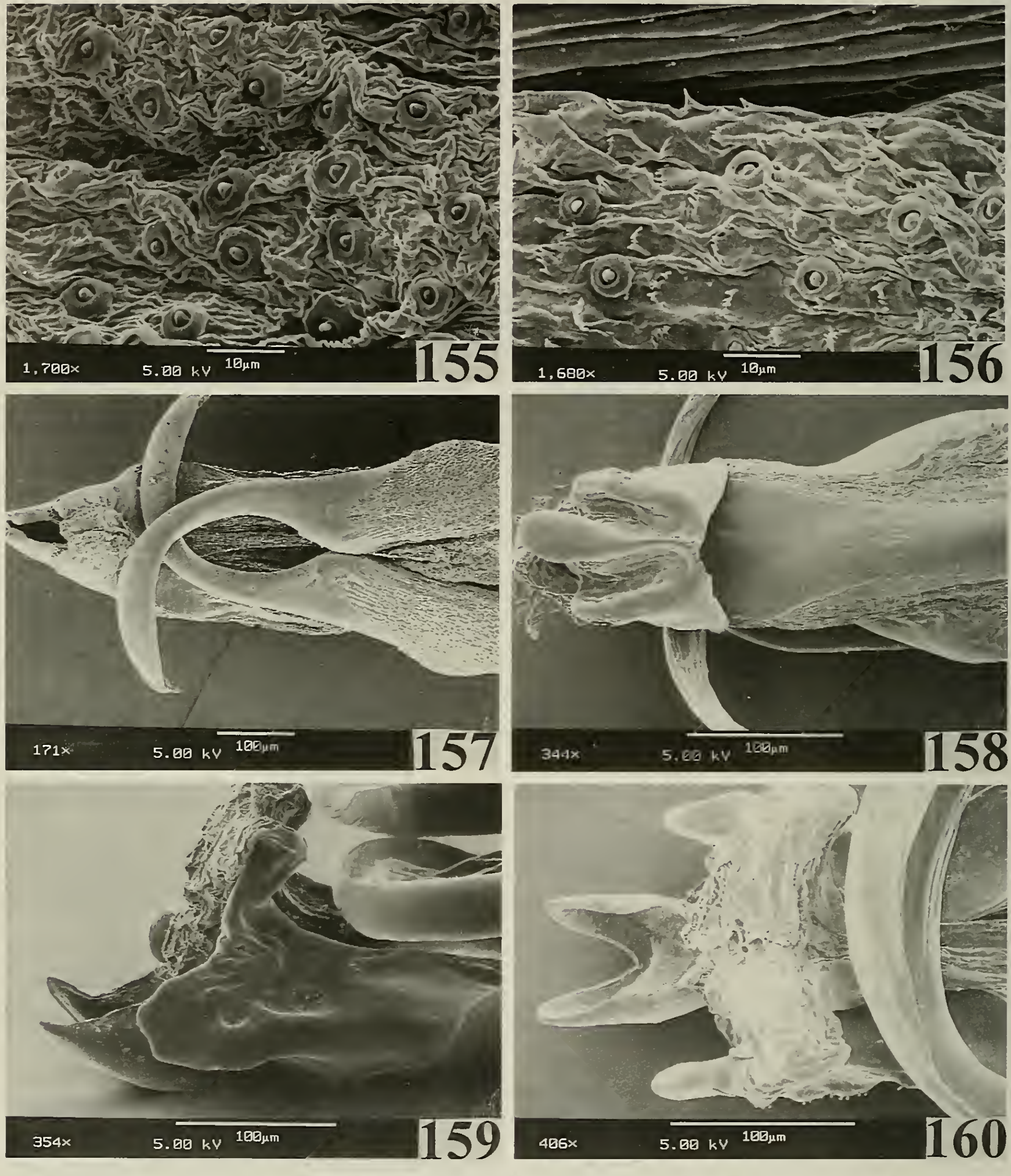
Types.—Holotype ♂ from Costa Rica, Alaquela, Rio Peje, ca. 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer (USNM). Paratype: Costa Rica: Cartago: Reserva Tapanti, Quebrada Palmitos, 1400 m, 24 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman 1 ♂ (UMSP). San Jose: Parque Nacional Carrillo, Rio Zurqui, 1650 m, 5 Feb 1986, J. Morse, W. Fasth, 1 ♂ (BPS).

Diagnosis.—See under *A. marca.*

Anacroneuria zapata, new species

Figs. 126–130

Adult habitus.—Diffuse V-shaped pattern extends from ocelli forward to M-line; lappets and anterior margin of head pale brown. Pronotum brown except for narrow



Figs. 155–160. *Anacroneuria* aedeagal structures. 155. *A. magnirufa* sensilla patch between hooks. 156. *A. benedetto* sensilla and microtrichia patch between hooks. The ridges above the patch are on the adjacent ventral sclerite. 157. *A. plutonis* ventral. 158. *A. curiosa* dorsal. 159. *A. acutipennis* apex, lateral. 160. *A. acutipennis* apex, ventral.

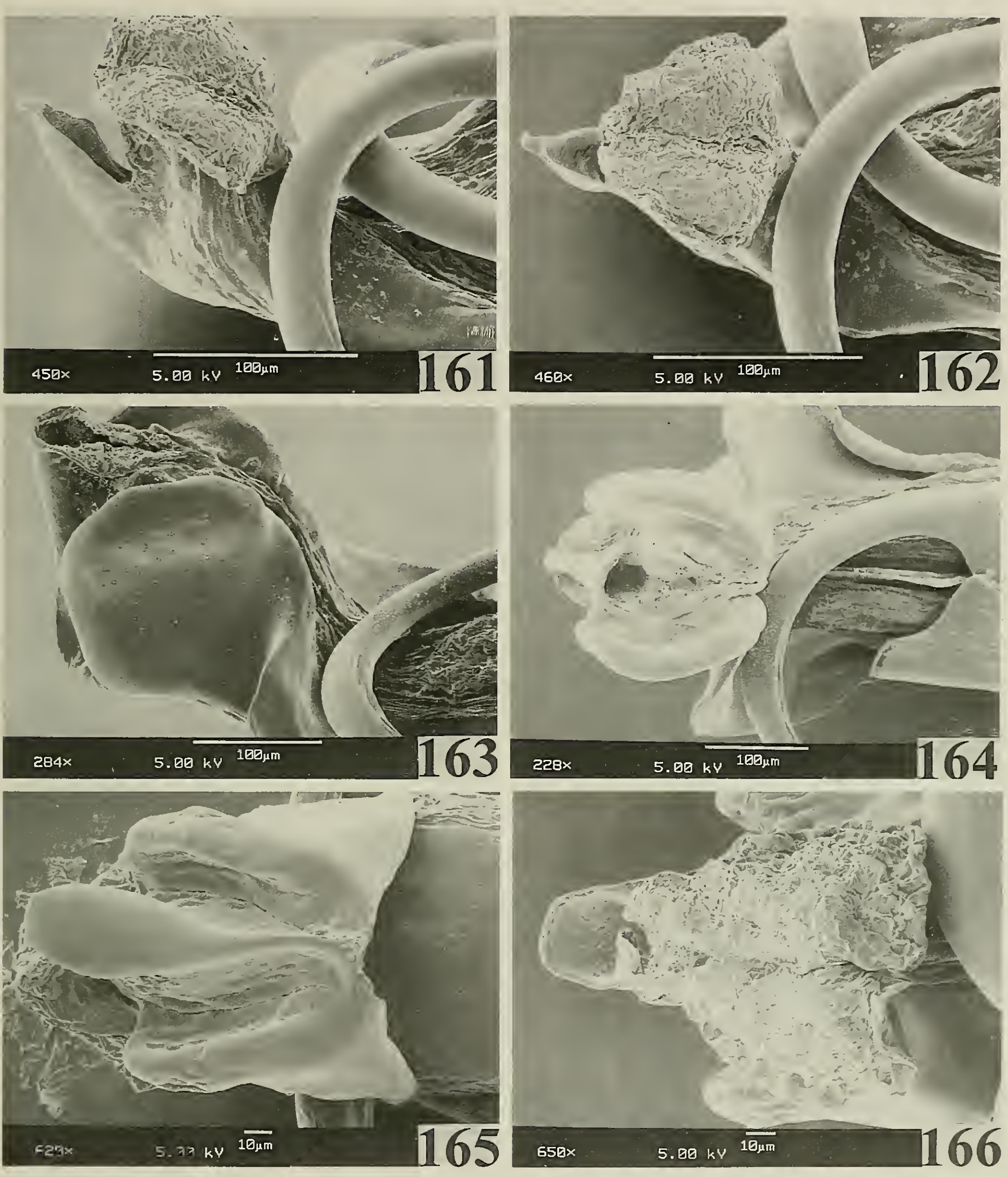
mesal stripe and anterolateral margins (Fig. 126). Wing membrane transparent, veins brown except for pale C and Sc.

Male.—Forewing length 13–14 mm. Hammer cylindrical (Fig. 127). Ventral aedeagal apex trilobed, hooks slender. Small dorsal keel projects apically along mesal lobe; lateral lobes of apex ear shaped (Figs. 128–130).

Female.—Unknown.

Nymph.—Unknown.

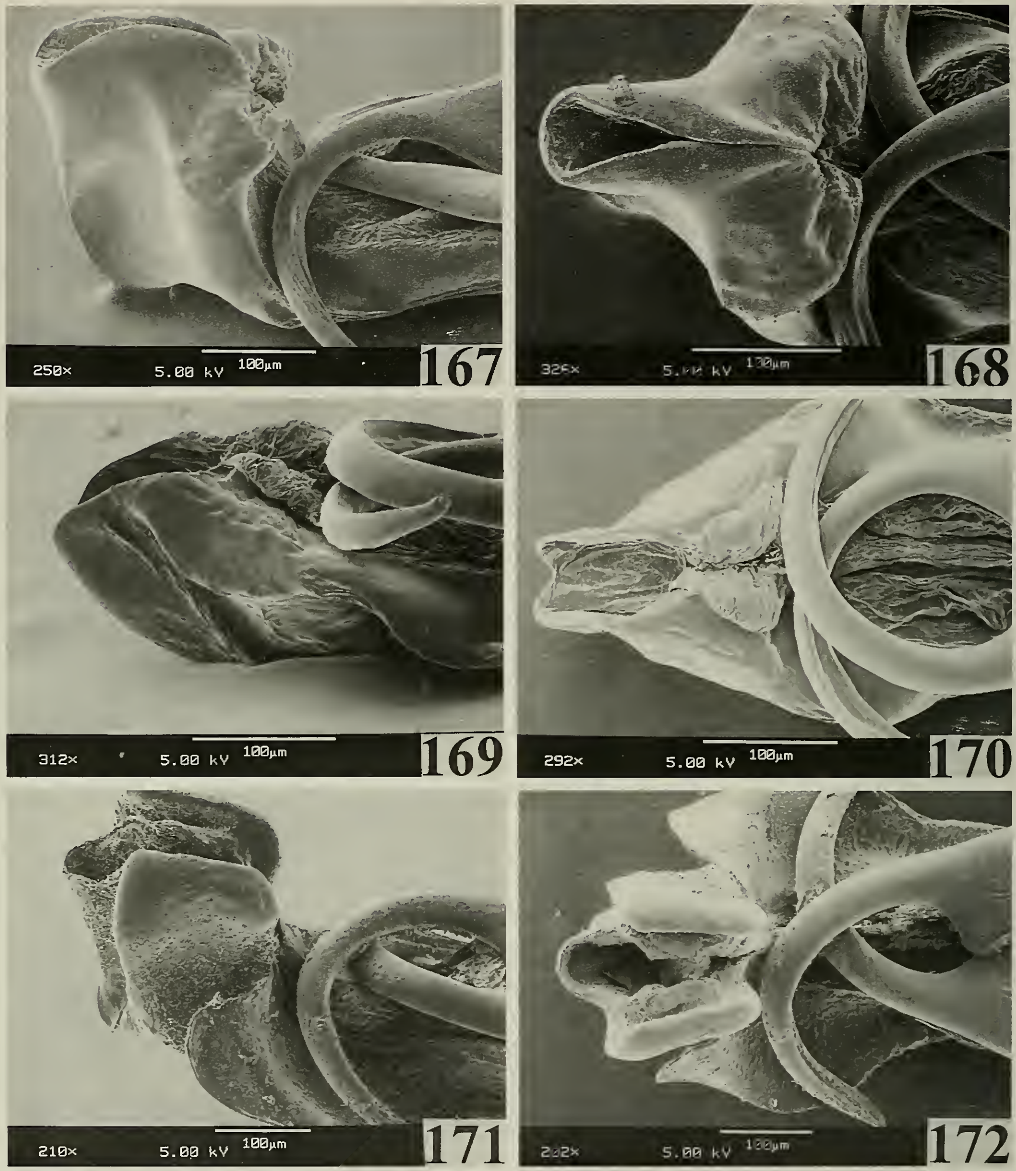
Etymology.—Zapata, Spanish for shoe,



Figs. 161–166. *Anacroneuria* aedeagal structures. 161. *A. annulipalpis* apex, lateral. 162. *A. annulipalpis* apex, ventral. 163. *A. benedettoi* apex, lateral. 164. *A. benedettoi* apex, dorsal. 165. *A. curiosa* apex, dorsal. 166. *A. curiosa* apex, ventral.

refers to the slipper shaped lateral aspect of the aedeagal apex and is used as a noun in apposition.

Types.—Holotype ♂ from Costa Rica, Alajuela, Rio Bochinche, Cerro Campana, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen (USNM). Paratypes: Costa Rica: Alajuela: Reserva Forestal San Ramon, Rio San Lorencito, 1090 m, 2–4 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (UMSP). Same location, 24–27 Feb 1987, I. Chacon, A. Chacon, 1 ♂ (USNM). Guanacaste: Estacion Maritza, Rio Tempisquito, 14 Jan 1990, 2 ♂



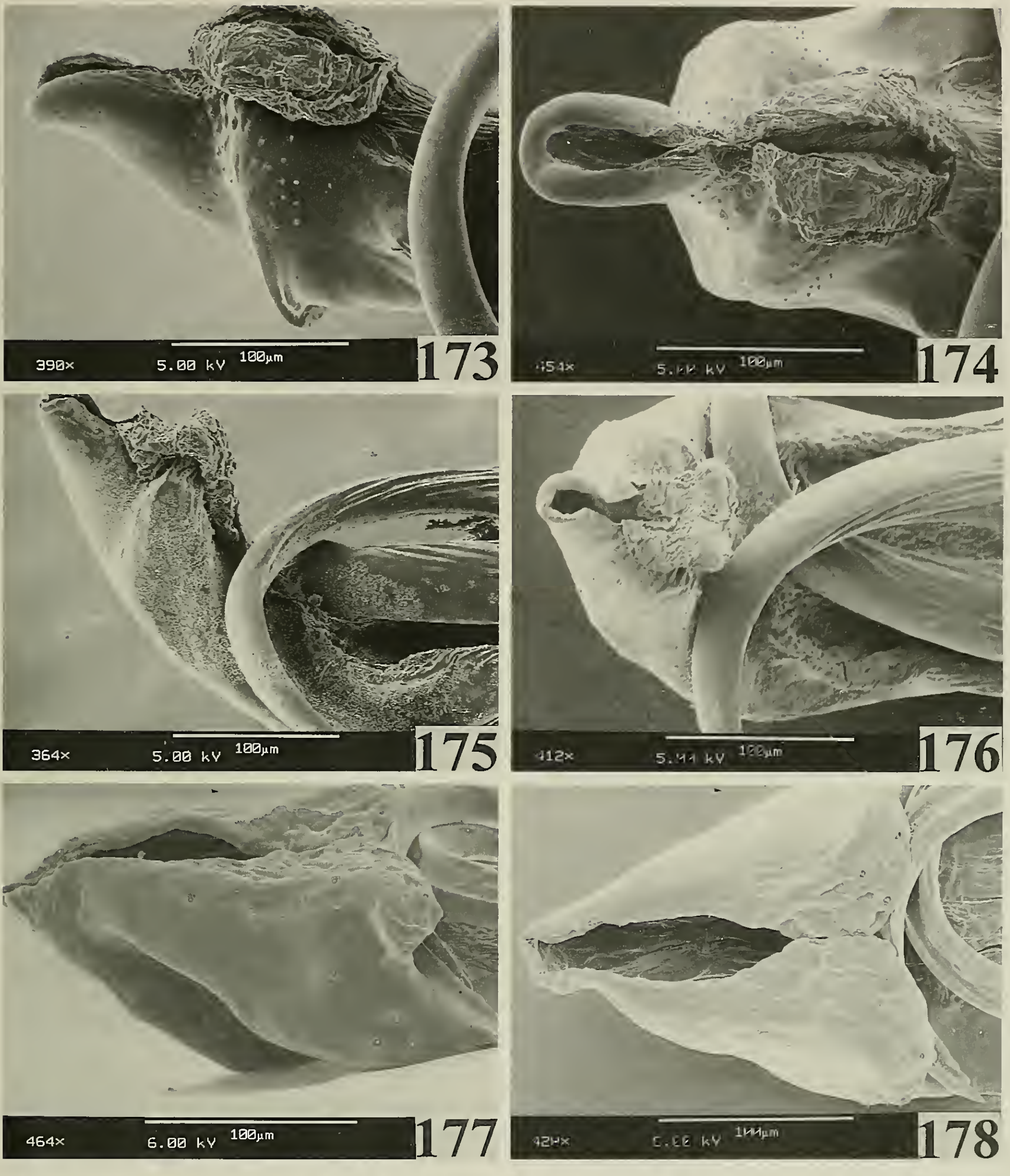
Figs. 167–172. *Anacroneuria* aedeagal structures. 167. *A. divisa* apex, lateral. 168. *A. divisa,* apex, ventral. 169. *A. hacha* apex, lateral. 170. *A. hacha* apex, ventral. 171. *A. holzenthali* apex, lateral. 172. *A. holzenthali* apex, ventral.

(SWRC). Same location, 17 Mar 1989, 1 ♂ (SWRC). Same location, 24 May 1989, 1 ♂ (INBIO). Same location, 22 Oct 1990, 3 ♂ (BPS, SWRC). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 2 ♂ (USNM, UMSP).

Diagnosis.—See under *A. marca.*

Anacroneuria zarpa, new species
Figs. 131–135

Adult habitus.—Head patterned with diffuse brown over most of frons; lappets



Figs. 173–178. *Anacroneuria* aedeagal structures. 173. *A. magnirufa* apex, lateral. 174. *A. magnirufa* apex, ventral. 175. *A. marca* apex, lateral. 176. *A. marca* apex, ventral. 177. *A. marginata* apex, lateral. 178. *A. marginata* apex, ventral.

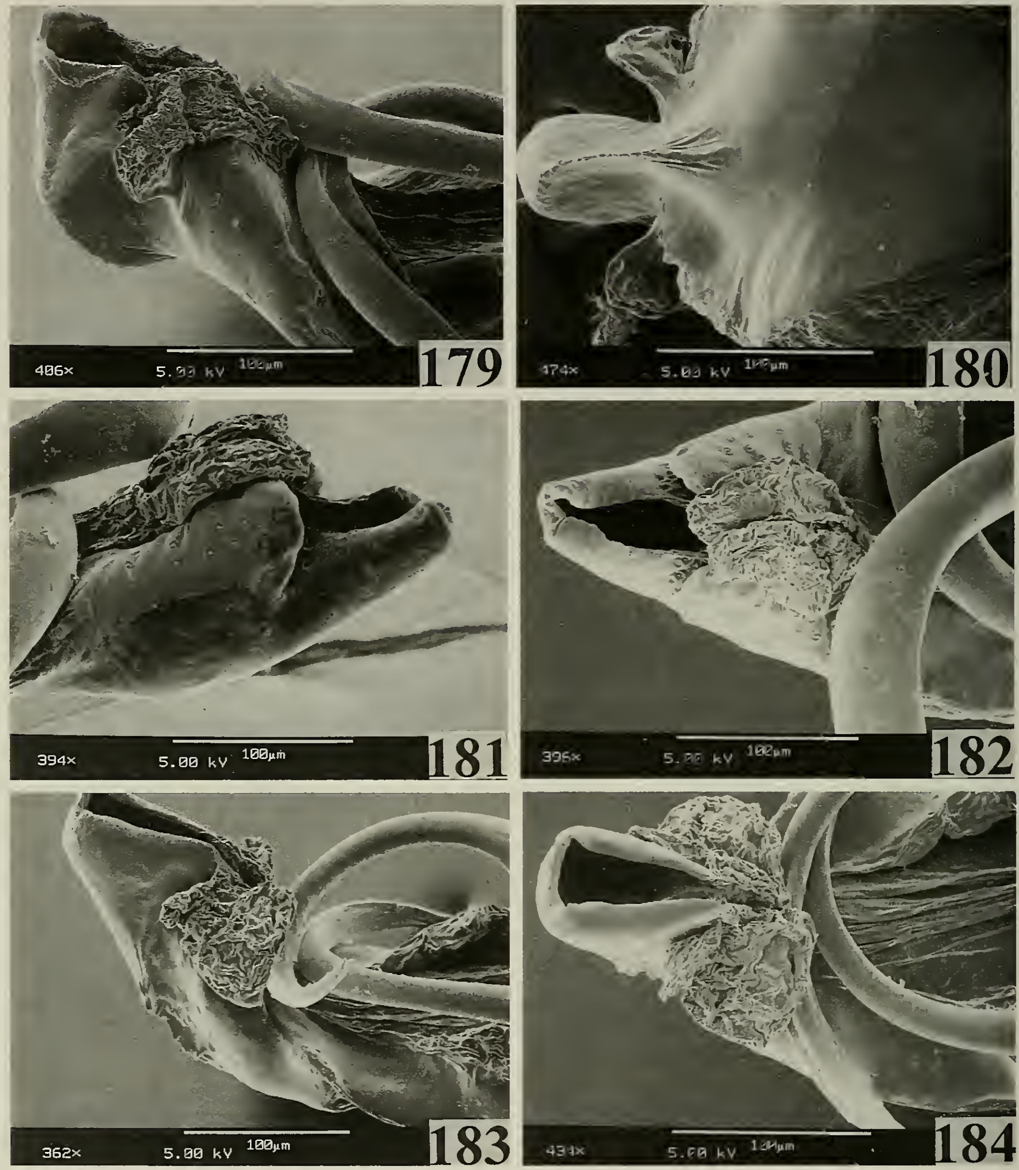
brown. Median pronotal stripe yellow, irregular lateral stripes pale brown with scattered rugosities; marginal rim black (Fig. 131). Wing membrane transparent, veins brown.

Male.—Forewing length 10 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 132). Aedeagal apex weakly trilobed and bearing a pair of dorsolateral clawlike lobes. Ventral aspect bearing prominent membranous lobes; tip rounded, hooks slender, keel absent (Figs. 133–135).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—Zarpa, Spanish for claw, re-



Figs. 179–184. *Anacroneuria* aedeagal structures. 179. *A. perplexa* apex, lateral. 180. *A. perplexa* apex, dorsal. 181. *A. plutonis* apex, lateral. 182. *A. plutonis* apex, ventral. 183. *A. varilla* apex, lateral. 184. *A. varilla* apex, ventral.

fers to the clawlike dorsolateral lobes of the aedeagal apex and is used as a noun in apposition.

Types.—Holotype ♂ from Panama, Bocas del Toro Province, Miramar, 21 Feb 1978, H. Wolda (USNM).

Diagnosis.—The color pattern of this species is not particularly distinctive but the bladelike dorsolateral aedeagal lobes (Fig. 134) distinguish this species from others.

Nomina dubia

Anacroneuria antica (Navas, 1924:71). Type locality Costa Rica.

The holotype ♀ is severely damaged. Benedetto (pers. comm.) provided notes of an attempted artistic "reconstruction" of the subgenital plate. Despite this I am unable to recognize this species.

Anacroneuria fulvipennis (Navas, 1934:17). Type locality San Jose, Costa Rica.

The holotype ♀ is in fragments and details of the subgenital plate are obscured (Benedetto, pers. comm.).

Anacroneuria proxima Klapálek, 1923:23. Type locality Surrubres, Costa Rica.

The syntypes consisting of a male and female from Costa Rica and a Mexican female have not been located (Benedetto, pers. comm.).

Acknowledgments

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111(3):604–612. 1998.

Studies in aquatic insects XIV: Description of eight new species of *Ochrotrichia* Mosely (Trichoptera: Hydroptilidae), from Costa Rica

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Abstract.—The species of the following microcaddisflies are described and their male genitalia are figured: *Ochrotrichia membrana, O. silva, O. avis, O. quebrada, O. dulce, O. vieja, O. ramona,* and *O. quinealensis.* These species were collected during an inventory of the Costa Rican Trichoptera fauna.

The exclusively New-World Tribe Ochrotrichiini was established by Marshall (1979) for the genera *Ochrotrichia (Ochrotrichia), Ochrotrichia (Metrichia)* and *Rhyacopsyche.* Wiggins (1996), noting larval characteristics that differentiated the two subgenera of *Ochrotriciha,* raised *Metrichia* to generic status, which we also accept. The species of *Ochrotrichia* are found from southern Canada to central Brazil and Peru, including all of the larger islands of the West Indies. Ross (1944), Denning & Blickle (1972), Blickle (1979), and Morse (1993) provided major reviews and checklists of the described North American species.

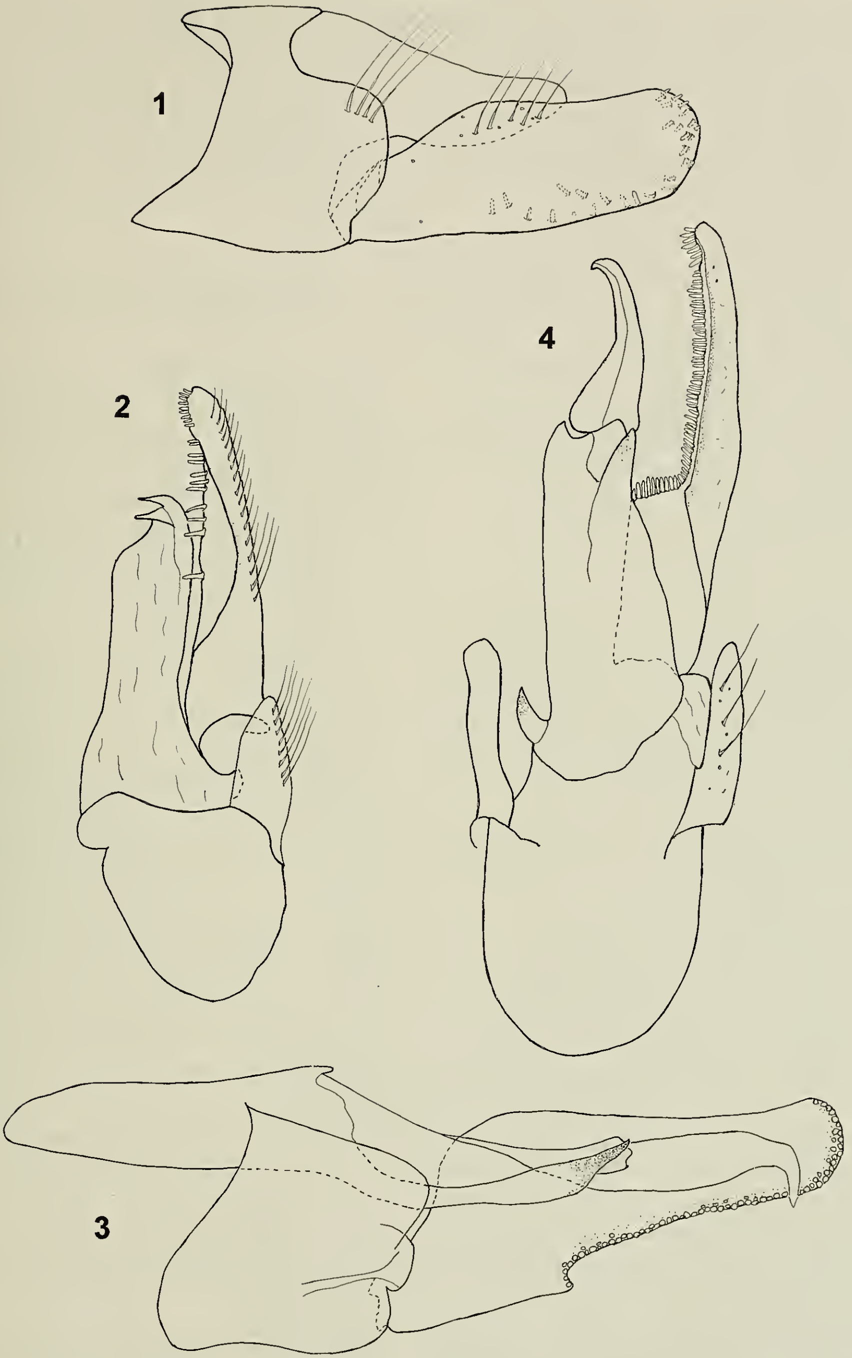
During the last 25 years, many new records and descriptions of new species in the genus *Ochrotrichia* Mosely from the Neotropical Region have been published (Botosaneanu & Alkins-Koo 1993; Botosaneanu 1991, 1995; Bueno-Soria & Santiago-Fragoso 1992, 1997; Flint 1972, 1981; Harris & Moulton 1993; Holzenthal 1988; Morse 1993). We are certain, however, that many more Neotropical species of *Ochrotrichia* remain to be described. Other species of *Ochrotrichia* described previously from Costa Rica are: *O. filiforma* Flint, *O. pacifica* Flint, and *O. tenanga* Flint.

In the present paper we describe eight new species, thereby increasing to 11 the number of species known from Costa Rica. The species described in this paper were collected during an inventory of the Trichoptera from Costa Rica conducted by Ralph Holzenthal and associates from 1986–1992. Morphological terminology used in the descriptions follows Marshall (1979). The holotypes will be deposited in the National Museum Natural History, Smithsonian Institution (USNM), Washington, D.C., and paratypes will be deposited in the collections of the University of Minnesota, St. Paul (UMSP) and Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM).

Ochrotrichia membrana, new species
Figs. 1–2

Diagnosis.—This species seems to be related to *Ochrotrichia flagellata* Flint, due to the shape of the simple, elongate membranous lobe of tergum X. However, *Ochrotrichia membrana,* can be distinguished from *O. flagellata* by the presence of 2 short hooklike processes on the left side of the apical process of tergum X.

Description of adult.—Length of forewing 2 mm. Color in alcohol stramineous. Male genitalia: Segment IX tubular, tergum slightly depressed but not produced anteriad. Tergum X a large, elongate membranous lobe, appearing as a cylindrical flat plate in dorsal view, with 2 short apical hooklike processes on the left side; in lateral view, tergum X ellipsoidal, apex round-



Figs. 1–4. Male genitalia of *Ochrotrichia membrana.* 1, Lateral view; 2, Dorsal view. Male genitalia of *Ochrotrichia silva.* 3, lateral view; 4, Dorsal view.

ed. Inferior appendage in lateral view, elongate, apex rounded; with clusters of black, peglike setae apicomesally and a row of black peglike setae ventromesally, ending in a few setae at the midbasal ridge. Phallus long, basal portion wide; apical portion narrow, apex truncate.

Material.—Holotype ♂; Costa Rica. Alajuela: Reserva Forestal San Ramón, Río San Lorencito and tribs. 10°12′96″N, 84°36′42″W, 30 Mar–1 Apr 1987, 980 m, Holzenthal, Hamilton, Heyn (USNM).

Etymology.—The species epithet, *membrana,* is Latin for membrane, in reference to membranous aspect of the tergum X.

Ochrotrichia silva, new species
Figs. 3–4

Diagnosis.—Based on the simple structure and shape of tergum X, *O. silva* appears distantly related to *O. quebrada,* new species. However, *O. silva* can be distinguished by the presence of a short, strong, hooklike process on the right side of the basal portion of tergum X, and by the presence of a long spinelike process on the left side, with its apex darker and touching the base of the apical process.

Description of adult.—Length of forewing, 2 mm. Color in alcohol stramineous. Male genitalia: Tergum IX depressed and produced anteriad. Tergum X in dorsal view with a short, strong hooklike process, situated on base of right side; middorsal portion appears membranous and cylindrical, with 1 long spinelike process on left side; apical process heavily sclerotized, slightly curved in dorsal view; in lateral view, apical process strongly curved ventrad apically. Inferior appendage in lateral view, elongate with mid portion narrower than anterior portion, apex rounded; apical and ventral margins with a row of black, peglike setae, ending in a midbasal ridge. Phallus long and threadlike.

Material.—Holotype ♂; Costa Rica. Alajuela: Reserva Forestal San Ramón Río San Lorencito and Tribs. 10°12′96″N, 84°36′42″W, 30 Mar–1 Apr 1987, 980 m, Holzenthal, Hamilton, Heyn (USNM).

Etymology.—The species epithet, *silva,* is a Latin word for forest, in reference to the type locality, Reserva Forestal San Ramón. The name is treated as a noun in apposition.

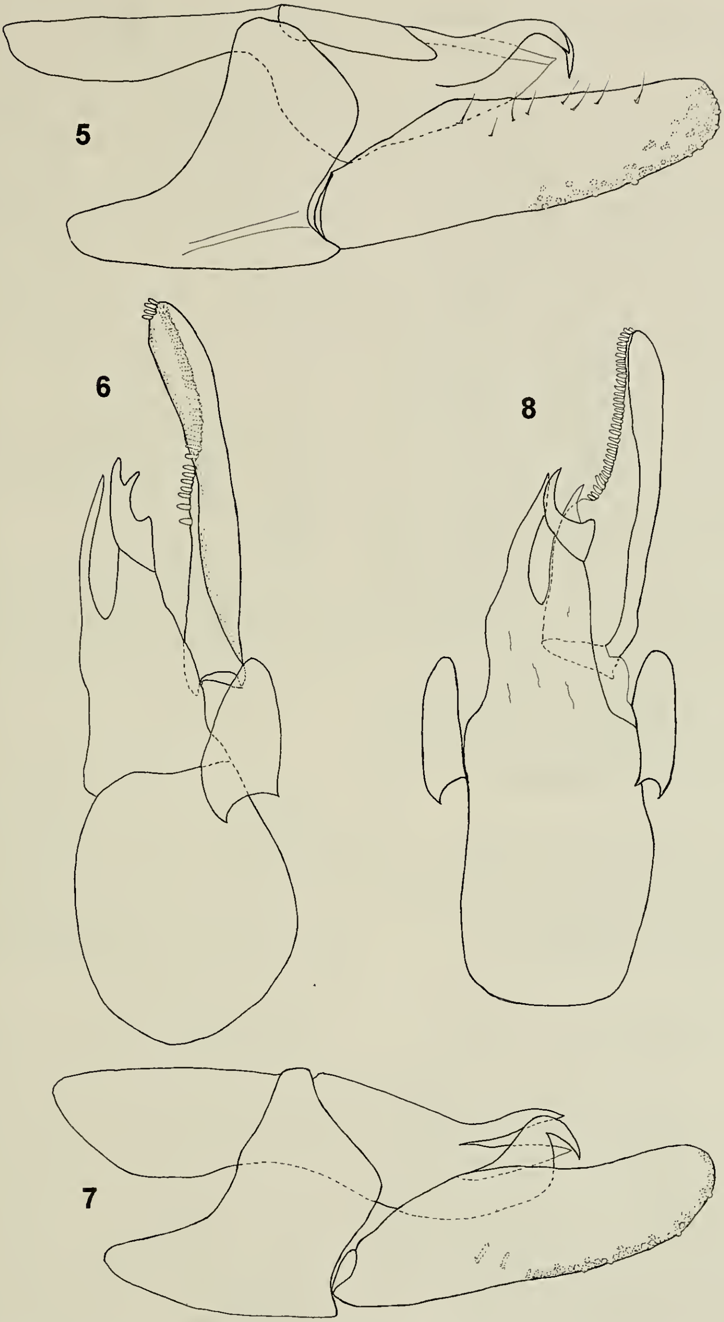
Ochrotrichia avis, new species
Figs. 5–6

Diagnosis.—Because of the shape of the inferior appendages in lateral view and the presence of a long spinelike process on the right side of the tergum X, *O. avis* is related to *O. quebrada,* new species. However, *O. avis* can be distinguished from that species by tergum X, which shows differences in the shape of the apical process, especially when viewed dorsally.

Description of adult.—Length of forewing 2 mm. Color in alcohol stramineous. Male genitalia: Sternum, IX in lateral view, produced anteriad; tergum IX depressed and produced anteriad. Tergum X in dorsal view with elongate middorsal spinelike process on right side, apical process bifurcated apically into 2 short hooklike processes; in lateral view, on right side, apical process appears hooklike with apex ventrally directed and elongate middorsal spinelike process almost touching apex of hooklike process; on left side, apical process appears elongate and ventrally curved, with a short preapical process giving appearance of a bird's neck. Inferior appendage in lateral view long, slender, with apex rounded; black peglike setae on apex and ventral margin. Phallus long with basal portion wider, at midlength surrounded and covered by a membranous structure; apical portion long and thin.

Material.—Holotype ♂; Costa Rica. Alajuela: Reserva Forestal San Ramón, Río San Lorencito and Tribs. 10°12′96″N, 84°36′42″W, 30 Mar–1 Apr 1987, 980 m, Holzenthal, Hamilton, Heyn (USNM). Paratype ♂, same data as holotype (UMSP).

Etymology.—The species epithet, *avis,* is



Figs. 5–8. Male genitalia of *Ochrotrichia avis.* 5, Right lateral view; 6, Dorsal view. Male genitalia of *Ochrotrichia quebrada.* 7, Right lateral view; 8, Dorsal view.

derived from the Latin avis meaning bird in allusion to the bird's neck shape of the apical process of tergum X. The name is treated as a noun in apposition.

Ochrotrichia quebrada, new species

Figs. 7–8

Diagnosis.—On the basis of the presence of an elongate spinelike process on the right side of tergum X and by the elongate inferior appendages, *O. quebrada* appears related to *O. avis.* However, *O. quebrada* can easily be distinguished from that species by the presence of a long, dextrally curved, preapical hooklike process on tergum X.

Description of adult.—Length of forewing 2 mm. Color in alcohol stramineous. Male genitalia: Tergum IX deeply depressed and produced anteriad; in lateral view, sternum IX ventrolaterally produced. Tergum X in dorsal view with long pointed process on right side; on left side a broad elongate process with apex acute and also a long dextrally curved preapical hooklike process. Inferior appendage elongate, apex rounded, with a row of black peglike setae around apex, along midventral margin and midbasal ridge. Phallus long, with basal portion wider than apical portion.

Material.—Holotype ♂; Costa Rica. Guanacaste: P. N. Rincón de la Vieja Quebrada Zopilote, 10°45′9″N, 83°18′54″W, 3 Mar 1986, 785 m, Holzenthal & Fasth (USNM).

Etymology.—The species epithet, *quebrada,* alludes to the type locality, Rincón de la Vieja quebrada Zopilote. The name is treated as a noun in apposition.

Ochrotrichia dulce, new species
Figs. 9–10

Diagnosis.—Based on the presence of the long process on the right side and a hooklike apical process of tergum X, *O. dulce* seems related to *O. tenanga* (Mosely). However, *O. dulce* can be distinguished from that species by the rectangular shape of the inferior appendage in lateral view with its angled anterodorsal margin.

Description of adult.—Length of forewing 2 mm. Color in alcohol stramineous. Male genitalia: Segment IX deeply depressed dorsally and produced anteriad. Tergum X in dorsal view with long, straight, rodlike process on right side; body of X with long, membranous process covering most of length of an apical process that is hooked apically; in lateral view, on left side, a dorsalmost process appears, wider, and apically curved, ventral process appears long, thinner, with its apex slightly curved upward. Inferior appendage in lateral view, anterodorsally angled, apical portion rounded, with several rows of black peglike setae; in dorsal view apex with several peglike setae and midbasal ridge with 3 black peglike setae. Phallus long, threadlike.

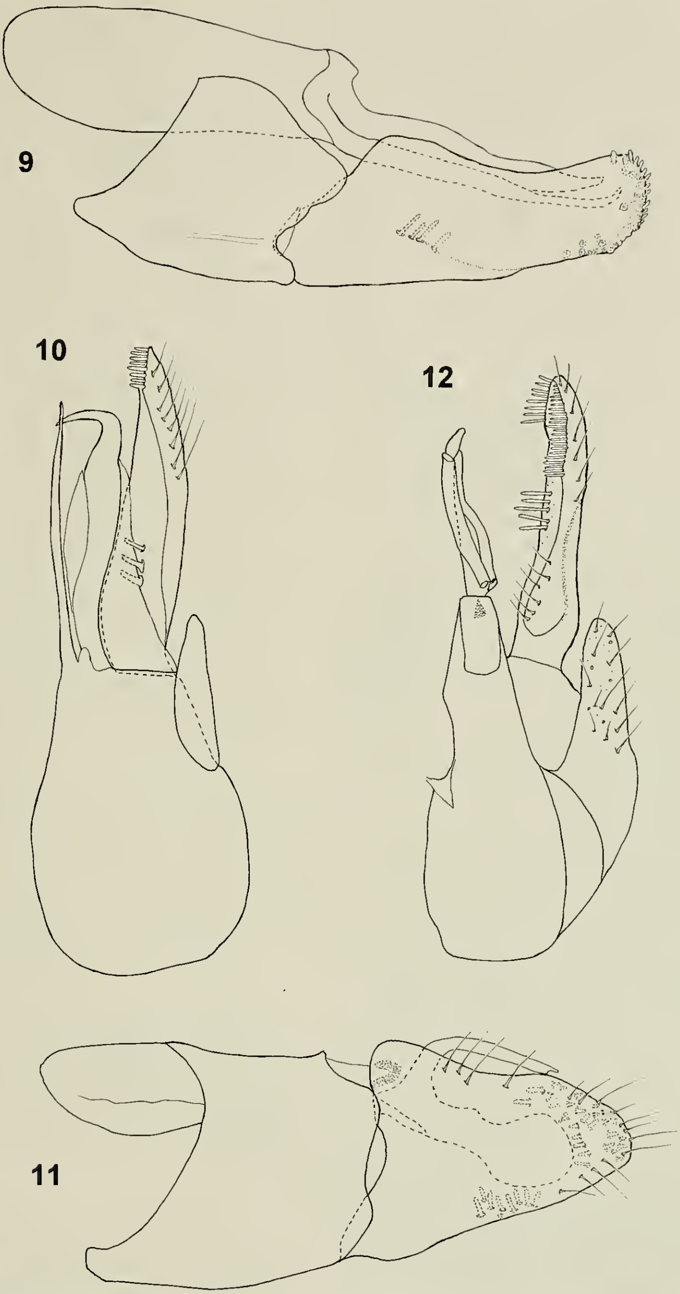
Material.—Holotype ♂; Costa Rica. Guanacaste: Río Tizate, 7.2 km N. E. Cañas Dulces, 10°43′98″N, 66°26′94″W, 28 Jun 1986, 275 m, Holzenthal, Heyn, Armitage (USNM).

Etymology.—The species epithet, *dulce,* is from the Spanish dulce, in allusion to the type locality (Cañas Dulces). The name is treated as a noun in apposition.

Ochrotrichia vieja, new species
Figs. 11–12

Diagnosis.—On the basis of the triangular shape of the inferior appendages in lateral view, *O. vieja* appears closely related to *O. cruces* Flint from Mexico. However, *O. vieja* can be distinguished from that species by the shape and presence of 1 long process on tergum X.

Description of adult.—Length of forewing 3 mm. Color in alcohol stramineous. Male genitalia: Tergum IX depressed and produced anteriad. Tergum X in dorsal view with first ⅔ of tergum smooth, long, apical portion rectangular; posterior ⅓ ending in a sinuous apical process; basal section of this portion with long, black tipped dorsal process, slightly curving to right apically, basal to this process is a broad thin plate middorsally, with a short black-tipped spine; in lateral view posterior third of sinuous process appears wide and rounded apically and basal section of this portion bears long, black-tipped, dorsal process; basally to this process a short black-tipped spine, and a very short spur on right and left sides at

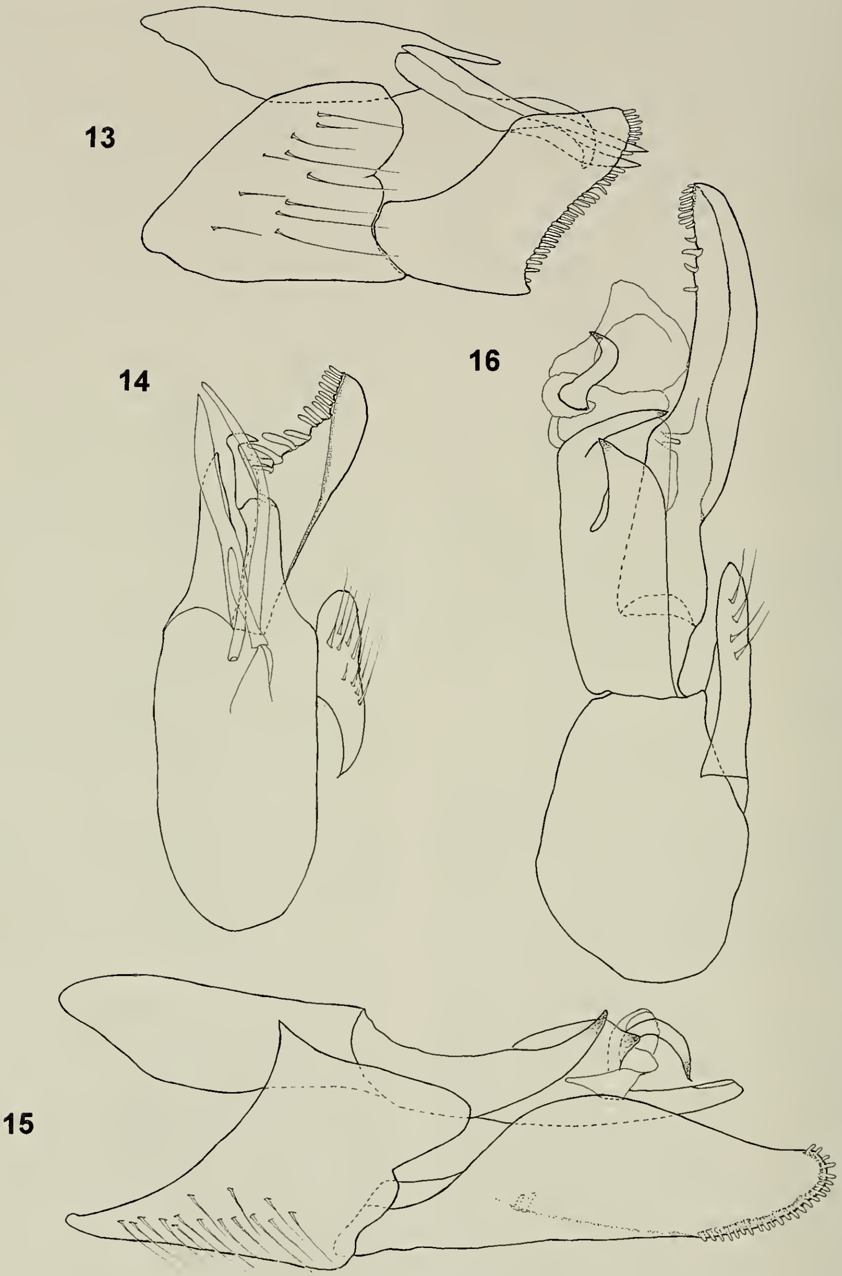


Figs. 9–12. Male genitalia of *Ochrotrichia dulce*. 9, Right lateral view; 10, Dorsal view. Male genitalia of *Ochrotrichia vieja*. 11, Right lateral view; 12, Dorsal view.

same level. Inferior appendage broadly triangular, apex rounded; with a band of black peglike setae apically and on midbasal ridge. Phallus slender, threadlike.

Material.—Holotype ♂; Costa Rica. Alajuela 10°46′14″N, 85°16′86″W, P. N. Rincón de la Vieja, Quebrada Provisión, 4 Mar 1896, 810 m, Holzenthal and Fasth (USNM).

Etymology.—The species epithet, *vieja,*



Figs. 13–16. Male genitalia of *Ochrotrichia ramona.* 13, Left lateral view; 14, Dorsal view. Male genitalia of *Ochrotrichia quinealensis.* 15, Right lateral view; 16, Dorsal view.

is from the Spanish vieja in allusion to the name of the locality, Rincón de la Vieja Provision. The name is treated as a noun in apposition.

Ochrotrichia ramona, new species
Figs. 13–14

Diagnosis.—Because of the presence of

2 long curved spinelike processes and 1 midbasal spine on tergum X, *O. ramona* seems to be related to *O. palitla* Flint and *O. felipe* Ross. However, *O. ramona* can be distinguished from these species by the rectangular shape of the inferior appendage in lateral aspect.

Description of adult.—Length of forewing 2 mm. Color in alcohol stramineous. Male genitalia: Tergum IX deeply depressed dorsally; sternum IX with a posterodorsal lobe. Tergum X in dorsal aspect with a small, basodorsal spine at center and 2 long, slightly curved, spines; membranous process ventrally, slightly twisted, with apex clearly curved to left; in lateral aspect small basodorsal spine and 2 long sinuous spines appear straight; apical portion of membranous process curved ventrad apically. Inferior appendage in lateral aspect rectangular, broadest apically with dorsal and posterior margin rectangular; posterior margin with many black, peglike setae. Phallus well developed, simple with long apical tubule.

Material.—Holotype ♂; Costa Rica. Alajuela: Reserva Forestal San Ramón Río San Lorencito and trib. 10°12′96″N, 84°36′42″W, 30 Mar–1 Apr 1987, 980 m, Holzenthal, Hamilton, Heyn (USNM). Paratypes: same data as holotype, 7 ♂ (UMSP).

Etymology.—The species epithet, *ramona,* is from Spanish 'Ramona', feminine form of 'Ramón' in allusion to the name of the type locality, Reserva Forestal San Ramón. The name is treated as a noun in apposition.

Ochrotrichia quinealensis, new species
Figs. 15–16

Diagnosis.—Because of the presence of the spines on tergum X and the elongate and broad appearance of the inferior appendages in lateral view, *O. quinealensis* is related to *O. palitla* Flint. However, *O. quinealensis* can be easily distinguished by the presence, in dorsal view, of a heavy, dark, spinelike process on tergum X, a character not observed in *O. palitla.*

Description of adult.—Length of forewing 2 mm. Color in alcohol stramineous. Male genitalia: Sternum IX in lateral view with dorsolateral lobe; tergum IX, depressed and produced anteriad. Tergum X in dorsal view a broad, flat plate; at midlength with a heavy, basally-wide spinelike process, its apex dark and directed to right; on right side, a long, slender process ending before membranous apical section, with a dark apex curved to left; apical section with a short, slender, twisted spinelike process, with dark apex curved to right; in lateral view on right side, heavy, basally-wide, spinelike process has its dark apex curved upward; twisted spinelike process of apical section appears strongly curved ventrad and partially covered by a membranous hoodlike structure; on left side, heavy and wide spinelike process appears with its apex slightly curved to right, long and slender process looks like a wide plate with dark apex situated before apical section of tergum X, short, twisted, spinelike process of apical section seems to emerge from a hoodlike structure and is strongly curved ventrad; apical process ending in a spoonlike lobe. Inferior appendage in lateral view, elongate, broad, apex rounded, with an apical band of black peglike setae and 2, black peglike setae on midbasal ridge. Phallus long, threadlike.

Material.—Holotype ♂; Costa Rica. Puntarenas; Río Guineal, Ca. 1 km (air) E. Finca Helechales, 9°4′56″N, 83°5′52″W, 22 Feb 1986, 840 m, Holzenthal, Morse, Fasth, (USNM). Paratypes 2♂; Alajuela: Reserva Forestal San Ramón, Río San Lorencito and tribs. 10°12′96″N, 84°36′42″W, 30 Mar–1 Apr 1987, 980 m, Holzenthal, Hamilton, Heyn (UMSP).

Etymology.—The species epithet, *quinealensis,* refers to the Río Guineal, the type locality.

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A new species of the genus *Gastrosaccus* (Crustacea: Mysidacea: Mysidae) from Oman

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Abstract.—A new species, *Gastrosaccus trilobatus,* is described based on specimens from sandy beaches of Oman. The new species is distinguished from known species of the genus by the carapace and telson. The carapace is provided with 3 posteriorly directed lobes on the posterodorsal margin, and the telson is armed with 2 distal conspicuously large spines and 4 or 5 spinules inserted between them.

The genus *Gastrosaccus* was established by Norman in 1868, and now contains 17 species as far as we can determine. List of these species, in company with their localities, are shown in Table 1. It is distinguished from related genera by the third male pleopod with the styliform exopod and the multi-segmented endopod, the uniramous female pleopods except for the first pair which is biramous, and the labrum without accessory spines in both sides of the median spiniform process. The present new species was collected during an ecological study of sandy beaches in Oman, Arabian Peninsula, by one of the authors (AM). The type specimens are deposited in the Zoological Museum, University of Copenhagen.

Gastrosaccus trilobatus, new species
Figs. 1–3

Type series.—Holotype (CRU 3411), adult male (6.0 mm); allotype (CRU 3412), gravid female (7.3 mm); paratypes (CRU 2419), 1 adult gravid female (5.8 mm), 3 immature males (4.6, 3.5, 3.3 mm) and 1 immature female (3.5 mm); Khaluf, Oman, 20°25′N, 58°00′E, sandy beach, 6 November 1995, coll. A. McLachlan. Other paratypes (CRU 2420), 2 adult males (5.6, 6.5 mm), 1 adult female (5.5 mm) and 1 immature female (5.4 mm), Majis, Oman, 24°30′N, 56°40′E, sandy beach, 27 September 1995, coll. A. McLachlan; 2 specimens of which, male of 6.5 mm and adult female, were dissected for drawing.

Description.—Rostrum low triangular with narrowly rounded apex, somewhat bent downwards, covering basal part of eyestalks (Fig. 1A, B). Anterolateral corner of carapace rounded. Posterior margin of carapace deeply emarginate, leaving last thoracic somite uncovered dorsally, split in each side of emargination, overlapping with posterolateral margin; emarginated part furnished with 3 lobes, median lobe elongate triangular with pointed apex, side lobes bill-shaped, directed posteriorly, not reflected; posterior and posterolateral margins from side lobe to posterolateral angle weakly serrated (Fig. 1C). Posterolateral angle of carapace rounded, covering side of first abdominal somite.

Eye well developed; cornea as wide as or slightly wider than stalk (Fig. 1A, B).

Antennular peduncle of male more robust than that of female; first segment shorter than combined length of second and third segments, with 4 short setae at anterolateral

Table 1.—List and localities of 18 *Gastrosaccus* species.

Species	Localities	Authorities
G. australis W. M. Tattersall	New Zealand	W. M. Tattersall 1923
G. bispinosa Wooldridge	S. Africa	Wooldridge 1978
G. brevifissura O. S. Tattersall	S. Africa	O. S. Tattersall 1952, 1962
G. daviei Băcescu & Udrescu	NE Australia	Băcescu & Udrescu 1982
G. dunckeri Zimmer	Between Ceylon and New Guinea	Zimmer 1915
	India	W. M. Tattersall 1922, Pillai 1973
	E. Africa	O. S. Tattersall 1958
	Singapore waters	O. S. Tattersall 1960
	S. China Sea	Ii 1964
G. kempi W. M. Tattersall	India	W. M. Tattersall 1922
	S. Africa	O. S. Tattersall 1962 (as *G. gordonae*)
	Arabian Gulf	Murano (1998)
G. longifissura Wooldridge	S. Africa	Wooldridge 1978
G. mediterraneus Băcescu	Mediterranean	Băcescu 1970
G. msangi Băcescu	Tanzania	Băcescu 1975
G. namibensis Wooldridge & McLachlan	Namibia	Wooldridge & McLachlan 1987
G. olivae Băcescu	Orange River estuary	O. S. Tattersall 1955 (as *G. sanctus*)
G. psammodytes O. S. Tattersall	S. Africa	O. S. Tattersall 1958
G. robusta Panampunnayil	SE Australia	Panampunnayil 1989
G. roscoffensis Băcescu	France	Băcescu 1970, Nouvel 1972
G. sanctus (van Beneden)	Atlantic coasts of Europe and Africa, Mediterranean	Tattersall & Tattersall 1951
G. sorrentoensis Wooldridge & McLachlan	W. Australia	Wooldridge & McLachlan 1986
G. spinifer (Goës)	Atlantic coasts of Europe and Africa, Mediterranean	Tattersall & Tattersall 1951, Lagardère & Nouvel 1980
G. trilobatus, new species	Oman	Present record

corner; second segment shortest, wider than long, with 3 spines on dorsolateral surface and 1 short and 1 long setae at inner distal corner; third segment 1.5 times longer than wide, with 2 spinules on dorsal surface, noticeable digitate process present on dorsal surface near base of outer flagellum. Female antennular peduncle with first segment as long as second and third segments combined, second segment with 2 long and 1 short setae at outer distal corner. Outer flagellum with basal lobe fringed with sensory setae (Fig. 1A, B).

Antennal scale extending to distal end of second segment of antennular peduncle in male, slightly less in female, slightly more than 3 times longer than broad; lateral margin slightly convex, naked, terminating in spine extending to apex of scale, distal suture distinct (Fig. 1D). Antennal peduncle shorter than antennular peduncle, longer than antennal scale; second segment longest, more than twice longer than broad, armed on inner margin with 4 plumose setae of which distal one is longest and thickest; third segment 0.4 as long as second, with 3 plumose setae on inner margin of which distal one is longest and thickest (Fig. 1D).

Labrum longer than broad, with long median spiniform process (Fig. 1H). Mandibular palp slender, third segment $\frac{4}{5}$ of second segment in length (Fig. 1E). Maxillule and maxilla as shown in Fig. 1F and G, respectively. Hook-shaped anteromedian process present on ventral side of clypeus (Fig. 1I).

First and second thoracic limbs with endopod rather slender (Fig. 2A, B). Endopods of third to eighth limbs similar in shape, ischium longer than merus, ischium

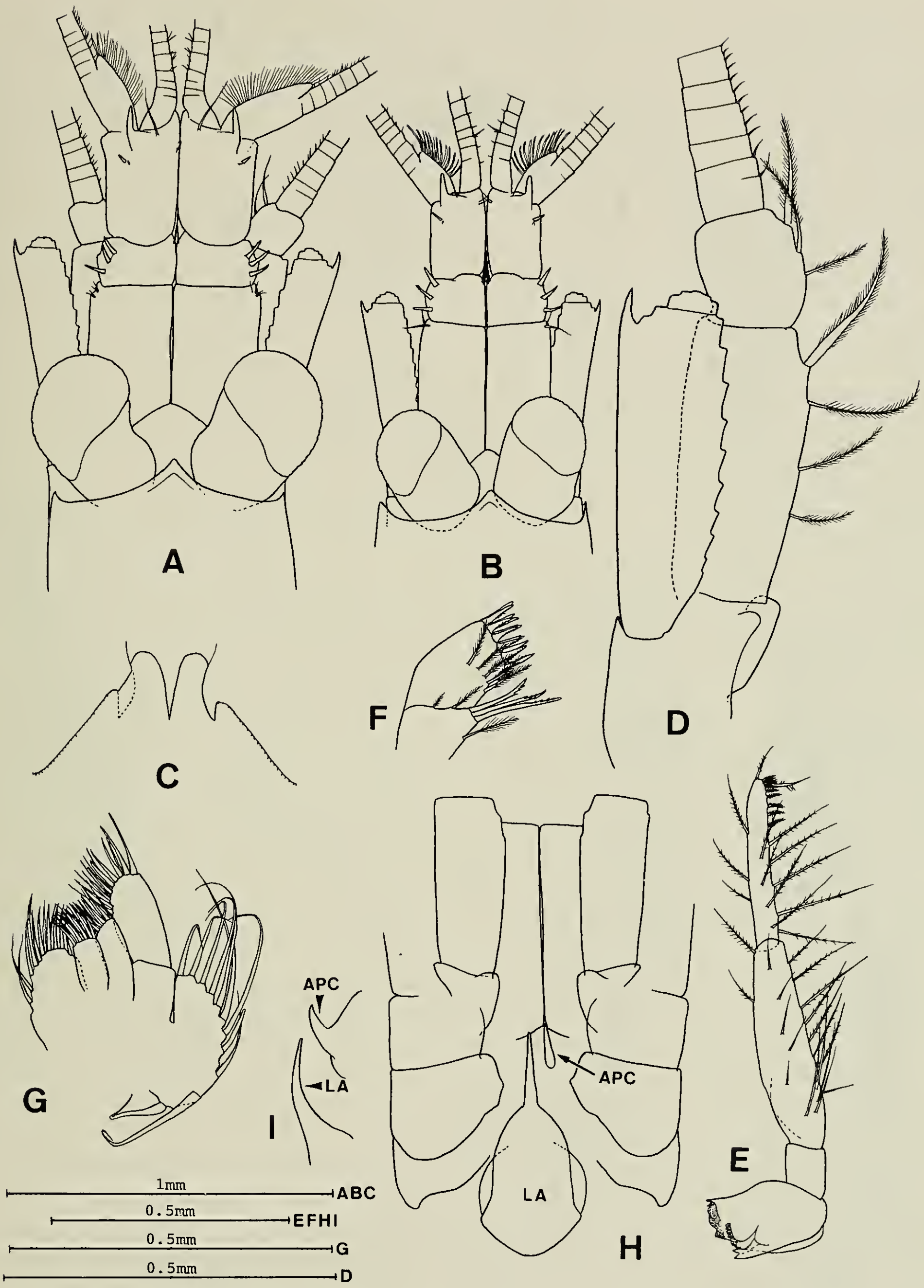

Fig. 1. *Gastrosaccus trilobatus,* new species, A, D, E, G, I, male (6.5 mm); B, C, F, H, female (5.5 mm). A, anterior end in dorsal view; B, anterior end in dorsal view; C, posterodorsal margin of carapace; D, antenna; E, mandible and mandibular palp; F, maxillule; G, maxilla; H, anterior end in ventral view; I, anteromedian process of clypeus (APC) and anterior part of labrum (LA) in lateral view.

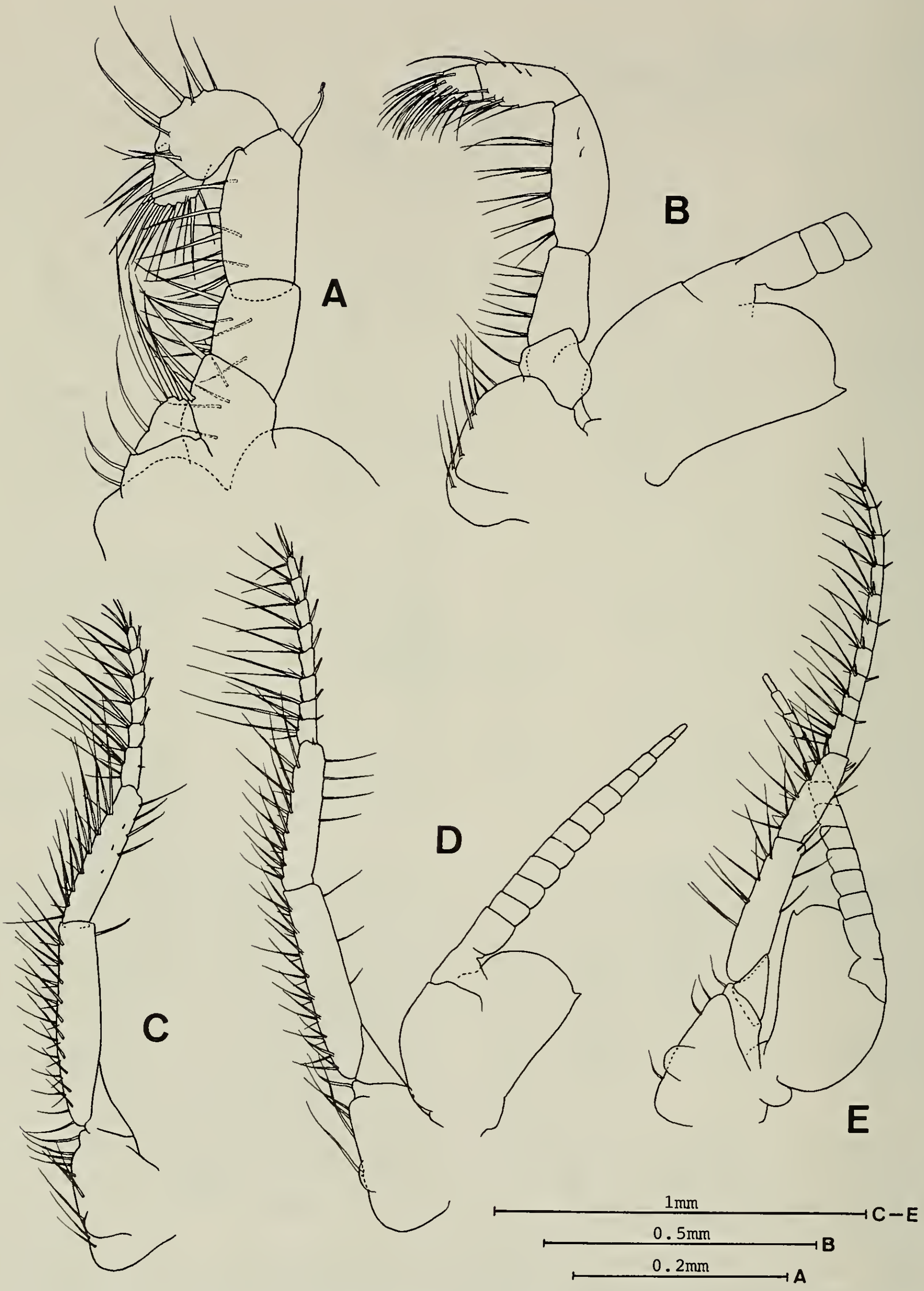

Fig. 2. *Gastrosaccus trilobatus,* new species, male (6.5 mm). A, endopod of first thoracic limb; B, endopod and proximal part of exopod of second thoracic limb; C, endopod of third thoracic limb; D, fifth thoracic limb; E, seventh thoracic limb.

and merus shortened and carpopropodus lengthened toward posterior pairs, carpopropodus subdivided into 6 to 10 subsegments increasing in number toward posterior pairs (Fig. 2C–E). Basal plate of thoracic exopods with distolateral corner pointed in second to seventh limbs (Fig. 2B, D, E) and rounded in first and eighth limbs. Flagella of thoracic exopods 10-segmented in first limb, 11 in second and third, 12 in fourth to eighth (Fig. 2D, E).

Abdomen with second and third somites shortest, fifth somite 1.5 times longer than fourth, sixth somite 1.2 times longer than fifth.

All pleopods of male biramous. First pleopod with 8-segmented exopod and unsegmented endopod, sympod with 9 plumose setae along lateral margin (Fig. 3A). Second pleopod with 7-segmented endopod and 8-segmented exopod, exopod much broader and longer than endopod, distal 3 segments extending beyond apex of endopod, each of proximal 4 segments armed at outer distal corner with thick seta, proximal part of which has undulate outer margin (Fig. 3B). Third pleopod: exopod extremely elongate, styliform, exceeding distal end of sixth abdominal somite, 4-segmented, first segment longest, indistinctly divided into about 4 subsegments, second segment as long as third and fourth segments together, second and third segments unarmed, fourth (distal) segment shortest, 0.37 as long as third, armed with 2 strong, subequal, barbed setae on distal end and short seta on distal third of lateral margin; endopod 6-segmented, extending beyond middle of first segment of exopod (Fig. 3C). Fourth pleopod with unsegmented endopod and 8-segmented exopod (Fig. 3D). Fifth pleopod allied to fourth but slightly smaller, endopod unsegmented, exopod 7-segmented (Fig. 3E). Female pleopods: first pleopod biramous, endopod unsegmented, shorter than exopod, with naked seta at tip; exopod unsegmented, with 3 plumose setae on distal end; sympod cylindrical, outer margin with 2 long setae near proximal end and 3 setae on distal end (Fig. 3F). Second to fifth pleopods uniramous, slender (Fig. 3G).

Endopod of uropod longer than exopod, with 8–10 strong spines on ventral inner margin from statocyst region to near distal end. Exopod of uropod truncate distally, as long as telson, armed along lateral margin with 12 strong spines arranged regularly (Fig. 3I).

Telson slightly longer than last abdominal somite, 2.3 times as long as maximum width at base; cleft more than ⅙ of telson length, armed with 15–20 spinules on either side; each apex of distal lobes with 1 strong spine; lateral margin nearly straight, with 6–7 large spines, distal one conspicuously larger than others and slightly larger than apical spine; 5 and 1 spinules inserted between apical spine and distal conspicuously large lateral spine and between fourth and fifth large spines, respectively (Fig. 3H); single spine present on median anteroventral line.

Etymology.—Derived from 3 lobes on the posterodorsal margin of the carapace.

Remarks.—In the new species the telson bears spinules between the apical spine and the distal spine of the lateral margin. To date, such a telson is recorded in 5 species of the genus *Gastrosaccus, G. bispinosa* Wooldridge, 1978, *G. brevifissura* O. S. Tattersall, 1952, *G. kempi* W. M. Tattersall, 1922, *G. longifissura* Wooldridge, 1978, and *G. msangi* Băcescu, 1975. The new species is easily distinguished from them by the 3 lobes on the posterodorsal margin of the carapace and the 2 conspicuously large distal spines on the telson.

There are intraspecific variations in the depth of the apical cleft and the armature on the lateral margin of the telson. In an adult female (5.8 mm) from Khaluf, the apical cleft of the telson is shallower (about ⅐ of telson length), more divergent posteriorly and the spinules are fewer in number. Moreover, the lateral margin of the telson is armed with 7 large spines, and the number of inserted spinules is one each in spaces between fourth and fifth, fifth and sixth,

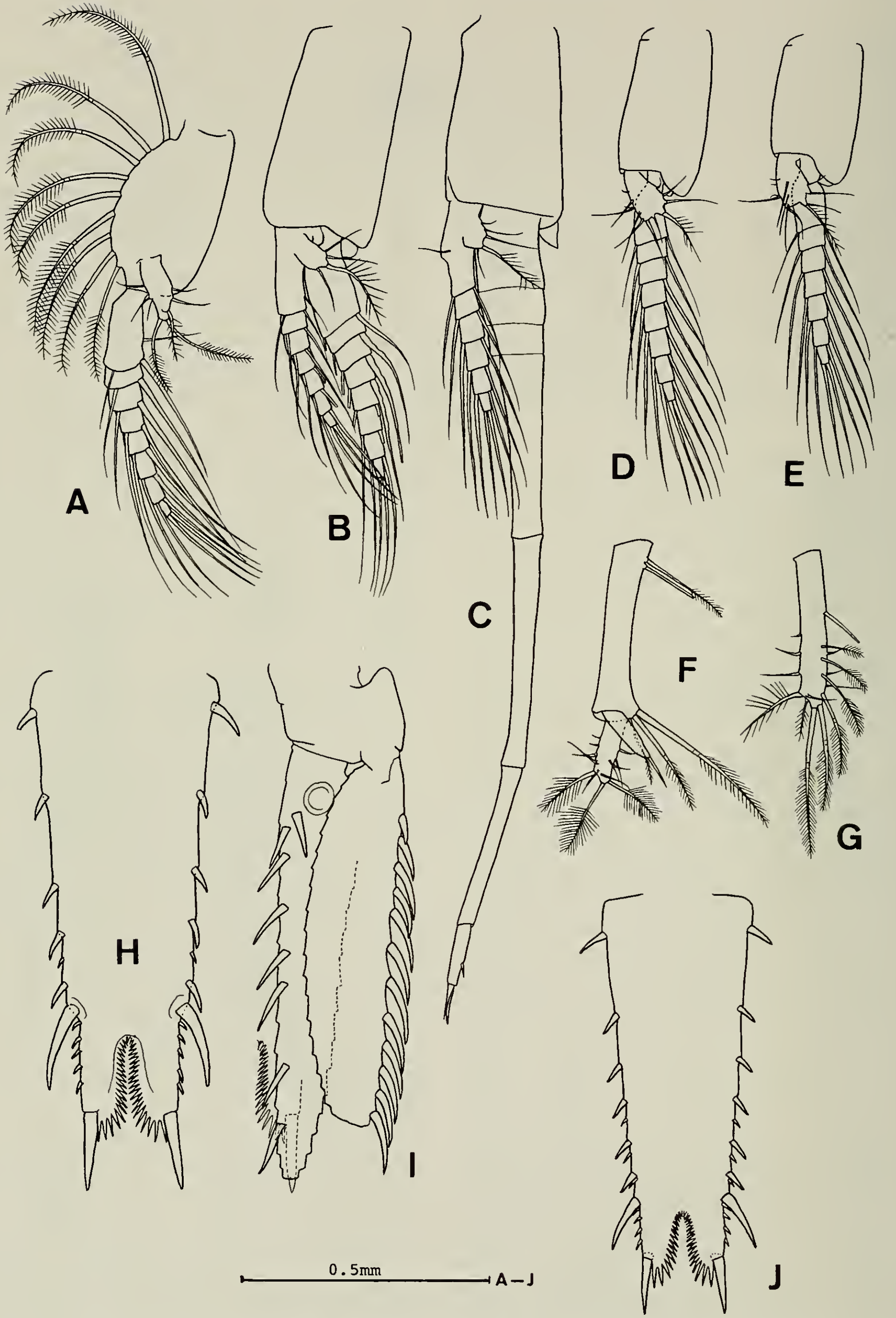

Fig. 3. *Gastrosaccus trilobatus,* new species, A–E, H, I, male (6.5 mm); F, G, female (5.5 mm); J, female (5.8 mm). A, first pleopod; B, second pleopod; C, third pleopod; D, fourth pleopod; E, fifth pleopod; F first pleopod; G, third pleopod; H, telson; I, uropod in ventral view; J, telson.

and sixth and seventh large spines and 4 in the space between the seventh and apical spines (Fig. 3J).

A prominent spine on the median line of the anteroventral surface of the telson was found in the new species. A similar spine was reported for *Gastrosaccus sorrentoensis* and *G. psammodytes.* As noted by Wooldridge & McLachlan (1986), it may be a common character in the genus *Gastrosaccus.*

Ecological note.—*Gastrosaccus trilobatus* was found on all 10 beaches surveyed in Oman in numbers ranging from 54–4128 per meter transect and up to 300 individuals/m^2. It tended to be more common on the most exposed beaches. Intertidal distribution of the mysids during low tide was across the saturated lower shore and into the surf zone. Numbers peaked between the mid tide and spring low tide levels. The beaches in Oman have fine sand and are mesotidal with a maximum tide range of 3 m. Wave energy is low except in the south. Water temperature and salinity on the sampling days were 27–33°C and 31–36 PSU, respectively. More ecological information is forthcoming.

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A new species of amphipod (Crustacea: Amphipoda: Lysianassoidea) from the Pacific Coast of North America

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Abstract.—A new species of lysianassoid amphipod, *Lepidepecreum serraculum,* is described. This species possesses a distinctive rudder-shaped convex carination of urosomite 1 that combined with a slightly carinate antenna 1, chelate gnathopod 2, and rounded corners of the epimera, distinguishes it from other species of *Lepidepecreum.* It occurs in a variety of substrata subtidally to 150 m depth from the Mexican–American border to Alaska.

An undescribed species of the lysianassoid amphipod *Lepidepecreum* has been encountered regularly in sublittoral surveys conducted in southern California during the past 20 years. This species was first recognized by Barnard (1969) who compared it with several *Lepidepecreum* species including *Lepidepecreum gurjanovae* Hurley, 1963. Barnard, noting that his specimens differed morphologically from *L. gurjanovae* and occurred in much shallower water, listed his material as *Lepidepecreum* ? *gurjanovae* pending further study. Subsequently, during Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) workshops conducted with the late J. Laurens Barnard, the species was recognized as distinct, both morphologically and ecologically. It was listed as *Lepidepecreum* sp. A prior to formal description (SCAMIT 1996).

Lepidepecreum serraculum, new species
Figs. 1–3

Material examined.—All specimens have been deposited in the Los Angeles County Museum of Natural History. Holotype: male, Santa Monica Bay, City of Los Angeles, Environmental Monitoring Division, station DN8, 33°51.02′N, 118°25.00′W, 7 Feb 1986, 22 m depth, LACMNH No 86-523.1. Paratypes: Huntington Beach, California, County Sanitation Districts of Orange County Station B4, 17 Jul 1980, 33°34.54′N, 117°59.75′W, 60 m depth, one female, LACMNH No. 80-162.1, Station B0(1) 5 Feb 1980 33°34.67′N, 118°00.54′W 60 m depth, one female, LACMNH No 80-163.1, and Station Control(1), 15 Jan 1981, 33°35.95′N, 118°03.79′W, 60 m depth, one female, LACMNH No 81-240.1; Santa Monica Bay, City of Los Angeles, Environmental Monitoring Division Station D3, 33°51.78′N, 118°35.25′W, 24 Jan 1994, 78 m depth, one female, LACMNH No 94-90.1 and Station E8, 33°54.30′N, 118°36.43′W, 29 Jul 1993, 151 m depth, two males, LACMNH No 93-143.1.

Diagnosis.—Coxae and pereopods 5–7 ornamented with fine setules. Antenna 1, article 1 slightly carinated, callynophore present in males. Metasomite 3 with posterodorsal carina. Urosomite 1 with pronounced rudder-shaped carina. Mandible with moderately developed setulose molar. Maxilla 1 outer plate spines well developed. Gnathopod 2 minutely chelate. Pereopods 5–7 article 2 posterior margins moderately serrate. Epimeron 3 posterior margin straight with rounded posteroventral corner. Uropods and telson spinose.

Description.—Male, body smooth with thick white integument, metasomite 3 bearing posterodorsal carina, urosomite 1 with pronounced rudder-shaped carina (Figs. 1a, b). Coxae 1–4 longer than broad, slightly expanded distally (ventrally), partially covered with fine setules and bordered with many setules; coxa 4 excavate posteriorly.

Head subequal in length to first pereonite, lateral lobes of head strongly produced, elongate eyes with deep reddish-brown pigmented ommatidea in alcohol. Antenna 1 short; peduncle robust, article 1 dorsal margin carinate bearing plumose setae dorsally and on distoventral corner, article 2 half as long as article 1, article 3 one third as long as article 1; accessory flagellum with 4 articles; main flagellum longer than peduncle, article 1 with callynophore of aesthetascs as long as the accessory flagellum (Fig. 1c). Antenna 2 long, nearly as long as body length; 8 setae subapically on outer ventrolateral margin of peduncular article 3, articles 4 and 5 both possessing a row of setules on dorsal margin and single plumose seta on anteroventral corner; flagellum at least 60-articulate, the first 40 calceolate (Fig. 1d). Epistome broadly rounded produced above upper lip. Mandible with moderately developed setulose molar, row of raker spines, incisor well defined with convex cutting edge; palp proximal to molar, 3-articulate, article 1 short, article 2 long bearing distal spines, article 3 half as long as article 2 with inner and distal spines (Fig. 1e). Maxilla 1: inner plate bearing distal plumose setae and many fine hair-like setae; outer plate with 11 multicuspidate spine-teeth; palp 2-articulate, article 2 longer having small distal teeth and a seta (Fig. 1f). Maxilla 2: inner plate with row of fine hair-like setae on inner proximal margin, several setae and serrated spines on inner distal margin; outer plate bearing closely bundled setae and serrate spines distally (Fig. 1g). Maxilliped: inner plate with apical stout teeth and spines on distal margin and plumose setae along inner margin; outer plate bearing basal setae, peg-like spines along the inner margin and small facial spines adjacent to peg-like spines; palp 4-articulate, article 2 longest with setae on inner margin and a distal seta on outer margin, article 3 similar to article 2 though shorter and bearing several distal setae, article 4 covered with striations or possibly short setules (not illustrated), prominent apicomedial seta on outer margin and small terminal nail (Fig. 1h).

Gnathopod 1 subchelate; dactyl with proximal tooth that forms a bifid process; article 6 sub-rectangular with distal setae, palmar margin bearing 2 medial teeth, terminating with 2 or more spines, dactyl with subterminal tooth; article 5 subequal in length to article 6; articles 3 and 4 short, subequal with distal setae; article 2 as long as articles 3–6 combined bearing several setules along anterior margin and setae on distoposterior corner (Fig. 2a). Gnathopod 2 minutely chelate; dactyl small, triangular bearing a single seta; article 6 anterior margin convex bearing 3 rows of serrate setae, lower margin straight, terminating in tooth armed with small spines; article 5 twice as long as article 6, anterior margin convex with many fine setules and setae distally, posterior margin expanded distally covered with a rasp of many scales; article 4 shorter than article 5, expanded distally with prominent anterior setae; article 3 length subequal to article 5; article 2 length subequal to combined length of articles 3–6 (Fig. 2b). Pereopod 3 simple; locking spines on distal end of article 6, article 4 expanded along anterior margin (Fig. 2c). Pereopod 4 similar to pereopod 3 in size and shape (Fig. 2d). Pereopod 5 shorter than pereopods 3 and 4; article 4 expanded distoposteriorly, lobe reaching over nearly half of article 5; article 2 ovoid, covered with fine setules, posterior margin moderately serrate; coxa subquadrate, covered with fine setules and short spines (Fig. 2e). Pereopod 6 length subequal to pereopod 5; article 4 expanded distoposteriorly; article 2 ovoid with posterior margin moderately serrate (Fig. 2f). Pereopod 7 shorter than pereopods 5 and 6; article 4 also expanded distoposteriorly; article 2 subquadrate, length

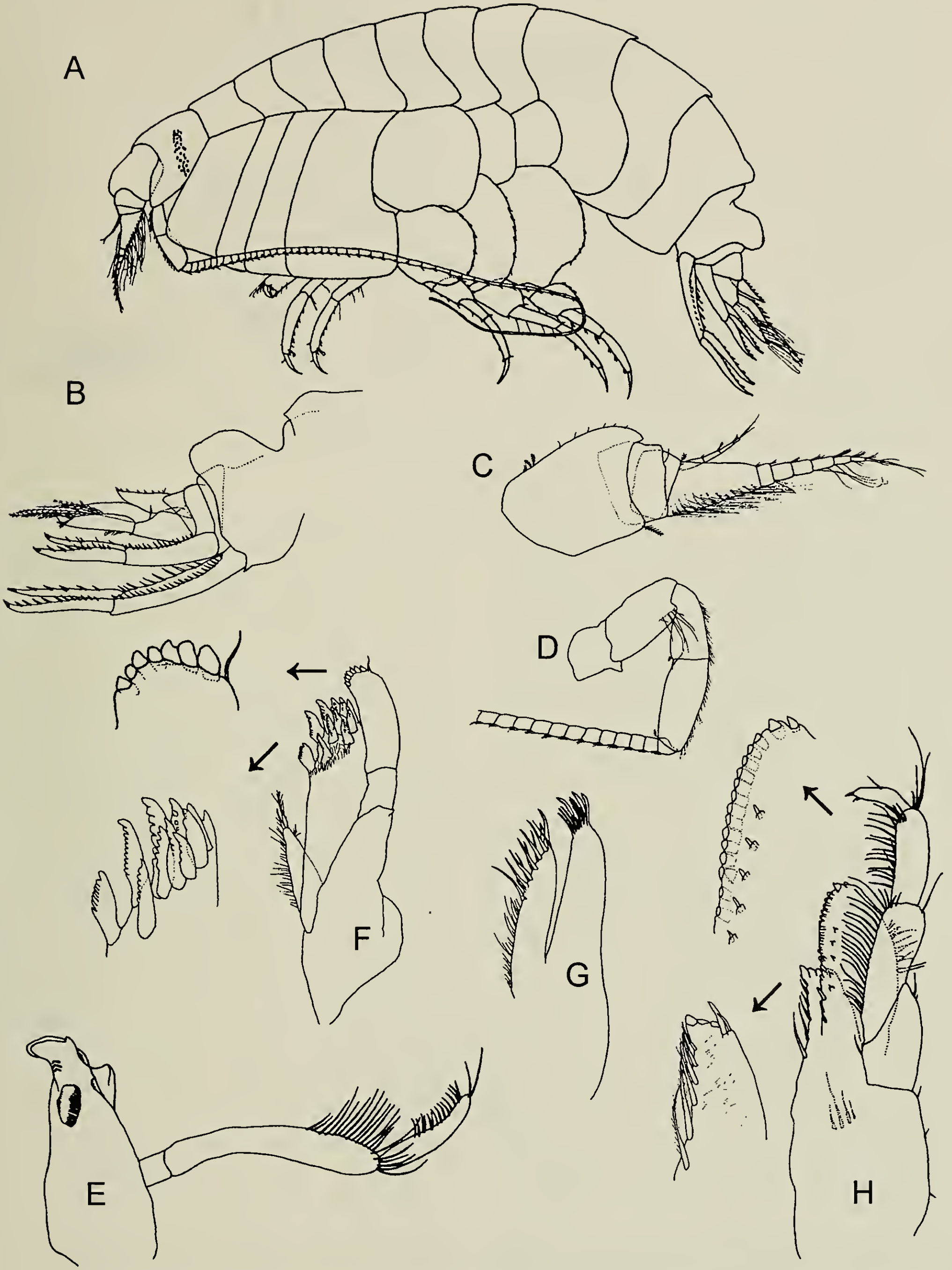

Fig. 1. *Lepidepecreum serraculum,* new species: a, entire holotype with antenna 2 placed outside coxal plates to illustrate relative length; b, urosome; c, antenna 1; d, antenna 2; e, mandible; f, maxilla 1; g, maxilla 2; h, maxilliped.

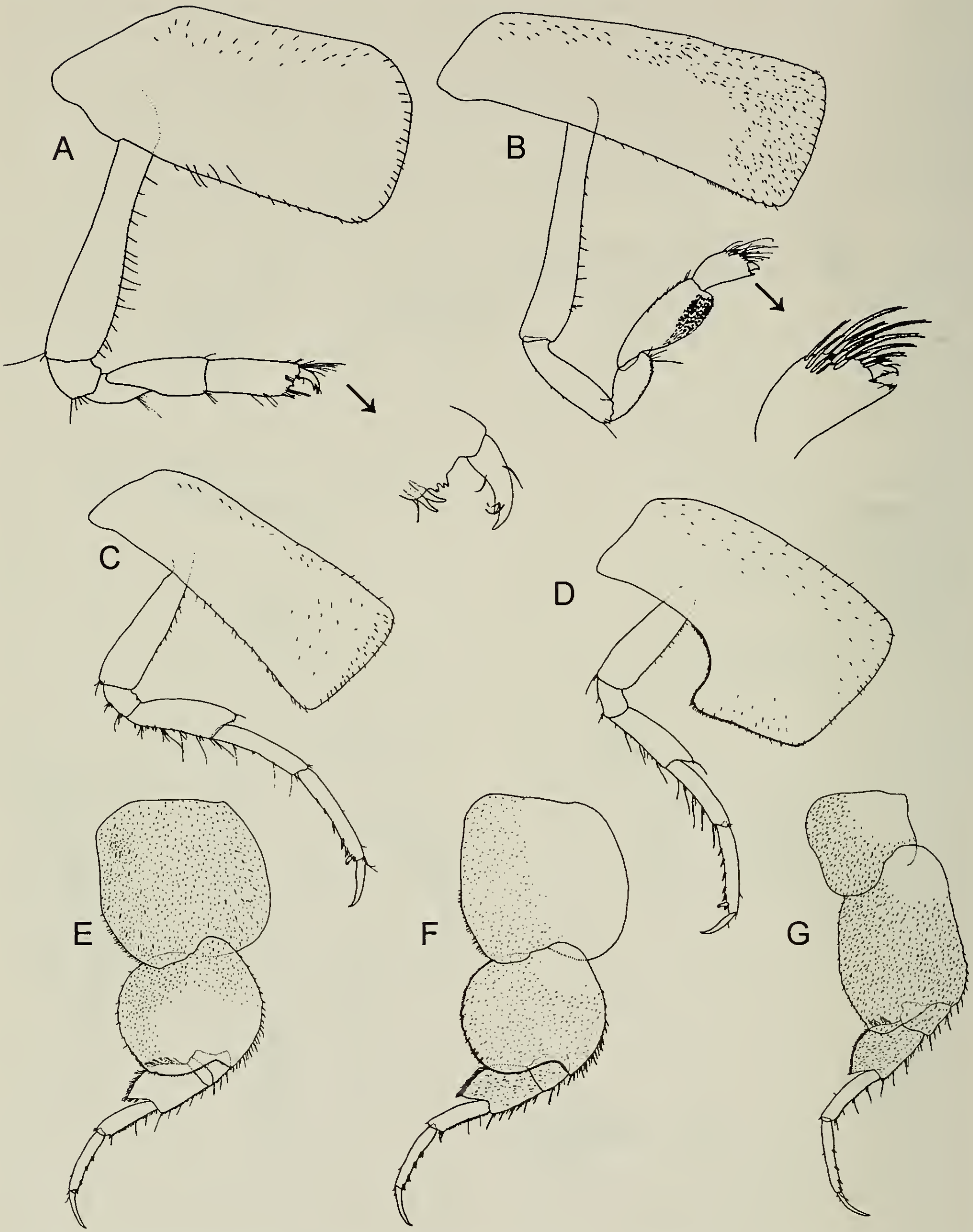

Fig. 2. *Lepidepecreum serraculum,* new species: a, gnathopod 1; b, gnathopod 2; c, pereopod 3; d, pereopod 4; e, pereopod 5; f, pereopod 6; g, pereopod 7.

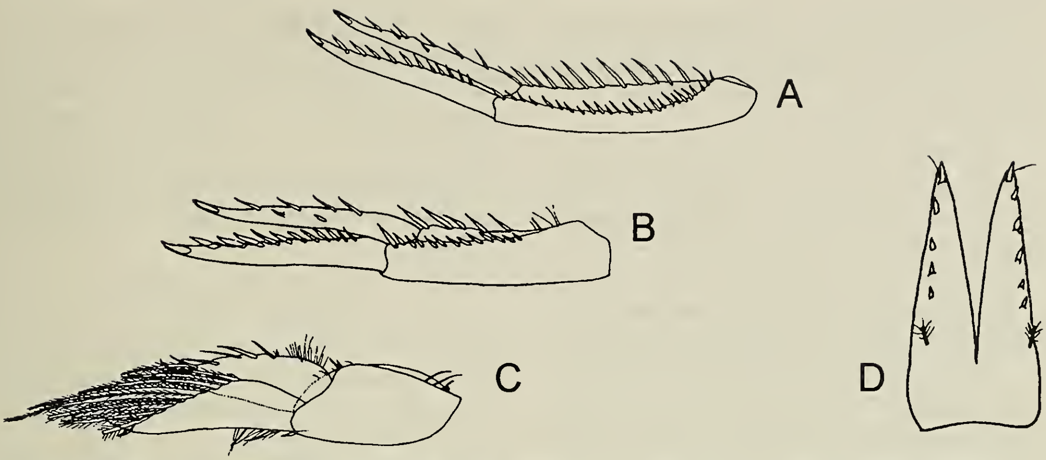

Fig. 3. *Lepidepecreum serraculum,* new species: a, uropod 1; b, uropod 2; c, uropod 3; and d, telson.

subequal to articles 4–7 combined, posterior margin moderately serrate with small, distoposterior excavation that varies in degree among and within individuals (Fig. 2g).

Epimera 1–2 posteroventrally convex; epimeron 3 (Fig. 1a) posterior margin straight with rounded posteroventral corner. Uropod 1 long; peduncle dorsally excavate with spinose margins; spinose rami slightly shorter than peduncle, both with spines and subterminal nail (Fig. 3a). Uropod 2 shorter than uropod 1; peduncle dorsally excavate with spines and setules on margins; rami spinose and subequal in length, both with subterminal nail (Fig. 3b). Uropod 3 peduncle shorter than uropod 1 peduncle, deeply excavate dorsally with setae on outer face and spines on medial margin; inner ramus subequal to peduncle in length, foliaceous, bearing setules on the proximal-lateral margin and spines on the apicolateral margin; outer ramus longer, foliaceous with many plumose setae on beveled apicolateral margin (Fig. 3c). Telson as long as uropod 3 outer ramus, longer than broad, incised three-fourths of its length, each lobe tapering distally, each with small apical plumose seta, apical spines and subterminal spine and setule (Fig. 3d).

Female, non-ovigerous: Like male but antenna 1 short, flagellum only 6-articulate, lacking callynophore; antenna 2 lacking calceoli; uropod 2 lacking plumose setae.

Remarks.—Other species differ from *L. serraculum* in cuticle ornamentation, body and antenna 1 carination, gnathopod chelation, pereopods 5–7 serration, uropod and telson spination. *Lepidepecreum serraculum* is most similar to *L. gurjanovae* which differs from the former by possessing forward directed carination on article 1 of the first antennal peduncle, a sub-chelate gnathopod 2, carination on all pereonites, subrectangular epimeron 3 pleon epimeron, and upturned carination of urosomite 1 (Hurley 1963). Although their geographic ranges overlap in the northeastern Pacific, the species are separated bathymetrically (*Lepidepecreum serraculum* subtidal to 150 m, *L. gurjanovae* >260 m). Another northeastern Pacific species *L. garthi* differs from *L. gurjanovae* by the absence of eyes, forward directed carina on article 1 of the first antennal peduncle, pronounced carination on all body segments, subchelate gnathopod 2, and fewer uropod and telson spines (Hurley 1963). Other northeastern Pacific species *L. comatum* and *L. vitjazi* differ from *L. serraculum* by possessing a coarser cuticle ornamentation; *L. alectum* and *L. kasatka* by lacking carination on antenna 1; *L. eoum* and *L. rostratum* by possessing greater body carination; and *L. nau-*

tilus and *L. umbo* in differing body carination and by lacking uropods and telson spines (Gurjanovae 1962, Hirayama 1985, Barnard and Karaman 1991).

A freshly preserved *Lepidepecreum serraculum* specimen had orange-pink dots at the base of coxal plates 1–3 and 5; orange-pink dots on the dorsum of pereonites 1–9 including a band across pereonite 8.

Etymology.—The specific epithet *serraculum* is a Latin neuter noun, meaning rudder, and is placed in apposition with the generic name. It alludes to the easily recognizable rudder-shaped dorsal carina on urosomite 1.

Distributional ecology.—This species occupies a wide range and variety of habitats. It occurs from the Mexican–American border and extends north along the Pacific Coast to Alaska. Typical specimens from southern California are 3 mm in length whereas those from northern range of distribution are twice as long (Norma Jarrett, pers. comm.). It is found in sediments ranging from fine (sandy silt) to coarse (red sands), off open ocean coast lines and in harbors. Depth range is from intertidal to 150 m.

Acknowledgments

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Metatiron bonaerensis, a new species (Crustacea: Amphipoda: Synopiidae) from the southwest Atlantic

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Abstract.–A new species, *Metatiron bonaerensis*, is described and illustrated from the south of Buenos Aires province, Argentine continental shelf, southwest Atlantic. The new species is assigned to *Metatiron* based on the absence of mandibular palp. *M. bonaerensis* is separated from *Tiron tropakis* by the laterally smooth pleonites 1–3, protuberant forehead, quadrate coxa 7 and maxilla 1 inner plate shape. The relationship with other species of the genus is discussed. The material was dredged at different depths and the grain size of the sediment was determined for each sampling station.

The new species described here was discovered from the El Rincón area of the Argentine continental shelf (Buenos Aires province), approximately 39° to 40°S and 61° to 62°W. Benthic samples were collected using a Van Veen dredge during the survey carried out by the R/V *El Austral* in 1993.

The type specimens are deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN).

Metatiron Rabindranath, 1972
Metatiron bonaerensis, new species
Figs. 1–49

Holotype.—Male 6.75 mm (MACN 34004), El Rincón, Buenos Aires: 39°39′40″S, 61°50′01″W (sta 24); depth 15 m; 2 Nov 1993.

Allotype.—Ovigerous female 9.6 mm (MACN 34005), El Rincón, Buenos Aires: 39°25′10″S, 61°34′57″W (sta 19); depth 18 m; 69% fine sand; 3 Nov 1993.

Paratypes.—1 male ca. 5.0 mm, 1 juvenile ca. 2.0 mm (MACN 34006), El Rincón, Buenos Aires: 39°05′36″S, 61°20′11″W (sta 3); depth 9.5 m; 78% medium sand; 3 Nov 1993. 1 ovigerous female 6.0 mm (MACN 34007), El Rincón, Buenos Aires: 39°20′08″S, 61°25′02″W (sta 15); depth 19 m; 69% fine sand; 3 Nov 1993. 1 immature female ca. 4.0 mm (MACN 34008), El Rincón, Buenos Aires: 39°30′07″S, 61°34′58″W (sta 22); depth 18 m; 75% fine sand; 3 Nov 1993. 1 female with oostegites ca. 6.0 mm, 1 immature male 6.0 mm (MACN 34009), same data as holotype. 1 ovigerous female 5.8 mm (MACN 34010), El Rincón, Buenos Aires; 39°40′07″S, 61°35′05″W (sta 25); depth 19 m; 67% fine sand; 2 Nov 1993.

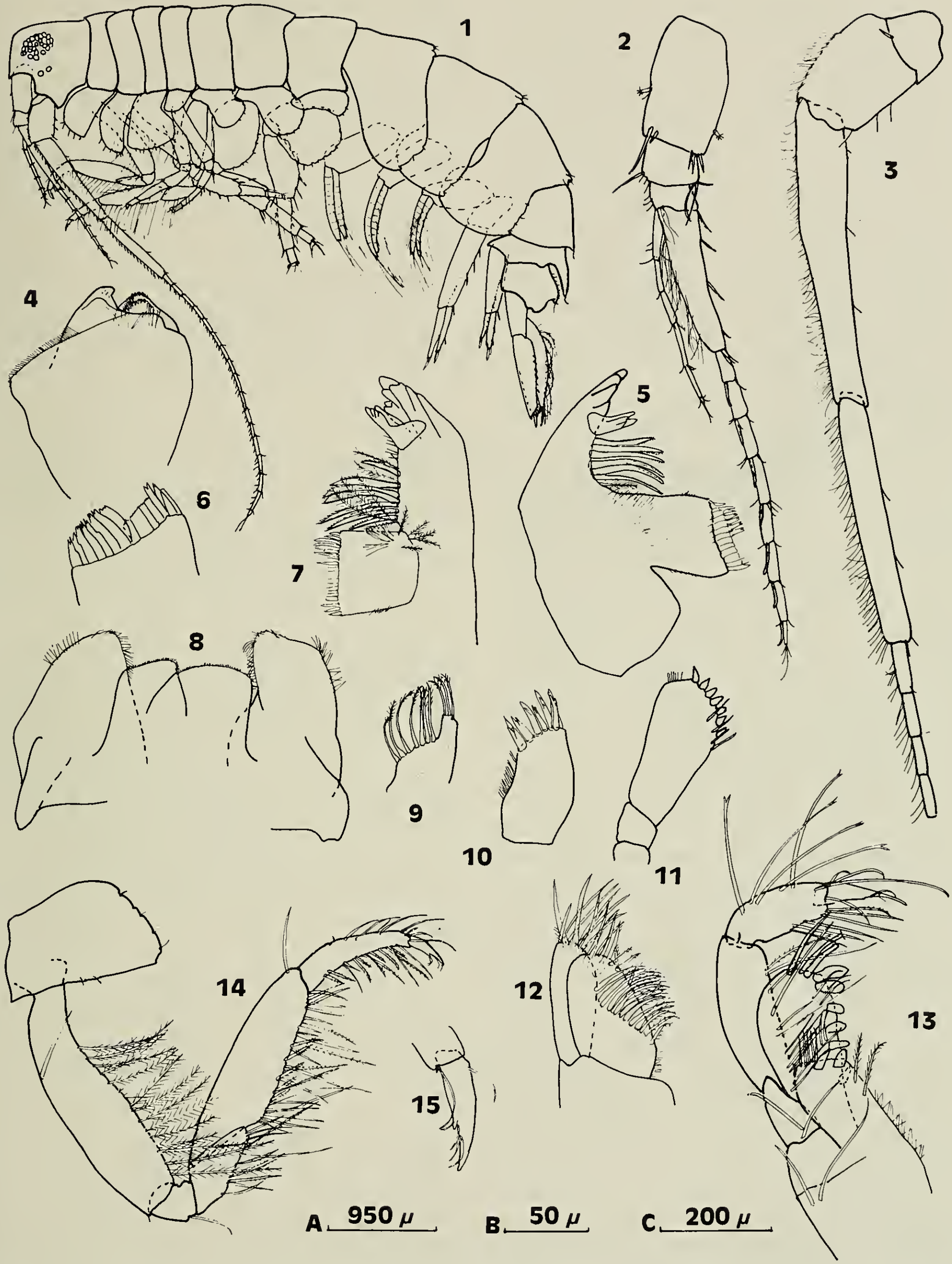
Description.—Male holotype, body length 6.75 mm. Head about as long as first 3 peraeonites combined; forehead protuberant, dorsal margin forming right angle anteriorly; rostrum short, pointing acutely over base of antenna 1; lateral cephalic lobe moderately produced. Eyes well-developed, of medium size; accessory eye composed of 2 separated ommatidia (Fig. 1). Antenna 1 somewhat shorter than peduncle of antenna 2; peduncle article 1 broad, longer than peduncle articles 2 and 3 combined, with single distal spine anteriorly, which is as long as peduncle article 2; peduncle article 2 about one-third as long as peduncle article 1; peduncle article 3 shorter than article 2, almost one-half the length of this latter; flagellum with 9 articles, article 1 elongate about one-third the length of flagellum, bearing fringe of setae; accessory flagellum with 6 articles, slightly longer than flagellum articles 1 and 2 combined (Fig. 2). Antenna 2 elongate, about as long as the body; peduncle articles with fine setae anteriorly; peduncle articles 4 and 5 very long, subequal in length; flagellum with 17 articles (Fig. 3). Upper lip and epistome as figured (Fig. 4). Mandible without palp; incisor with 4 teeth on right mandible and 2 more accessory teeth on the left; molar prominent, columnar, with triturating surface and plumose setae; lacinia mobilis large and dentate; spine row consisting of 6 spines subequally elongate on right mandible and 7 spines on the left mandible, being one of them shorter than the other ones (Figs. 5–7). Lower lip with well-developed mandibular lobes, inner lobes present and separate from each other (Fig. 8). Maxilla 1, inner plate fully setose, bearing 3 setae at the apex separated from the rest of medial setae by a smooth acclivity (Fig. 9); outer plate with 7 apical spines (Fig. 10); palp carrying 7 terminal tooth-spines and 4 subterminal setae (Fig. 11). Maxilla 2, inner plate broader than outer with dense medial and submarginal setal row (Fig. 12). Maxilliped as illustrated (Fig. 13).

Gnathopods 1 and 2 similar, simple; propodus thin, about 0.5 length of carpus, posterior margin with pectinate spines; dactylus bearing inner tooth. Gnathopod 1, coxa distally expanded; basis shorter than the next 3 articles combined, slightly broader medially, with long plumose setae along anterior margin; carpus elongate, posterior margin with pectinate spines (Figs. 14, 15). Gnathopod 2, coxa narrow; basis about as long as the next 3 articles combined, almost straight, with long plumose setae on distal half of anterior margin and along posterior margin; carpus elongate, posterior margin armed with spines and long plumose setae (Figs. 16, 17). Peraeopods 3–7, propodus short and broad; dactylus stubby and bearing an inner tooth. Peraeopods 3 and 4 small (Figs. 18–21), similar except for coxa; coxa of peraeopod 3 large, distally expanded and posteriorly with a lobe; coxa of peraeopod 4 small, short and broad; dactylus of both appendages imbeded in end of propodus, forming a subspherical disk with hooked tooth, a long seta matching curve of hook, and an accessory small spine at base of hook. Peraeopods 5 and 6 similar; coxa with posterior lobe; basis ovate, longer than wide, with distal posterior lobe (Figs. 22–25). Peraeopod 7, coxa nearly oval; basis broader than long, almost quadrate, weakly crenellate posteriorly; merus broader than on peraeopods 5 and 6 (Figs. 26, 27). Peraeopods 5–7, dactylus not spherical basally and only hooked distally.

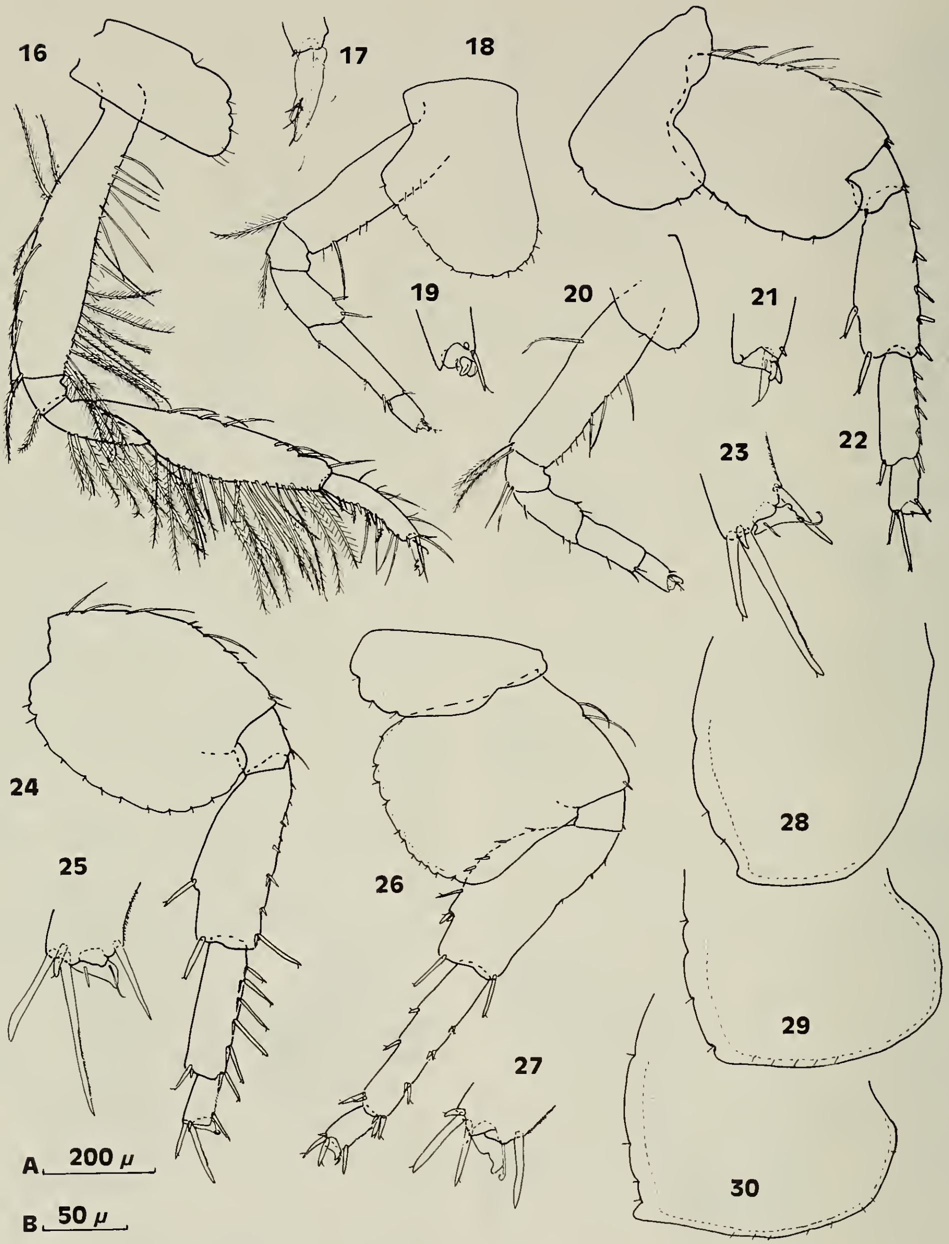
Pleonal epimera 1–3, posteroventral corners slightly produced, posterior margins bearing some notches with setules (Figs. 28–30). Pleonites 1–3 crenellate posteriorly on dorsal edge, crenellations superimposed, almost indistinguishable, small and rounded; lateral segmental margins evenly smooth (Fig. 31).

Urosomites 1 and 2 with medium and large dorsal teeth, respectively; urosomite 3 with dorsal hump. Uropod 1 elongate, peduncle much longer than rami; rami subequal in length (Figs. 32, 33). Uropod 2 shorter than uropod 1, peduncle slightly longer than inner ramus; outer ramus shorter than inner ramus (Figs. 34, 35). Uropod 3, peduncle broad and short; rami subequal in length, elongate, apically obliquely truncate (Figs. 36, 37). Telson long and slender, cleft almost to base, with short dorsal spines sparsely distributed in medial row and 1 terminal longer spine on each lobe (Figs. 38, 39).

Allotype, ovigerous female, body length 9.6 mm. Similar to holotype, but differs from it as follows. Eyes smaller (Fig. 40). Antenna 1, peduncle articles 1–3 longer; flagellum article 1 short (Fig. 41). Antenna 2 much shorter. Mandibles, spine row bearing 9 spines. Maxilla 1, inner lobe with more numerous medial setae (Fig. 42). Maxilliped as that of holotype: inner plate



Figs. 1–15. *Metatiron bonaerensis,* new species. Holotype, adult male. 1, Lateral view; 2, 3, Antennae 1, 2; 4, Upper lip; 5, Right mandible; 6, Right molar; 7, Left mandible; 8, Lower lip; 9, Inner plate of maxilla 1; 10, Outer plate of maxilla 1; 11, Palp of maxilla 1; 12, Maxilla 2; 13, Maxilliped; 14, Gnathopod 1; 15, Dactylus of gnathopod 1. Scales: A, Fig. 1; B, Figs. 4–13, 15; C, Figs. 2, 3, 14.



Figs. 16–30. *Metatiron bonaerensis*, new species. Holotype, adult male. 16, Gnathopod 2; 17, Dactylus of gnathopod 2; 18, Peraeopod 3; 19, Dactylus of peraeopod 3; 20, Peraeopod 4; 21, Dactylus of peraeopod 4; 22, Peraeopod 5; 23, Dactylus of peraeopod 5; 24, Peraeopod 6; 25, Dactylus of peraeopod 6; 26, Peraeopod 7; 27, Dactylus of peraeopod 7; 28–30, Epimera 1–3. Scales: A, Figs. 16, 18, 20, 22, 24, 26, 28–30; B, Figs. 17, 19, 21, 23, 25, 27.

with 2 apical tooth-like spines and several submarginal plumose setae; outer plate broad, carrying 3 apical long spines, 6 short, stout medial spines and submarginal setae; palp slender, with 4 articles, article 4 almost as long as article 3, bearing a distal nail (Figs. 43, 44).

Peraeopods 3–7 similar, but bearing more setae.

Pleonal epimera 1 and 3, posteroventral corners more rounded than male Fully developed oostegites elongate, narrow, marginally setose, attached to coxae 2–5 (Fig. 45).

Urosomites 1 and 2 dorsally less elevated than in male; urosomite 3 without dorsal hump (Fig. 46). Telson with numerous longer dorsal spines arranged in row on each lobe; one lobe bearing 2 subapical spines, other lobe with 1 subapical spine (Figs. 47–49).

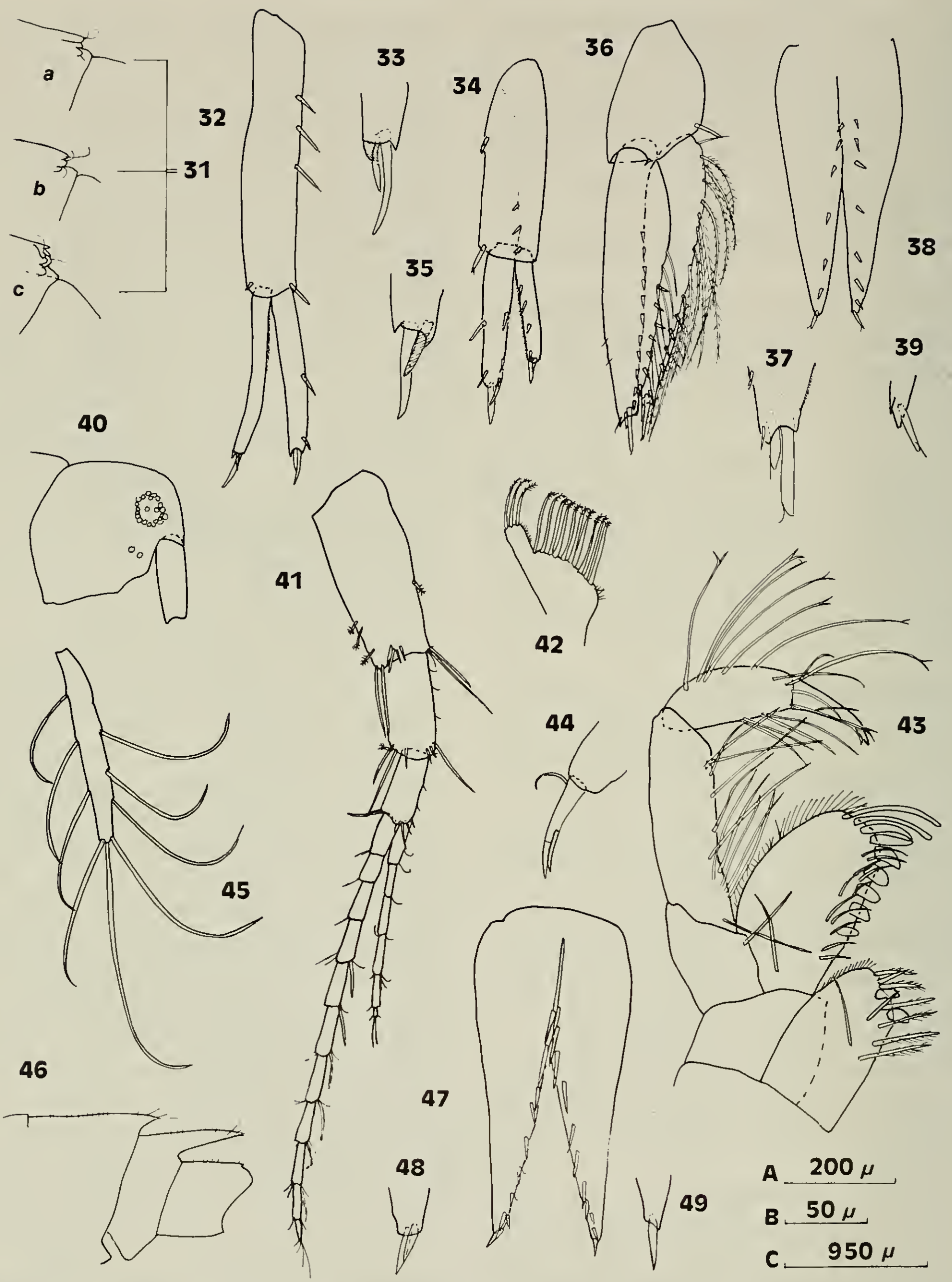
Paratypic males and females at different stages of maturity; general appearance of pleonites 1–3 and urosomites 1–3 as in holotype and allotype; no morphological variations were observed.

Habitat.—The specimens were dredged from sand bottom, at depths of 9.5–19 m. Fine grain size sand prevailed, but one sampling station contained a high percentage of medium grain size sand. No fractions of lime or clay were found (salinity 32.46–33.05‰; temperature 14.1–15.4°C).

Etymology.—The species is named in reference to the biogeographical zone, the Bonaerensian district, where the specimens were found.

Remarks.—The new species, *Metatiron bonaerensis,* is assigned to the genus *Metatiron* Rabindranath, 1972, based on the absence of mandibular palp. Barnard (1972) in his review of the family Synopiidae described the genus *Tiron* Liljeborg, 1865, mentioning the presence of a mandibular palp; he made a brief diagnoses of all its known species; some of them had a mandibular palp while others [like *T. brevidactylus* (Pillai 1957) and *T. tropakis* Barnard 1972] the palp was absent, or its condition was unknown. More recently, other authors including Just (1981), Goeke (1982) and Hirayama (1988) have placed new species that lacked a palp on the mandible in *Tiron.* Barnard & Karaman (1991) diagnosed the genera *Metatiron* and *Tiron,* but did not allocate species to *Metatiron*; these authors separated both genera by the absence of a mandibular palp and the presence of mid-dorsal tooth on pleonites 1–3 in *Metatiron.* The new species described in this paper is assigned to *Metatiron,* primarily because of the absence of a palp on the mandible, and secondarily because of dorsal crenulations on pleonites 1–3. Ledoyer (1979) supported the proposal of Rabindranath (1972) that the lack of the palp in *Metatiron* was a character of generic value, as did Thomas (1993) in his identification manual for marine amphipods of South Florida.

Metatiron bonaerensis is most closely related to *Tiron tropakis* Barnard, 1972. They resemble each other in their general appearance; they have the accessory eye formed of two separate ommatidia, both lack the palp on the mandible, the peraeopods possess stubby dactyli, and the male and female telsons bear similar dorsal spines. *Metatiron bonaerensis* is easily distinguished from *T. tropakis* by the laterally smooth pleonites 1–3 which are serrated in the other species, and the forehead protuberance compared with the evenly rounded forehead in *T. tropakis*; in addition, coxa 7 is more quadrate in the new species, and maxilla 1 inner plate is morphologically different in both taxa. *Metatiron brevidactylus* (Pillai 1957) (transfered by Rabindranath 1972), *M. caecus* Ledoyer 1979, *M. triocellatus* (Goeke 1982) (transfered by Thomas 1993), *T. ovatibasis* Hirayama, 1988 and *T. galeatus* Hirayama, 1988 also lack a mandibular palp, but they can be separated from the new species as follows: *M. brevidactylus* has maxilla 1 inner plate small without setae and telson with only one spine at the middle of each lobe; *M. caecus, T. ovatibasis* and *T. galeatus* lack accessory eyes, whereas *M. triocellatus* has



Figs. 31–49. *Metatiron bonaerensis*, new species. Holotype, adult male. 31 (a–c), Pleonites 1–3; 32, Uropod 1; 33, Ramus tip of uropod 1; 34, Uropod 2; 35, Ramus tip of uropod 2; 36, Uropod 3; 37, Ramus tip of uropod 3; 38, Telson; 39, Apical lobe of telson. Allotype, ovigerous female. 40, Head; 41, Antenna 1; 42, Inner lobe of maxilla 1; 43, Maxilliped; 44, Fourth article of maxilliped; 45, Oostegite; 46, Urosomites 1–3; 47, Telson; 48, 49, Apical lobes of telson. Scales: A, Figs. 31, 32, 34, 36, 38, 41, 45, 47; B, Figs. 33, 35, 37, 39, 42–44, 48, 49; C, Figs. 40, 46.

accessory eyes composed of three ommatidia, instead of two as in *M. bonaerensis.*

Acknowledgments

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A new genus and species of "goneplacid-like" brachyuran crab (Crustacea: Decapoda) from the Gulf of California, Mexico, and a proposal for the use of the family Pseudorhombilidae Alcock, 1900

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Abstract.—A new genus and species of crab, *Bathyrhombila furcata,* are described from localities in the Gulf of California, western coast of Mexico. The new genus is close to *Pseudorhombila* H. Milne Edwards and belongs to a group of three genera tentatively assigned to the subfamily Pseudorhombilinae Alcock, 1900 by Guinot in 1969. The affinity of *Bathyrhombila,* new genus, with other genera of "Goneplacidae" (*Euphrosynoplax* Guinot, *Pseudorhombila* H. Milne Edwards, *Nanoplax* Guinot, *Oediplax* Rathbun, and *Chacellus* Guinot) is discussed, noting that they all represent primitive transitional forms between the cyclometopous and the catometopous abdomen-sternum organization, and a similar "xanthoid-goneplacid" facies. On the basis of these affinities, it is proposed that these six genera be included into the family Pseudorhombilidae Alcock, within the Heterotremata Guinot, 1977.

Resúmen.—Se describe un nuevo género y una nueva especie de cangrejo, *Bathyrhombila furcata,* recolectado en localidades de el golfo de California, costa oeste de México. El nuevo género se parece a *Pseudorhombila* H. Milne Edwards y pertenece a un grupo de tres géneros tentativamente asignados a la subfamilia Pseudorhombilidae Alcock, 1900 por Guinot en 1969. Se discute la afinidad de *Bathyrhombila,* nuevo género, con otros género de "Goneplacidae" (*Euphrosynoplax* Guinot, *Pseudorhombila* H. Milne-Edwards, *Nanoplax* Guinot, *Oediplax* Rathbun, y *Chacellus* Guinot), señalando que todos ellos representan formas primitivas de transición entre la organización abdomen-esternón cyclometopes y catametopes, y una apariencia similar de tipo "xanthoideo-goneplacideo". En base a estas afinidades, se propone que estos seis géneros sean incluídos en la familia Pseudorhombilidae Alcock, dentro del grupo de los Heterotremata Guinot, 1977.

Two common and widely distributed families of brachyuran crabs, the Xanthidae and Goneplacidae (sensu Balss 1957) have long been recognized as containing heterogeneous groups of genera (see Guinot 1970, 1977, 1978; Serène 1984; Williams 1984; Martin & Abele 1986). In the last twenty years, the organization of the Xanthidae sensu Balss has been subject to many changes. The concept of a superfamily Xanthoidea proposed by Guinot (1978) emphasized the sternal position of female openings ("sternitrèmes") coupled with the coxal or coxo-sternal position of male genital openings, thus relating the Xanthoidea with the heterotremateous arrangement (Heterotremata, as defined by Guinot 1977). Guinot (1978) insisted on the fact that among the Xanthoidea, two groups of families should be considered: one with male opening coxal, and another in which the male opening progressively migrates to a coxo-sternal position. In the later group, the evolutionary process is associated with a modification of the facies, which becomes goneplacid-like (Guinot 1978:266). Guinot (1978) also suggested that when all genera of Goneplacidae sensu Balss will have been reviewed, new families might be added to the second, goneplacid-like group of Xanthoidea (i.e., those genera with a coxo-sternal male openings).

A group of goneplacid-like brachyuran crabs presently included in the Goneplacidae has long been recognized as representing an intermediate step towards the transformation of the cyclometopous (heterotrematous) abdomen-sternum arrangement (male genital opening coxal; abdominal somites 1–2 covering entirely the space between the coxa of P5; sternite plate 8 entirely covered by these abdominal somites and not visible ventrally) into a catometopous arrangement (male opening sternal; sternite plates 7 and 8 widened, ventrally united and visible ventrally; abdominal segments 1–2 reduced, clearly separated from coxa of P5) (Guinot 1969a, 1978, 1979). For Guinot (1969b, 1970) this group of genera represents an evolutionary step towards the more advanced catometopous (thoracotrematous) organization in which the sternum occupies an increasingly wider area between the basal abdominal somites and the coxa of P5, and the male opening moves progressively towards a sternal position. Guinot (1970: 1076, 1080) suggested that several of these genera (i.e., *Pseudorhombila* H. Milne Edwards, 1837, *Oediplax* Rathbun, 1893, and possibly *Nanoplax* Guinot, 1967) could be integrated in the subfamily Pseudorhombilidae Alcock, 1900 pro parte.

Guinot (1969b: 721) also described the genus *Chacellus* Guinot, 1969b, monotypic at that time, which she considered "... [a genus with] une organisation très proche de l'organisation cyclométopienne et fait sans doute partie des Crabes formant le passage entre Cyclométopes et Catométopes [an organization close to the cyclometopous organization and probably belonging to the crabs linking the cyclometopous to the catametopous]." A second species of *Chacellus* was added by Hendrickx (1989a) who, despite of a "rather xanthoid facies," included it in the Goneplacidae with a "primitive catometopous organization." Another genus, *Euphrosynoplax* Guinot, 1969b was also described by Guinot (1969b:720), to accommodate an undescribed species of crab from Florida: *E. clausa* Guinot, 1969b. Again, Guinot (1969b) emphasized the primitive catometopous stage of this genus, relatively close to the cyclometopous arrangement. A second species of *Euphrosynoplax* was recently described by Vázquez-Bader & Gracia (1991) from the Gulf of Mexico. Although these authors did not clearly illustrate sternite eight, they refer to a (what appears as a primitive) catometopous organization of their species, *E. campechiensis,* with a "... male opening coxal [and] a small portion of sternite 8 not covered by the second abdominal somite."

The present paper deals with a new species of crab that present morphological similarities with those in the above cited genera. It is herein considered that this new species requires a new genus. Furthermore, the use of the family Pseudorhombilidae Alcock, 1900, is proposed for a group of six genera with a "xanthoid-goneplacid" facies representing primitive transitional forms between the cyclometopous and the catometopous abdomen-sternum organization.

Abbreviations used in this paper are: CW, carapace width; CL, carapace length; P2 to P5, pereiopods; Pl1 and Pl2, male first and second pleopods (gonopods), respectively; SEM, Scanning Electron Microscope; EMU, Estación Mazatlán UNAM, invertebrate reference collection; SIO, SCRIPPS Institution of Oceanography, invertebrates collection, La Jolla, California, U.S.A.; LACM, Los Angeles County Museum of

Natural History, Los Angeles, California, U.S.A.

Drawings were made with a camera lucida (Fig. 2). Holotype was photographed using a Kodak TMAX 100 ASA black and white film (Fig. 1), and SEM microphotographs of male gonopods were obtained using the classical technique of acetone dehydrated, gold-palladium coated gonopods extracted from type material (Fig. 3).

Bathyrhombila, new genus

Diagnosis.—Carapace 1.4 to 1.5 broader than long, anteriorly convex, slightly convex and narrower posteriorly; general shape "xanthoid". Antero-lateral margin arched, with 4 teeth, excluding the outer orbital tooth which is well-defined and slightly projecting; second and outer orbital teeth fused, forming an almost straight slightly projecting margin; length of this margin almost half the frontal width. Postero-lateral border converging posteriorly. Regions relatively well marked. Front narrow, less than ⅓ maximum width of carapace, slightly projecting forwards, with a shallow median depression, margin sinuous, with a well-marked notch between the external corner and the inner orbital tooth. Orbits reduced in size; eyes relatively small. Upper orbital margin slightly concave, with 2 distinct sutures; lower orbital margin with 2 strong teeth, inner one acute, outer one rounded. Antennal flagellum long, entering orbit; basal article of antenna relatively long, slightly oblique, in contact with front; a small apophyse intercalated between basal article and epistome (pterygostomian upper border); palp folding horizontaly. Interantennular septum broadly triangular. Third maxilliped with merus about 0.5 times length of ischium, antero-external angle slightly produced; palp articulating at inner distal angle of merus. Chelipeds large and robust, not markedly unequal in large males, subequal in females; carpus with a blunt, moderately large spine at inner angle; pincers very large, fingers flattened, pointed, tips recurved, gap between fingers reduced. A very conspicuous, strong pterygostomian ridge in front of cheliped articulation. Walking legs slender, long, flattened. Sternum moderately wide, narrowing in front of P1. Abdomen narrow in its base; segment 2 not overlapping coxa of P5. Abdominal segments 3–5 incompletely fused; suture 3–4 distinguishable, a remaining notch on both extremities; suture 4–5 obsolete, a remaining notch on both extremities. A small portion of sternite 8 visible, close to articular condyle of P5, not in contact with sternite plate 7. A shallow depresion in front of the abdominal telson. Male genital opening coxal and gonopod 1 free. Pl1 long, slender, with slightly curved apex; stiff subterminal spines, with stout and long lateral (apical) process and shorter, hook-like apical process. Pl2 short, sigmoid.

Type species.—*Bathyrhombila furcata,* new species, by original designation and monotypy.

Ethymology.—The name of the genus is a combination of *rhombila* and *bathys,* to indicate affinities with the genus *Pseudorhombila* H. Milne Edwards and the fact that most specimens were collected in the bathybenthic region.

Bathyrhombila furcata, new species

Figs 1–3

Material examined.—Holotype, male (CW 24.6 mm; CL 17.5 mm), 05 Jul 1965, station SIO 65-257, La Paz Bay (24°19′N, 110°26′W), Baja California, Mexico, otter trawl, 55–80 m (coll. W. Baldwin) (SIO C-2116).

Paratypes: male (CW 20.3 mm; CL 14.45 mm), 18 Jan 1968, station MV68-I-59, Gulf of California, north of Angel de La Guarda Island (29°41′N, 113°56′W), Baja California, Mexico, 566–644 m, otter trawl, R/V *T. Washington* (coll. C. Hubbs) (SIO C-5669A). Male, slightly damaged (CW 22.8 mm; CL 16.35 mm), 18 Jan 1968, station MV68-I-59, Gulf of California, north of Angel de La Guarda Island (29°41′N, 113°56′W), Baja California, Mexico, 566–644 m, otter trawl, R/V *T. Washington* (coll. C. Hubbs) (LACM-68-464.1, ex-SIO C-5669).

Non-paratypes: 1 soft shell male (cw 25.95 mm; CL 17.95 mm), 1 damaged soft-shell ovigerous female (CW ca. 17.9 mm; CL ca. 13.0 mm), 18 Jan 1968, station MV68-I-59, Gulf of California, north of Angel de La Guarda Island (29°41′N, 113°56′W), Baja California, Mexico, 566–644 m, otter trawl, R/V *T. Washington* (coll. C. Hubbs) (SIO-5669C).

Description.—Carapace wide (CW/CL ratio 1.40–1.46). Front narrow (7.05 mm wide in holotype), sinuous; fronto-orbital width (13.4 mm in holotype) about half the carapace width. Carapace anteriorly convex and mostly covered with small flattened granules, without setae; granules more numerous and rounded close to edges and on antero-lateral teeth. Antero-lateral margin with five teeth (including the outerorbital tooth), the posterior three large to medium-sized, conical; second teeth reduced, fused with the outerorbital tooth and forming an almost straight, little projecting margin; outerorbital tooth little produced, distinct. Fifth tooth smaller than the preceeding two; fourth teeth acute, pointing upward; third teeth wider that fourth and fifth, its sides at a right angle, flattened compared to fourth. Orbital lobe well-marked; upper orbital margin somewhat irregular, with small rounded granules and two conspicuous sutures (median and lateral); lower orbital margin with granulated inner tooth and outer lobe, both granulated. Outer orbital tooth well-defined, little projecting. Pterygostomian and subhepatic regions granulated. Pterygostomian ridge coarsely granulated.

Distal border of merus of third maxilliped sinuous, with a marked median concavity; antero-external angle little produced; merus coarsely granulated; ischium with more flattened granules, its distal border produced internally in a lobe; palp coarse.

Cheliped very strong, long (length of major cheliped ca. 1.75 CW); claw heavy and long (length of major claw about equal to CW), right claw being slightly higher (right/left claw maximum height ratio 1.09 to 1.12). Merus with granules on anterior and posterior sides, a dorsal row of granules and a blunt superior subterminal angle, produced in a low tubercle. Carpus strong, obliquely subquadrate in dorsal view, surface slightly irregular dorsally; clusters of granules arranged in rugae (well defined in the holotype) on outer slope; a blunt, moderately large spine at inner angle; a well-defined sulcus parallel to distal border. Manus inflated, smooth (microscopically punctated). Fingers long, flattened, pointed, strongly incurving and with recurved tips, gap between fingers reduced; length of dactylus of major claw ca. 0.4 times length of claw; dorsal margin of dactylus of major claw almost straight, that of major claw only slightly curved. Cutting edge of dactylus of both claws sharp, that of major claw with a strong, projecting subrectangular proximal tooth, followed by a series of irregular, smaller teeth; cutting edge of polex with a series of irregular teeth; cutting edges of smaller claw with reduced teeth.

Pereiopods 2–5 long, slender, flattened; merus covered with dense granules on lower and upper margin, sides almost smooth; carpus and propodus partly covered with granules on upper margin; a low, longitudinal granulated crest on upper margin of carpus; dactylus about same length as propodus, with longitudinal rows of setae, tip short, corneous. Pereiopods 2–4 subequal in length (P2 = 1.66 times CW; P3 = 1.69 times CW; P4 = 1.63 times CW), fifth pereiopod notably shorter (1.39 times CW).

A small portion of sternite eight of male abdomen visible between second and third abdominal somites; first and third somites slightly wider than second, second and third of about the same length and with subacute lateral margins; sixth somite wider than long, sides concave, narrower medially, distal and proximal margin equal; seventh somite (telson) as long as sixth, posteriorly

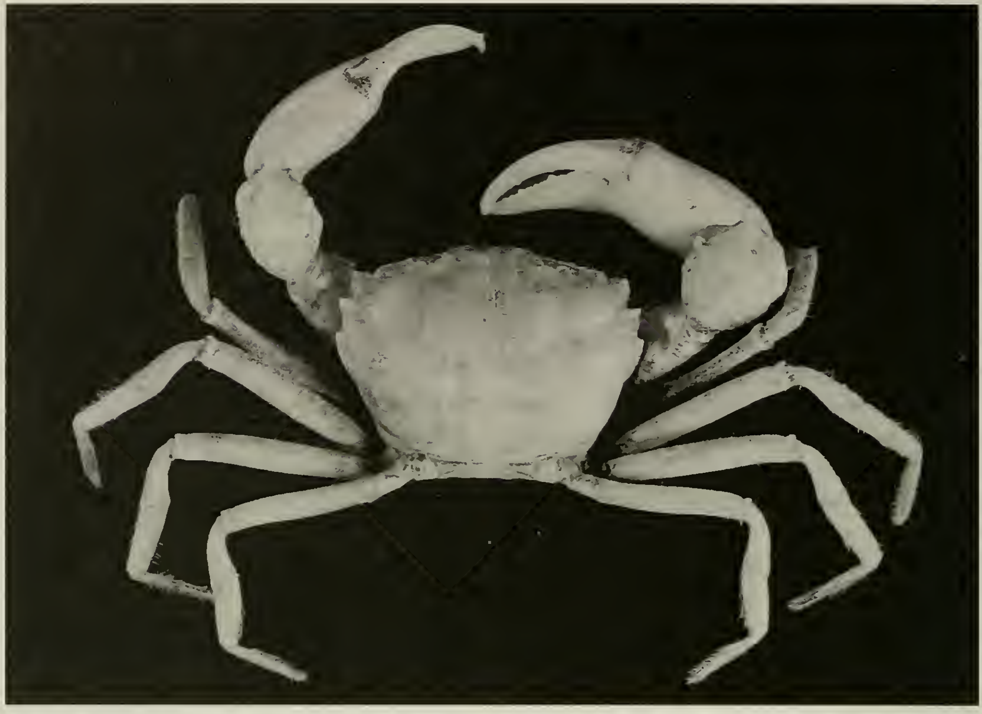

Fig. 1. Holotype, male, CW 24.6 mm, CL 17.5 mm, dorsal view, La Paz Bay, Baja California, Mexico (SIO C-2116).

rounded. First somite and lateral portion of second coarsely granulated; other somites with fewer flattened granules or almost smooth.

Female gonopores longitudinally oval; opening vertical.

First pleopod of male long, slender, bending and slightly curved distally. Two rows of small spines on the shaft; two series of 3 and 5 much longer distal spines on each side of the fold, close to the apex; a strong, spine-like subterminal process, and a terminal, hook-shaped shorter process; a cluster of spines on the side opposite to the fold; an obscure third lobe, covered with tiny spines, in front of the hooked process.

Ethymology.—The name of the species refers to the peculiar arrangement of the subapical setae of the male first pleopod, simulating a fork (*furca*).

Remarks.—The smaller male features more marked heterochely, the right claw being about 1.34 times the maximum height of the smallest whereas it is 1.11 in the holotype. The soft-shell male is also the largest male available but due to the lack of calcification this specimen has not been used as holotype. The only available female also features a soft-shell, and although basic characteristics match the description of the species, it was not designated as type material either. The bathymetric range of *B. furcata* is rather wide; the holotype was taken in trawl between 55 and 80 m, while the rest of the material was obtained in a single trawl from a depth of 566–644 m.

Discussion

Like several other genera included in the Goneplacidae or "Goneplacid-like" group (i.e., *Pseudorhombila, Nanoplax, Oediplax,* and *Chacellus*), *Bathyrhombila* represents a primitive evolutionary step towards a catometopous stage, in which an uncovered expanded sternite 8 unites to sternite 7. In

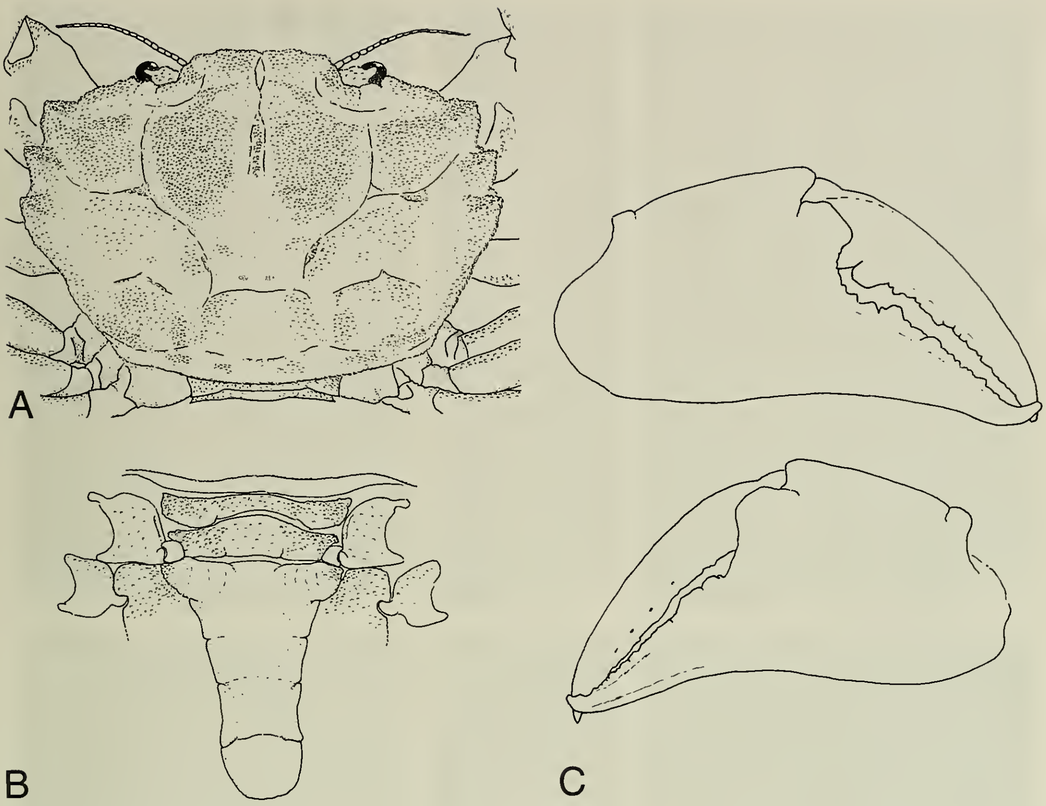

Fig. 2. Holotype male, CW 24.6 mm, CL 17.5 mm (SIO C-2116). A, dorsal view of carapace; B, dorsal view of abdomen and sternal plates 7–8; C, right (upper) (SIO C-2116) and left (lower) claws, frontal view.

the former four genera, the abdominal somite 2 is: notably reduced, its lateral margin straight and clearly separated from the coxa of P5 (e.g., *Oediplax granulata* Rathbun, 1893, type species of the genus; *Pseudorhombila xanthiformis* Garth, 1940; *P. octodentata* Rathbun, 1906); reduced but antero-laterally acute, in such a way that the acute corner is close to the coxa of P5 (e.g., *Chacellus pacificus* Hendrickx, 1989a); or antero-laterally acute and touching the coxa of P5 (e.g., *Nanoplax xanthiformis* A. Milne Edwards, 1880). In all cases, somite 2 leaves a reduced portion of sternite 8 visible at the basis of coxa of pereiopod 5. In *Bathyrhombila* the antero-laterally produced corner of somite 2 is almost in contact with the coxa of P5. In his study of *Bathyplax typhlus oculiferus* Miers, 1886, Tavares (1996: 420) note that the size of vissible portion of sternite 8 varies among specimens of a same species; data related to other genera, however, are lacking. *Pseudorhombila, Nanoplax* and *Oediplax* are considered by Guinot (1969b, 1970) as potential members of a series of "Goneplacidae" related to the Xanthidae, equivalent to the Pseudorhombilinae Alcock, 1900. Among the species of *Pseudorhombila,* the abdomen-sternum organization itself varies from a primitive step (sternites 7 and 8 appear not in contact in ventral view, male opening coxal: *P. xanthiformis*) to a more advanced phase [sternites 7–8 in contact on a short distance, in ventral view, displacement of the male opening towards a sternal position: *P. quadridentata* (Latreille, 1828), *P. octodentata* (Rathbun, 1906), and *P.*

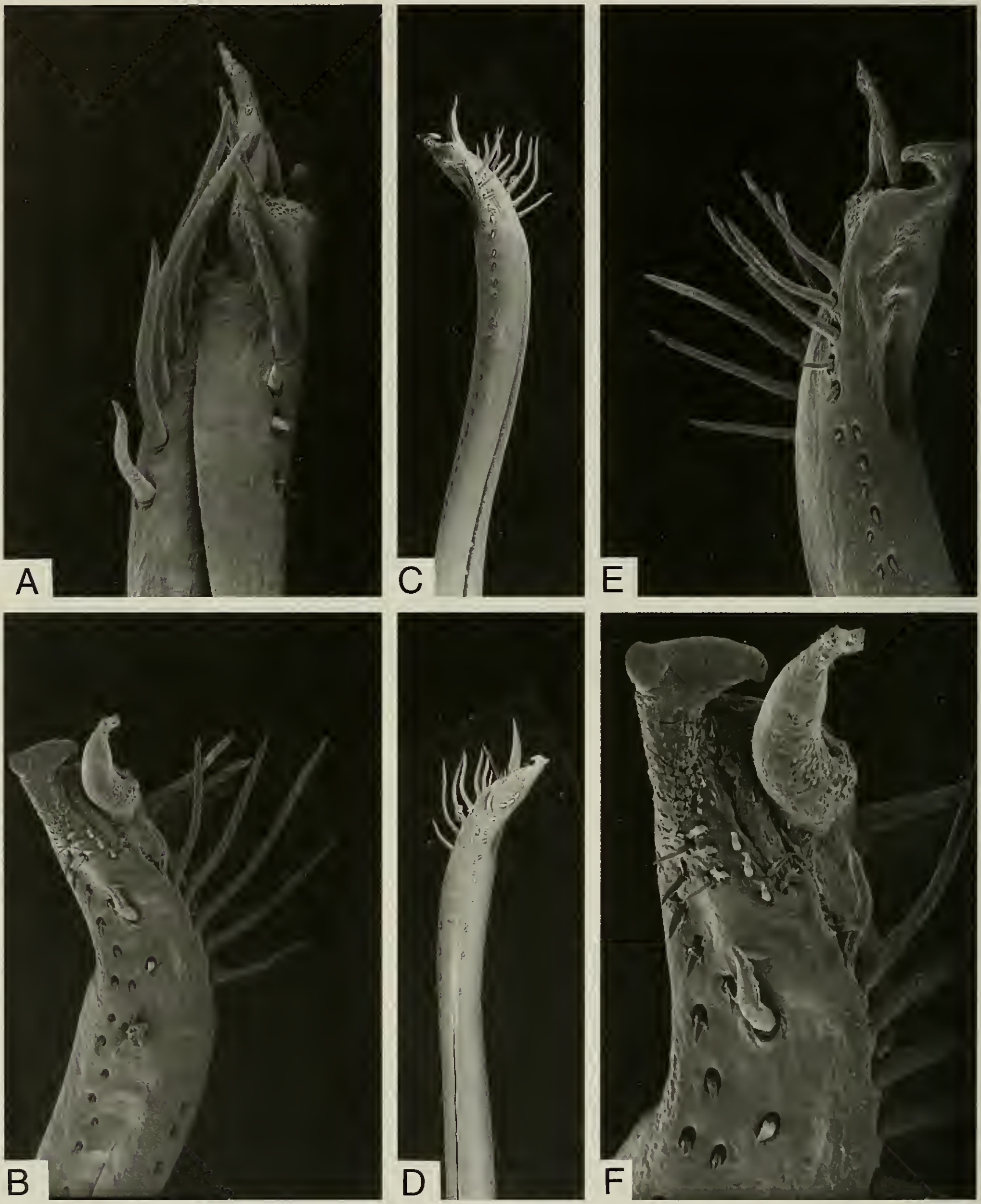

Fig. 3. Microphotographs (SEM) of male first gonopod (Pl1). A, B and E, F, paratype, male, CW 22.8 mm, CL 16.35 mm (LACMNH 68-464.1), slightly damaged, station MV68-I-59, Gulf of California, north of Angel de la Guarda Island (29°41′N–113°56′W), Baja California, Mexico, detail of extremity; C, D, holotype, male, CW 24.6 mm, CL 17.5 mm (SIO C-2116) distal portion (SEM photographs) (scale: A, F, 100×; B, E, 72×; C, D, 25×).

ometlanti Vázquez-Bader & Gracia, 1995]; this would make *Pseudorhombila* the most advanced genus of all.

The "faciès goneplacien" referred to by Guinot (1969a, b) is distinguishable in all the above mentioned genera (in particular considering the shape of the cheliped) and the pterygostomian ridge, also referred to by Guinot (1969a, 242) as a "... caractère assez constant [in Goneplacidae], rarement signalé ..." [a rather constant feature, rarely reported], is also present in all four genera (strong and sharp in *Oediplax*; strong and granulated in *Bathyrhombila*; strong to moderate in *Pseudorhombila*; weak in *Chacellus*). In the case of *B. furcata,* the general aspect of the crab relates it to species of *Pseudorhombila*; the carapace is similar, notably wider than long, with distinguishable regions and convex in lateral view. Both genera feature large to very large (*Bathyrhombila*), heavy chelipeds, although the heterochely is more marked in *Pseudorhombila.* Orbits and eyes are small. Structure of the frontal and antennular regions and of the bucal frame is similar, as is the shape of the third maxilliped, although the antero-lateral angle of the merus is not so produced in *Bathyrhombila* (in this respect, closer to *Oediplax*). Both genera also feature long (*Pseudorhombila*) to very long (*Bathyrhombila*), flattened, slender P2–P5. *Bathyrhombila,* however, differs from *Pseudorhombila* in the following characters: the exorbital and second teeth of carapace are fused, forming a wide, almost straight slightly projecting margin (exorbital tooth almost wanting in *Pseudorhombila*); the pterygostomian ridge, in front of the cheliped articulation, is much stronger in *Bathyrhombila*; the second abdominal segment is wider in *Bathyrhombila*; and the structure of the male Pl1 is strikingly different (Fig. 3). Considering the shape of the male gonopods, the slender Pl1 of *Bathyrhombila* is closer to Pl1 of *Chacellus* (*Pseudorhombila* and *Oediplax* possess a shorter, more massive Pl1). Ornamentation of the tip of Pl1 however, shows affinities with some species of Panopeidae Ortmann, 1893 such as *Lophopanopeus frontalis* Rathbun (see Martin & Abele 1986: fig. 1N). Although the "third" lobe (typical of Panopeidae) in *Bathyrhombila furcata,* new species is hardly distinguishable, the other two processes are strongly developed. In contrast, long subterminal spines (present on the Pl1 of *B. furcata*) are also observed on Pl1 of species of *Pseudorhombila* and on the type-species of *Nanoplax* [i.e., *N. xanthiformis* (A. Milne Edwards, 1880)] (Hendrickx 1995), with a single cluster of subterminal spines in the later.

Another genus close to the "Pseudorhombilid" organization is *Euphrosynoplax* Guinot. The visible portion of sternite 8, however, is smaller in *E. clausa* (the type-species of the genus) than in *Pseudorhombila, Bathyrhombila* and *Oediplax*; and is similar in size to sternite 8 of *Nanoplax xanthiformis* and the two known species of *Chacelus.*

When all these species are compared, they present striking similarities as far as their general shape and aspect is concerned. On the basis of these considerations, and following the suggestion of Guinot (1970; 1080), the use of the family-group name Pseudorhombilidae Alcock, 1900, is proposed for those genera of "goneplacid-xanthid" crabs.

Pseudorhombilidae Alcock, 1900

Pseudorhombilinae Alcock, 1900:286, 292, 297, pro parte.

Pseudorhombilinae.—Guinot, 1969b:706; 1971:1080.

Type genus.—Pseudorhombila.

Included genera.—Bathyrhombila new genus, *Chacellus, Euphrosynoplax, Nanoplax, Oediplax,* and *Pseudorhombila.*

Definition.—Carapace xanthoid, wider than long, with 3–5 (including outer orbital) antero-lateral teeth. Bucal frame widening anteriorly. Orbits of moderate or reduced size, oval. Chelipeds goneplacids, long, heavy, with long, strongly to moderately incurving fingers. Pterygostomian ridge (in front of chelipeds) strong to moderate. Abdominal somites 3–5 at least partially fused, sutures usually visible. Second abdominal somite reduced, its antero-lateral margin in contact with (anterior angle produced) or separated (margin straight) from basis of coxa of P5. Sternal plate wide and slightly to moderately depressed between P1 (minimum width between P1 equal to 0.60–0.63 times maximum width between P2). A small to relatively large piece of sternite 8 visible ventrally; sternite 8 not touching sternite 7 in ventral view (Pl1 coxal) or in contact over a short distance (Pl1 displaced towards a sternal position). Pl1 long and slender or moderately long and strong; ornamentation variable. Pl2 short, strongly or moderately sigmoid.

Genera.—The family is divided into three groups of genera. Group A includes the most primitive catometopous forms (i.e., *Nanoplax, Chacellus, Bathyrhombila* and *Euphrosynoplax*); group B includes species with a larger visible piece of sternite 8 (*Pseudorhombila* pro parte and *Oediplax*); group C includes species with a larger visible piece of sternite 8 in contact over a short distance with sternite 7 (*Pseudorhombila* pro parte).

Remarks.—Among the Pseudorhombilidae, several species present a subtriangular hiatus between the ischium and the merus of the third maxilliped (e.g., *Chacellus pacificus*; both species of *Euphrosynoplax*; *Oediplax granulata*; *Pseudorhombila xanthiformis, P. quadridentata* and *P. guinotae* Hernández-Aguilera, 1982) while other species (e.g., *Chacellus filiformis* Guinot, 1969b; *Pseudorhombila ometlanti*) possess an anteriorly expanded lobe at the inner angle of the ischium that makes contact with the proximal margin of the merus (Hendrickx 1989a: table 1). The third maxilliped of other species have not been illustrated in the literature and specimens have not been available for examination. In *Nanoplax,* the partially-fused outerorbital and second teeth are much narrower than in any other genus included in the Pseudorhombilidae, although still separated by a shallow notch. The carapace of species of *Pseudorhombila* and *Oediplax* features a reduced to unconspicuous first anterolateral tooth and the fifth tooth varies from well (e.g., *P. octodentata*) to poorly developed (or obsolete) (e.g., *P. quadridentata*).

Provisional key to genera of Pseudorhombilidae

1. Distance between outer orbital and first anterolateral teeth much shorter than orbit width; these tooth partially-fused, separated by a shallow notch. Extremity of male Pl1 with a strong longitudinally projecting flange . . . . *Nanoplax*
– Distance between outer orbital and first anterolateral teeth about equal to orbit width 2
2. Pl1 of male long, very slender and tapering, with only a few minute spines along the shaft . . . . *Chacelus*
– Pl1 of male stout, strong, twisted, with median to large spines along the shaft and distal part 3
3. Outer orbital and first anterolateral teeth coalesced, forming an almost straight slightly projecting margin. Extremity of male Pl1 with two longitudinal series of very long spines . . . . *Bathyrhombila*
– Outer orbital and first anterolateral teeth reduced, separated by a granulated space; granules coarse to minute 4
4. Merus of MXP3 not produced antero-laterally . . . . *Oediplax*
– Merus of third maxilliped strongly produced antero-laterally 5
5. Extremity of male Pl1 with a strong subterminal or lateral upturned flange; a patch of strong spines just below the flange and series of weaker spines along shaft . . . . *Pseudorhombila*
– Extremity of male Pl1 with a lateral flange; no patch of strong subterminal spines below the flange, but a series of moderate size spines along the shaft . . . . *Euphrosynoplax*

Relationships between Pseudorhombilidae Alcock and the Panopeidae Ortmann are difficult to establish. As emphasized by Guinot (1969a:249, 250, and in lit.) this is due basically to the complexity of the Panopeidae sensu lato, of which a first group presents a xanthid facies and coxal male opening (e.g., *Eurypanopeus, Panopeus*), while a second group presents a goneplacid facies and coxal or coxo-sternal male opening (e.g., *Cyrtoplax, Glyptoplax*). Some species of the Panopeinae second group (e.g., *Glyptoplax pugnax* Smith, 1870, the type species of the genus, and *G. consagae* Hendrickx, 1989b) present a sternum-abdomen organization more advanced towards a catometopous organization, with uncovered section of sternites seven and eight widely in contact and covering a groove through which the penis passes (see Hendrickx 1989b: 653). All members of the Panopeidae, including *Glyptoplax,* however, feature the typical "Panopeid" Pl1 ornamentation.

Specimens of the monospecific genera *Thalassoplax* Guinot and *Robertsella* Guinot were not available during this study. Both genera were briefly described by Guinot (1969b) to accomodate specimens erroneously identified by Rathbun (1918) as *Pilumnoplax elata* (A. Milne Edwards, 1880). Both genera are very similar primitive catometopous and feature distinctive male Pl1. Shape of carapace (see Guinot 1969: plate V) of both genera is apparently different from typical pseudorhombilids (carapace more squarish; wider front and orbits). Further studies will be needed to show if these two genera belong to the Pseudorhombilidae or not.

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A new crayfish of the genus *Orconectes* from the Blood River drainage of western Kentucky and Tennessee (Decapoda: Cambaridae)

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Abstract.—A new crayfish, *Orconectes burri,* is described from the Blood River drainage of western Kentucky and Tennessee. The species occurs in small to medium-sized streams with substrates of gravel and sand. Form I males of *O. burri* differ from all other members of the genus *Orconectes* in possessing a first pleopod with terminal elements that comprise 22 to 29% of the total length of the pleopod, and a central projection with a tip that terminates at an 90° angle to the main shaft of the pleopod, which is either directly above or slightly overhanging the distal end of the mesial process.

Field work conducted in western Tennessee in the spring of 1996 revealed the presence of an undescribed species of crayfish in the headwaters of the Blood River drainage. Subsequent field work in western Kentucky and Tennessee and examination of material housed at the National Museum of Natural History, Smithsonian Institution, indicated that this undescribed form was endemic to the Blood River drainage. Based on the morphology of the form I male pleopod, this new species, described herein as *Orconectes burri,* is assigned to the Rafinesquei group (Fitzpatrick 1987) of the subgenus *Crockerinus* Fitzpatrick 1987. Members of the Rafinesquei group inhabit lotic habitats and are distributed across the western half of Kentucky and extreme southern Illinois. Fitzpatrick (1987) included the following as members of the Rafinesquei group: *Orconectes bisectus* Rhoades, 1944, *O. illinoiensis* Brown, 1956, *O. rafinesquei* Rhoades, 1944, *O. tricuspis* Rhoades, 1944.

Orconectes burri, new species
Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented. Rostrum slightly concave dorsally, terminating in short acumen (see Variation); weak median carina present. Rostral margins thickened; distal halves straight and slightly converging, proximal halves slightly convex; terminating in spines (Fig. 1D). Areola 28.8–34.0% ($\bar{X}$ = 31.0, *n* = 28, *SD* = 1.3) of total length of carapace, narrowest part slightly anterior of midpoint, 4.4–7.5 ($\bar{X}$ = 5.7, *n* = 28, *SD* = 0.9) times as long as wide with 5 to 8 (mode = 6, *n* = 28, *SD* = 0.7) punctations across narrowest part (Fig. 1D). One corneous cervical spine on each side of carapace (Fig. 1D). Postorbital ridges well developed, terminating in corneous spines (Fig. 1D). Suborbital angle weakly developed, forming broadly rounded projection. Antennal scale broadest distal to midlength, distal margin at 90° angle to lateral margin, thickened lateral margin terminating in large corneous spine (Fig. 1F). Ischia of third pereiopods of males with hooks; hooks overreaching basioischial articulation in form I males only. Chela with 2 rows of tubercles (see Variation) along mesial margin of palm, usually 8 or 9 tubercles in mesial row and 6 or 7 in dorsomesial row; small tufts of setae over mesial margin of palm, dorsomesial

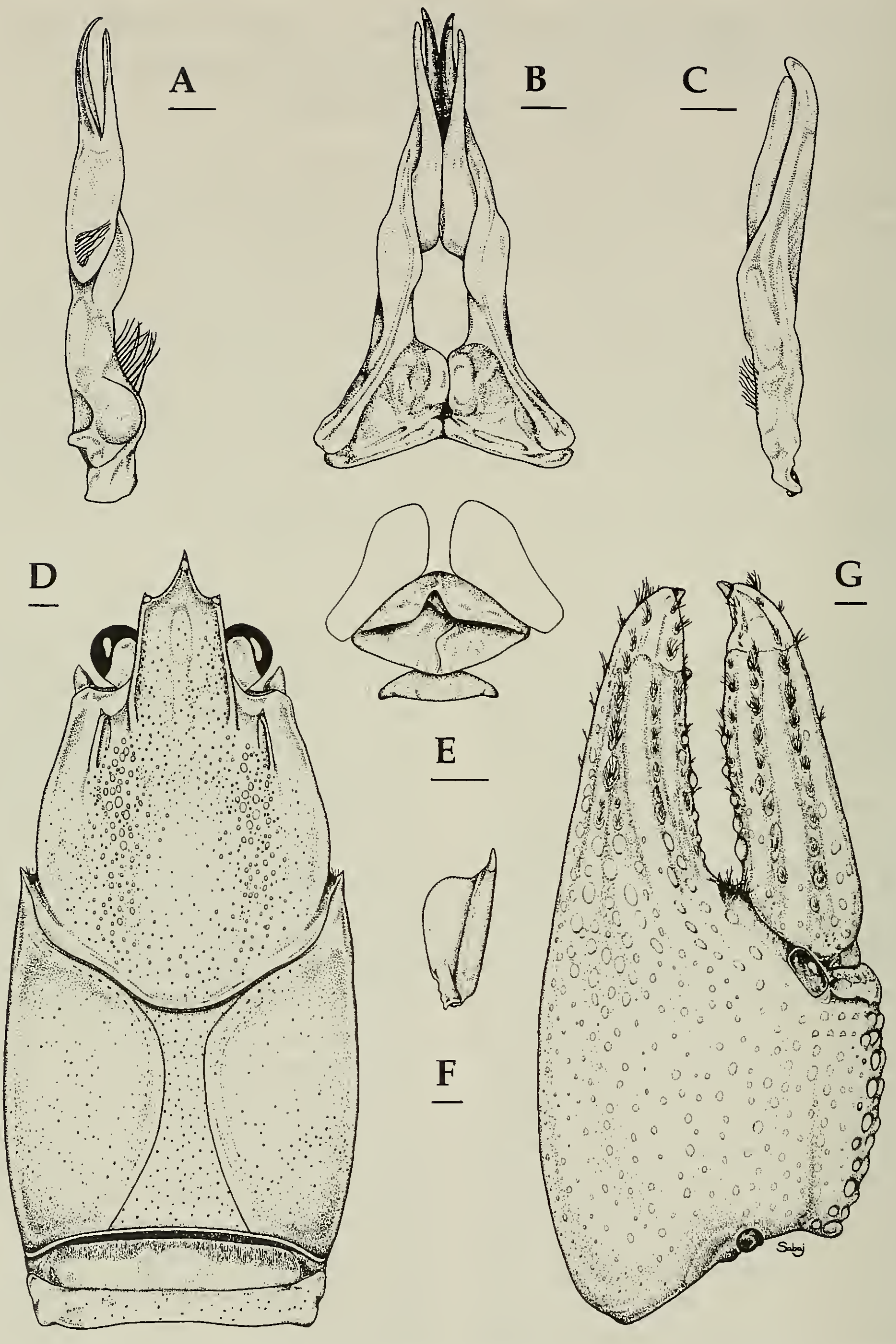

Fig. 1. *Orconectes burri,* new species: A, Mesial view of first pleopod of form I male; B, caudal view of first pleopods of form I male; C, Lateral view of first pleopod of form II male; D, Dorsal view of carapace; E, Annulus ventralis; F, Dorsal view of right antennal scale; G, Dorsal view of left chela (note- small tufts of setae over mesial margin of palm, dorsal, dorsomesial, and dorsolateral surfaces not shown). A, D, F, G of holotype (INHS 6663); B, topotype (INHS 6662); C, morphotype (INHS 6659); E, allotype (INHS 6664). Scale bars beneath letters equal 1 mm.

Table 1.—Measurements (mm) of *Orconectes burri,* new species.

	Holotype	Allotype	Morphotype
Carapace			
Total length	26.7	24.1	21.9
Postorbital length	21.3	18.8	16.7
Width	13.9	12.7	10.6
Height	12.2	10.8	9.3
Areola			
Width	1.5	1.4	1.4
Length	8.7	7.4	6.7
Rostrum			
Width	3.8	3.5	3.3
Length	6.4	6.0	5.5
Chela, left			
Length, palm mesial margin	8.5	5.7	4.8
Palm width	10.7	7.2	6.0
Length, lateral margin	23.3	15.5	14.2
Dactyl length	12.8	8.3	7.8
Abdomen			
Width	12.5	12.8	9.2
Length	30.4	27.8	23.7

and dorsolateral surfaces, and fingers; dorsal surfaces of fingers with well defined longitudinal ridges (Fig. 1G). First pleopods of form I male symmetrical, extending to posterior edge of bases of second pereiopods when abdomen flexed. First pleopod of form I male without shoulder on cephalic surface at base of central projection; central projection corneous, constituting 22.2–29.2% ($\bar{X} = 26.4$, $n = 9$, $SD = 2.1$) of total length of first pleopod, arched caudodistally, tapering to a pointed tip, tip at 90° angle to main shaft of pleopod and extending to or slightly overhanging distal end of mesial process; mesial process straight and slightly subequal in length to central projection, non-corneous, tapering to an acute tip (Fig. 1A). First pleopod of form II male non-corneous, extending to posterior edge of bases of second pereiopods when abdomen flexed; central projection weakly arched caudodistally, mesial process straight and subequal in length; both elements tapering to rounded tips (Fig. 1C). Annulus ventralis immovable, subrhomboidal; cephalic half with wide median trough and 2 caudally directed protuberances overhanging centrally located fossa; sinuate sinus running from left corner of fossa to caudal edge (Fig. 1E).

Description of holotypic male, form I.—Body slightly depressed dorsoventrally, carapace wider than abdomen (13.9 and 12.5 mm, respectively). Greatest width of carapace larger than height at caudodorsal margin of cervical groove (13.9 and 12.2 mm, respectively). Postorbital carapace length 80.0% of length of carapace. Areola 5.8 times longer (8.7 mm) than wide (1.5 mm) with 6 punctations across narrowest part; length of areola 32.6% of total length of carapace. Rostrum densely covered by setiferous punctations, slightly excavated dorsally, weak carina present; margins thickened, distal halves straight and slightly converging, terminating in corneous spines, proximal halves slightly convex. Acumen terminating in upturned corneous spine and reaching midpoint of antennular peduncle. Postorbital ridges well developed, terminating in corneous spines. Suborbital angles weakly developed, forming broadly rounded projections. Cervical spines corneous; dorsal and branchiostegal areas of carapace densely punctate.

Abdomen longer than carapace (30.4 and 26.7 mm, respectively). Cephalic section of telson with 1 movable and 1 immovable spine in each caudolateral corner. Protopodite of uropod with spine extending over endopodite and spine in caudolateral corner extending over exopodite. Caudal margin of cephalic section of exopodite with numerous fixed spines (13) and 1 movable spine in caudolateral corner. Lateral margin of endopodite terminating in spine; endopodite with prominent median ridge terminating in premarginal spine. Dorsal surfaces of telson and uropods setiferous.

Antennal scale broadest distal to midlength, distal margin at 90° angle to lateral margin, thickened lateral margin terminating in large corneous spine. Right antennal scale 5.5 mm long, 2.3 mm wide.

Mesial surface of palm of left chela with 2 rows of tubercles, 9 tubercles in mesial row, 9 tubercles in dorsomesial row, and 3 small widely interspersed tubercles lateral to dorsomesial row. Mesial, dorsal, and lateral surfaces of chela covered with numerous setiferous punctations; ventral surface with scattered punctations. Dorsal and ventral surfaces of finger of propodus with submedian longitudinal ridges flanked by setiferous punctations; basal half of opposable margin with 1 weakly developed tubercle and 4 well developed tubercles; 1 corneous tubercle at midlength between distal-most tubercle and distal tip of finger. Dorsal and ventral surfaces of dactyl with submedian longitudinal ridges flanked by setiferous punctations; basal half of opposable margin with 5 well developed tubercles, first and fourth tubercle from base of dactyl slightly larger than remaining 3. Finger of propodus and dactyl with subterminal corneous tip.

Carpus with deep oblique furrow dorsally; mesial margin with 1 large corneous procurved spine just distal to midlength; ventral surface with 1 corneous spine just lateral to midlength of distal margin, 1 spine just mesial to midlength of distal margin. Dorsodistal surface of merus with 2 corneous spines: ventral surface with 2 large corneous spines just distal to midlength of ventrolateral margin and mesial row of 7 spines, some corneous; row terminating in large corneous spine; small corneous tubercle at distolateral corner. Ischium with 1 corneous spine just proximal to midlength of mesial margin and 1 large tubercle on distal end of mesial margin.

Hook on ischium of third pereiopod only; hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. First pleopod as in Diagnosis, reaching to posterior edge of base of second pereiopods when abdomen flexed.

Description of allotypic female.—Differing from holotype as follows. Areola constituting 30.1% of length of carapace and 5.3 times longer than wide with 7 punctations across narrowest part. Postorbital carapace length 77.2% of length of carapace. Dorsomesial row of tubercles along palm of left chela with 6 tubercles. Tuft of long setae at base of finger of propodus. Ventral surface of left carpus with 2 corneous spines along distal margin. Ventrolateral margin of left merus with mesial row of 5 spines, some corneous. Ventral surface of merus with large corneous spine at distolateral corner.

Sternum between third and fourth pereiopods narrowly V-shaped. Postannular sclerite 1/2 as wide as annulus ventralis (described in Diagnosis). First pleopod uniramous, barely reaching caudal margin of annulus when abdomen flexed.

Description of morphotypic male, form II.—Differing from holotype as follows. Areola constituting 30.6% of length of carapace and 4.8 times longer than wide. Postorbital carapace length 77.0% of length of carapace. Dorsomesial row of tubercles along palm of left chela with 8 tubercles. Dorsodistal margin of carpus with 1 corneous spine just mesial to carpus/chela articulation joint.

Hook on ischium of third pereiopod not overreaching basioischial articulation. Left fourth and fifth pereiopods detached, right fifth pereiopod detached. First pleopod as described in Diagnosis.

Size.—The largest specimen examined is a 33.5 mm total carapace length (CL) form I male. Females (n = 11) range in size from 13.0 to 29.7 mm CL. Form I males (n = 10) range from 14.9 to 33.5 mm CL. Form II males (n = 7) range from 14.0 to 25.2 mm CL.

Color.—Dorsal and lateral surfaces of cephalothorax, abdomen, and tail fan densely mottled with tan, light brown, and dark brown patches of varying size. Dorsum with one large laterally elongate dark brown patch just anterior to areola. Cephalothorax with dark brown dorsolateral U-shaped saddle connected at caudal margin and extending to midlength of lateral surfaces. Saddle discontinuous and mottled anterior to midlength. Dorsal and lateral surfaces of chelae, carpus, and merus mottled as cephalothorax and abdomen. Large rounded tubercle at carpus/chela articulation joint at dorsoposterior margin of chelae dark blue to black. Fingers of chelae with orange tips followed proximally by wide black bands. Dorsal surfaces of pereiopods tan and mottled with small light brown patches. Ventral surfaces of chelae, cephalothorax, and abdomen cream to white.

Type locality.—Wildcat Creek at Kentucky Hwy. 280, 12.6 km E Murray, Calloway County, Kentucky. Holotype was collected from under an exposed tree root mass along the north bank, approximately 5 m downstream of the bridge. The allotype was collected from woody debris that had accumulated just upstream of the bridge. At the time of collection, Wildcat Creek ranged in width from 8–10 m with an average depth of 0.4 m. A small exposed shoal with woody vegetation occurred just upstream of the bridge. Substrate at the type locality was dominated by sand and gravel. Gravel substrates were predominantly found in shallow riffles while sand was found in slower flowing runs and pools. Stream banks were generally steep and well vegetated.

Disposition of types.—The holotype, allotype, and morphotype are deposited in the Illinois Natural History Survey Crustacean Collection (INHS 6663, INHS 6664, and INHS 6659, respectively), as are the following paratypes; 2 ♂ I, 1 ♂ II, and 1 ♀ (INHS 6665). Paratypes consisting of 1 ♂ I and 2 ♂ II (USNM 260869) and 2 ♂ II, 11 juvenile ♂, 1 female, and 2 juvenile ♀ (USNM 148718) are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. The localities and dates of collection are provided in the following Range and specimens examined section.

Range and specimens examined.—*Orconectes burri,* new species, is confined to the Blood River system (Tennessee River Drainage) in western Kentucky and Tennessee (Fig. 2). From its headwaters originating in Henry County, Tennessee, the Blood River flows northeasterly across the state line and through Calloway County, Kentucky. This relatively small drainage is best characterized as lowland stream habitat with minimal gradient (Burr and Warren 1986). A large portion of the main channel is embayed at its mouth by Kentucky Lake. Headwaters and tributaries of the Blood River drain Tertiary Porters Creek Clay/Clayton formations and Cretaceous McNairy Sand formations while the main channel flows through Quaternary Alluvial deposits. In western Kentucky and Tennessee the Porters Creek Clay/Clayton and McNairy Sand formations occur as a thin (16–32 km wide) strip of land that roughly coincides with the divide between eastward flowing tributaries of the lower Tennessee River (and the northern flowing Clarks River) and westward flowing tributaries of the Mississippi River. Extensive collecting in the lower Tennessee River drainage of western Tennessee and Kentucky by the authors and a search of holdings in the National Museum of Natural History have failed to document the presence of *O. burri* outside the Blood River drainage. In tributaries of the Tennessee River south of the Blood River, the species is replaced by *Orconectes* (*Orconectes*) *pagei* Taylor & Sabaj, 1997. To the north, *O. burri* is replaced by a disjunct population of *O.* (*Procericambarus*) *durelli* Bouchard & Bouchard, 1995.

A total of 92 specimens has been examined from the following six locations in Tennessee and Kentucky: TENNESSEE: Henry County: 1) INHS 5815, North Fork Blood River at Blood River Rd., 6.4 km ENE Puryear, 15 Jul 1996 (6 juvenile ♂, 2 ♀, 10 juvenile ♀); 2) INHS 6659, INHS 5822, USNM 260869, Middle Fork Blood River at Mt. Pleasant Rd., 6.4 km E Puryear, 8 May 1996 (morphotype; 3 ♂ I, 10 ♂ II; 1 ♂ I, 2 ♂ II paratypes to USNM); KENTUCKY: Calloway County: 3) INHS 6663, INHS 6664, INHS 6665, INHS 6662,

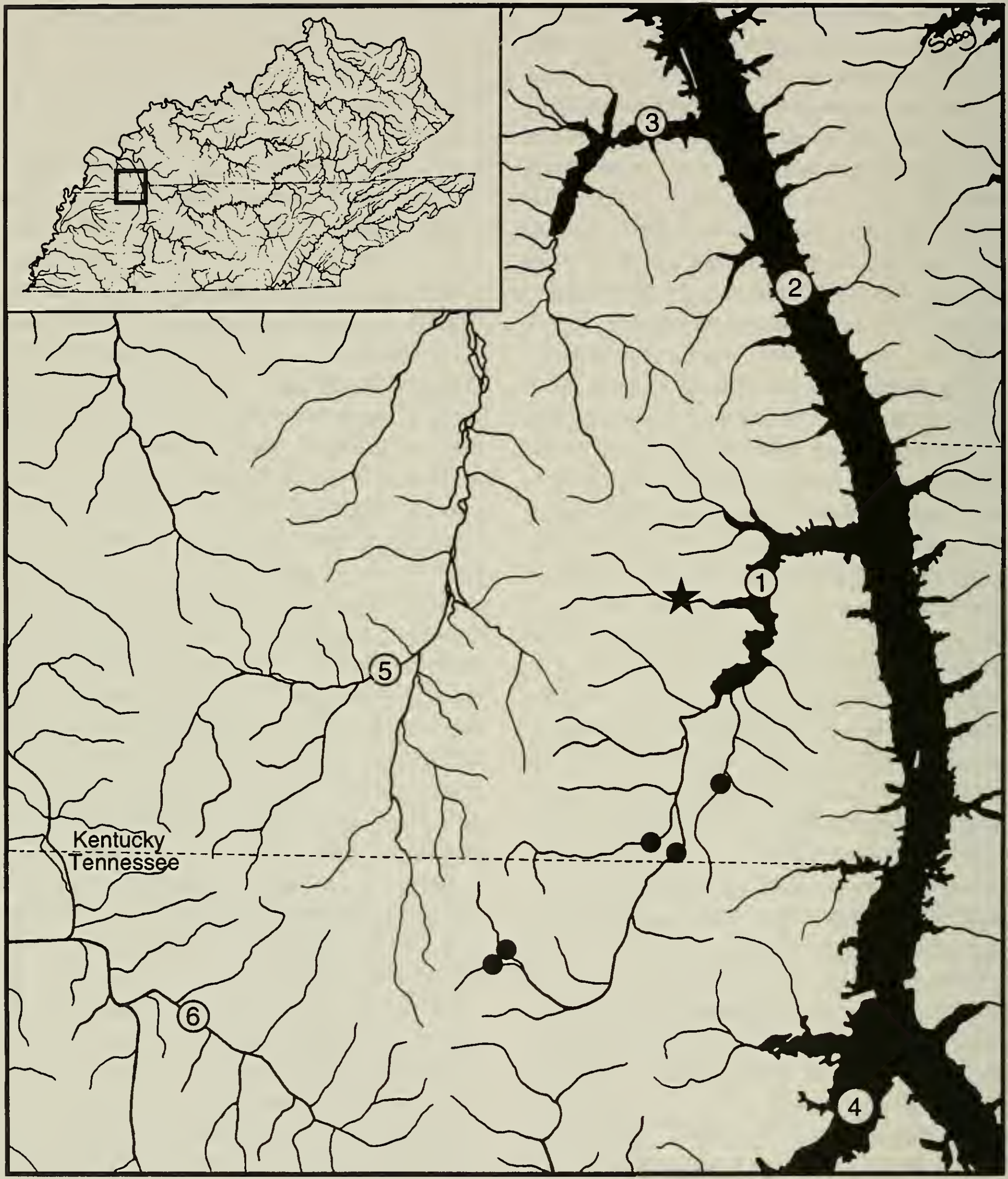

Fig. 2. Known range of *Orconectes burri*, new species. Type locality denoted by star. 1 = Blood River, 2 = Tennessee River (Kentucky Lake), 3 = Jonathan Creek, 4 = Big Sandy River, 5 = East Fork Clarks River, 6 = North Fork Obion River.

Wildcat Creek at KY Hwy. 280, 12.6 km E Murray (type locality), 26 Oct 1997 (holotype; allotype; 2 ♂ I, 1 ♂ II, 1 ♀ paratypes; 4 ♂ I, 4 ♂ II, 16 ♀, 3 juvenile ♀); 4) INHS 6667, Beechy Creek at KY Hwy. 121, 7.7 km SW Hamlin, 26 Oct 1997 (2 ♂ I, 2 ♀); 5) INHS 6669, McCullough Fork at State Line Rd., 5.2 km SSW New Concord, 26 Oct 1997 (1 ♂ I, 4 ♀, 1 juvenile ♀); USNM 148718 (2 ♂ II, 11 juvenile ♂, 1 ♀, 2 juvenile ♀, all paratypes); 6) INHS 5919, Blood River at Grubbs Rd., 0.3 km N KY-TN state line, 31 Mar 1997 (2 ♂ I).

Etymology.—Named in honor of Dr. Brooks M. Burr, Professor of Zoology and Curator of Fishes at Southern Illinois University at Carbondale. Dr. Burr is an avid naturalist with an intense interest in all aquatic organisms. This interest, coupled with his extensive collecting in the creeks and rivers of Kentucky over the past 20 years, has contributed greatly to our knowledge of the crayfishes and other aquatic species within the state.

Habitat and life-history notes.—*Orconectes burri,* new species, occurs in small to medium-sized streams with substrates of sand and gravel. Within these streams, the species was most commonly encountered in woody debris piles or woody vegetation root masses along stream banks. At site #2 (see Range and specimens examined) the species was collected from under large riprap immediately downstream of the bridge.

Form I males have been collected in the months of March, May, and October. Juveniles were commonly encountered in July. Most *O. burri* collections were composed of two distinct year classes, strongly suggesting a two-year life cycle for the species. No ovigerous females or females bearing young have been collected.

Crayfish associates.—The following species were collected from habitats containing *O. burri: Cambarus* (*Lacunicambarus*) *diogenes* Girard, 1852, and *Procambarus* (*Ortmannicus*) *acutus* (Girard 1852).

Variation.—Several ontogenetic variations are observed in *O. burri,* new species, none of which shows any geographic patterns of distribution. In smaller individuals the acumen is usually longer, the U-shaped saddle pattern on the cephalothorax is more clearly defined, and fewer tubercles occur along the mesial margin of the palm. In addition to the ontogenetic variation, a few individuals had two or three tubercles lateral to the dorsomesial row of tubercles along the mesial margin of the palm, and several females had a sinuate sinus running from the right corner of the fossa of the annulus ventralis.

Comparisons.—*Orconectes burri* differs from all other members of the genus *Orconectes* in the shape of the form I male pleopod. The pleopod of *O. burri* in unique in possessing the following combination of characteristics: terminal elements moderately long, central projection comprising 22 to 29% of total length of pleopod; both elements subparallel to main shaft of pleopod; central projection weakly arched caudodistally, tapering to a pointed tip, tip at 90° angle to main shaft of pleopod and either even with or slightly overhanging distal end of mesial process. In addition to the unique shape of the form I pleopod, *O. burri,* new species, differs from other members of the subgenus *Crockerinus* by possessing an antennal scale that is widest distal to midlength and with a distal margin forming a 90° angle with lateral margin.

Relationships.—The form I male pleopod of *O. burri* is most similar in length and general shape to those of members of the subgenus *Crockerinus,* and we assign *O. burri,* new species, to that subgenus. In his subgeneric reorganization of the genus *Orconectes,* Fitzpatrick (1987) subdivided *Crockerinus* into five groups: Sanbornii, Marchandi, Propinquus, Rafinesquei, and Shoupi. Following Fitzpatrick's (1987) hypothesis that characters associated with amplexus are most useful for inferring phylogenetic relationships, we believe that *O. burri,* new species, most likely belongs to the Rafinesquei group. *Orconectes burri,* new species, shares with other members of the Rafinesquei group the following characters: central projection of form I male pleopod comprising 22 to 29% of total length of pleopod, distal tip of central projection arched caudally, and distinct trough through cephalic half of annulus ventralis. The placement of *O. burri,* new species, in the Rafinesquei group also is supported biogeographically given that it occupies a range closer to those of other members of the Rafinesquei group than to other members of the subgenus. With the exception of *O. rafinesquei,* which inhabits the upper Rough River drainage of west-central Kentucky, all members of the Rafinesquei group occur in the lower Cumberland, Tennessee, and Ohio river drainages of extreme western Kentucky and southern Illinois (Hobbs 1989). Using morphology alone, we are unable to determine the closest relative of *O. burri,* new species, because the shape of its form I pleopod is equally different from the pleopods of all other members of the Rafinesquei group. Other characters such as the shape of the rostrum, areola, and chelae offer no additional clues to relationships. The rostrum of *O. burri,* new species, is similar to those of all other members of the group while the areola and chelae are unique to the group in that the areola is generally wider and the chelae are stockier with shorter fingers.

Acknowledgments

We are grateful to T. J. Near and L. M. Page for assistance in collecting specimens and to L. M. Page and C. H. Dietrich for reviewing an earlier version of this manuscript. We are also indebted to J. Dexter for photographic assistance and to K. Reed for graciously providing records from and access to the crustacean collections at the National Museum of Natural History, Smithsonian Institution.

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Two new species of *Erugosquilla* from the Indo-West Pacific (Crustacea: Stomatopoda: Squillidae)

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Abstract.—The fifth and sixth species of *Erugosquilla* to be recognized are *E. grahami,* new species, from Australia and Taiwan; and *E. serenei,* new species, from Vietnam. Both species resemble *E. woodmasoni* (Kemp) in lacking distinct tubercles adjacent to the median carina of the telson, and in this feature differ from *E. massavensis* (Kossmann) and *E. hesperia* (Manning), both from the western Indian Ocean. The two new species differ from *E. woodmasoni* in having the anterior margin of the ophthalmic somite trapezoidal rather than rounded in shape; and the outer inferodistal angle of the raptorial merus produced into a blunt angle rather than a spine. *Erugosquilla grahami* and *E. serenei* can be distinguished by the length of the prelateral lobe of the telson and the color in life of the antennal peduncle.

Erugosquilla Manning, 1995 was erected for species of the *Oratosquilla woodmasoni* species group. *Erugosquilla* is distinguished from other species of *Oratosquilla* and allies by the combination of the broad carapace, smooth dorsum, suppression of the anterior bifurcation of the median carina of the carapace and the apically spinulate anterior margin of the ophthalmic somite.

Manning (1995) recognized *Erugosquilla* for four species: *E. septemdentata* (Ahyong 1994), *E. woodmasoni* (Kemp 1911), *E. massavensis* (Kossman 1880), and *E. hesperia* (Manning 1968). Recent sampling from Australia as part of revisionary work on the Australian fauna and restudy of Vietnamese material collected by Raoul Serène revealed two new species of *Erugosquilla,* one from Australia and Taiwan, and one from Vietnam, described below.

The following abbreviations are used: A1, antennule; A2, antenna; AS, abdominal somite; CI, corneal index (CI), 100CL divided by cornea width; CL, carapace length, measured along the midline, excluding the rostral plate; coll., collector or collected by; F.R.V., Fisheries Research Vessel; IM, intermediate; LT, lateral; m, meter(s); MD, median; MG, marginal; mm, millimeter(s); MXP, maxilliped; n, number; NSW, New South Wales; PLP, pleopod; SM, submedian; St, stomatopod catalogue, MNHN, Paris; TL, total length, measured on the midline, from the anterior margin of the rostral plate to a line between the apices of the submedian teeth of the telson; TS, thoracic somite; WA, Western Australia. Terminology and size descriptors typically follow the conventions of Manning (1969, 1978), supplemented by some abbreviations proposed by Makarov (1979). All measurements are in millimeters.

Type material is deposited in the Australian Museum, Sydney (AM); Muséum National d'Histoire Naturelle, Paris (MNHN); National Taiwan Ocean University (NTOU), Keelung; and the National Museum of Natural History, Smithsonian Institution, Washington (USNM).

Family Squillidae Latreille, 1803

Erugosquilla Manning, 1995

Erugosquilla grahami, new species

Figs. 1, 2, 3A

Oratosquilla woodmasoni.—Graham et al., 1993:73 [list; not *Oratosquilla woodmasoni* (Kemp 1911)].

Material.—Holotype: Australia: AM P4276, 1 ♂, TL 139 mm, off Patonga, NSW, 32°34′S, 151°17′E, trawled, 7–10 m, coll. S. T. Ahyong.

Paratypes: Australia: AM P42767 (to USNM), 1 ♂, TL 133 mm, type locality, coll. S. T. Ahyong, 29 Jan 1994; AM P42762–66, 3 ♂♂, TL 92–141 mm, 2 ♀♀, TL 102–145 mm, type locality, coll. S. T. Ahyong, 12 Feb 1994; AM P42768–70, 3 ♂♂, TL 136–151 mm, type locality, coll. S. T. Ahyong, 12 Feb 1994

Other material.—AM P19332, 2 ♂♂, TL 115–134 mm, 30 miles south of Carnarvon [24°52′S, 113°38′E], WA, sandy mud with *Posidonia* and *Cymodocea* banks, 14–18 m, coll. N. Coleman, 3 Jun 1972; AM P19333, 1 ♀, TL 123 mm, off Carnarvon, WA, 23 m, coll. A. Nickol, May 1972; AM P41798, 1 ♂, TL 134 mm, east of Port Hunter, Newcastle, NSW, 32°55′S, 157°56′E, 66 m, F.R.V. *Kapala,* coll. K. Graham, Jun 1990; AM P41799, 1 ♂, TL 140 mm, southeast of Brunswick Heads, NSW, 28°35′S, 153°34′E, 12–15 m, F.R.V. *Kapala,* coll. K. Graham, 11 Aug 1991; AM P42955, 1 ♂, TL 125 mm, off Newcastle, NSW, 32°55′S, 151°56′E, 69–73 m, F.R.V. *Kapala,* coll. K. Graham, 3 Dec 1990; AM P42956–58, 1 ♂, TL 144 mm, 2 ♀♀, TL 101–141 mm, off Clarence river, NSW, 30°48′S, 153°02′E, 22–30 m, F.R.V. *Kapala,* coll. K. Graham, 5 Nov 1991; AM P42949, 1 ♀, TL 94 mm, Port Jackson, NSW, 33°55′S, 151°15′E, coll. M. Beatson, 7 Mar 1994; AM P42950, 1 ♀, TL 74 mm, Port Jackson, NSW, 33°55′S, 151°15′E, coll. M. Beatson, 7 Mar 1994; AM P42951–54, 2 ♂♂, TL 64–116 mm, 2 ♀♀, TL 122–146 mm, Port Jackson, NSW, 33°51′S, 151°15′E, coll. M. Beatson, 7 Mar 1994.

Taiwan: NTOU, 1 ♂, TL 91 mm, western Taiwan, 50 m, on sand, commercial trawler, 6 Jul 1996.

Description.—Size large, TL of adults to at least 150 mm. Dorsal surface smooth, polished.

Eye large, not extending beyond A1 peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 295-403 (holotype 373).

Ophthalmic somite anterior margin trapezoid, with median spinule. Ocular scales separate, subtruncate.

A1 peduncle subequal to CL. A1 somite dorsal processes trianguloid, apices acute, directed anterolaterally. A2 scale slender, length 0.5–0.7 CL.

Rostral plate broader than long, trapezoid; lateral margins upturned, convergent, straight; apex truncate; dorsal surface lacking MD carina.

Carapace anterior width 0.6 CL; anterolateral spines not extending beyond base of rostral plate; MD carina very low, indistinct; anterior bifurcation absent; with normal complement of carinae (MD, SM, LT, MG); posterior median projection very low or absent.

Raptorial claw dactylus with 6 teeth, outer margin sinuous, lacking basal notch or lobe; carpus dorsal carina irregularl tuberculate; propodus opposable margin evenly pectinate, distal margin lacking stout tooth; merus outer inferodistal angle at most a blunt angle.

Mandibular palp 3-segmented. MXP1–4 each with epipod. MXP5 basal segment with ventrally directed spine.

TS6–8 each with SM and IM carinae, former indistinct. TS5 lateral process bilobed, anterior lobe a slender spine directed anterolaterally, posterior lobe short, triangular, apex acute, directed laterally.

TS6 lateral process bilobed; anterior lobe much smaller than posterior, slender, apex blunt; posterior lobe broad, triangular, anterior margin straight, apex acute.

TS7 lateral process bilobed, anterior lobe much smaller than posterior, latter lobe

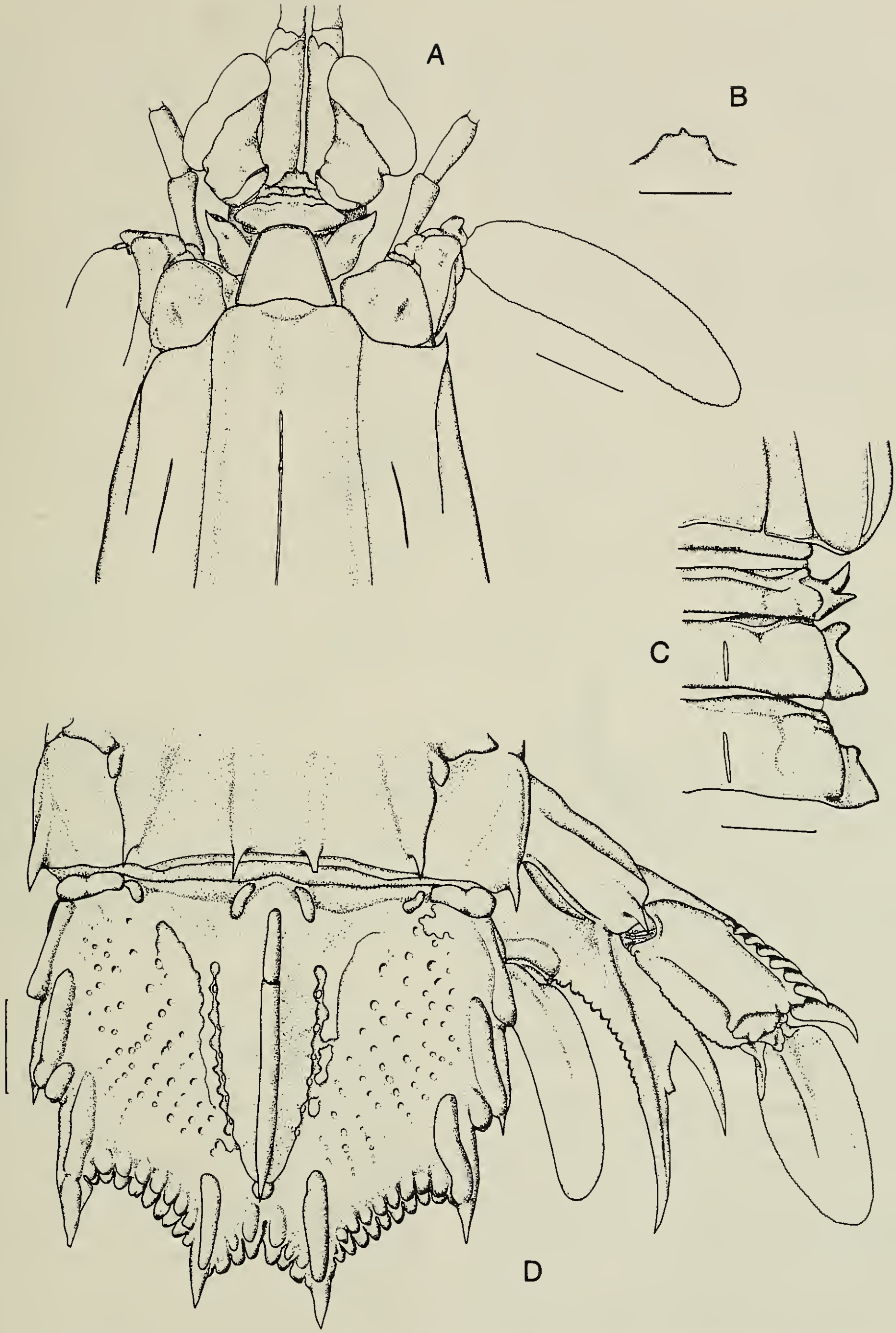

Fig. 1. *Erugosquilla grahami,* new species, male holotype, TL 139 mm, AM P42761. A, Anterior part of body; B, Anterior margin of ophthalmic somite, enlarged; C, Lateral processes of TS5–7; D, AS6, telson, and right uropod. (Setae omitted). Scale: A,C,D, 5 mm; B, 2.5 mm.

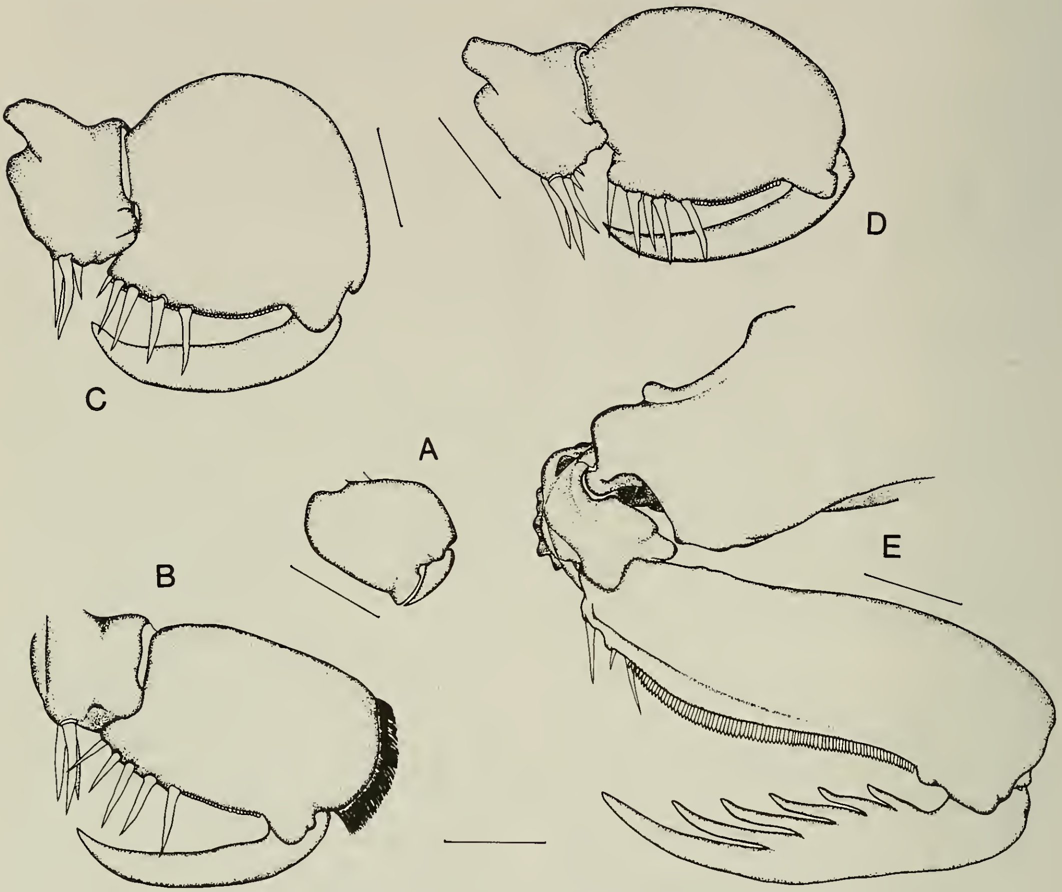

Fig. 2. *Erugosquilla grahami*, new species, male holotype, TL 139 mm, AM P42761. Distal three segments of MXP1–5. A, MXP1; B, MXP5; C, MXP4; D, MXP3; E, MXP2. (Setae omitted). Scale: A–D, 2.5 mm; E, 5 mm.

broad, triangular, anterior margin straight, apex blunt.

TS8 anterolateral margin quadrate, apex blunt; sternal keel rounded.

AS1–5 each with normal complement of carinae (SM, IM, LT, MG). SM carinae low, indistinct; divergent on AS5. AS6 with distinct SM, IM, and LT carinae; with ventrolateral spine anterior to uropodal articulation. Abdominal carinae spined on the following somites: SM 5–6; IM 3–6; LT (2)3–6; MG 1–5.

Male PLP1 endopod with hook process approximately half length of tube process; apex blunt.

Telson flattened, subquadrate, slightly broader than long; with 3 pairs of primary marginal teeth, apices fixed; prelateral lobe subequal to or longer than margin of LT tooth; denticles SM 3–4, IM 8–10, LT 1, rounded, each with dorsal tubercle; carinae of MG teeth slightly inflated in adult males; MD carina interrupted proximally, armed posteriorly with apical spine overhanging 2 blunt tubercles; posteriorly convergent, pitted groove present on each side of MD, lateral margin raised, irregular, but not formed by distinct tubercles; dorsolateral surface with curved rows of shallow pits; ventral surface with postanal carina.

Uropod protopod terminating in 2 slender spines, dorsally and ventrally carinate,

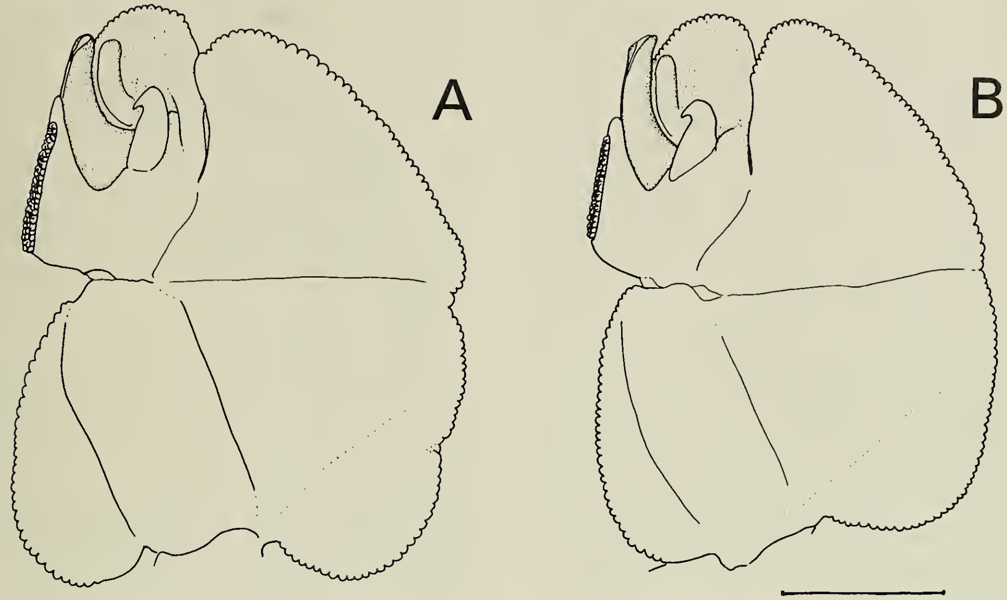

Fig. 3. Endopod of first male PLP (gonopod). A, *Erugosquilla grahami,* new species, male holotype, TL 139 mm, AM P42761; B, *E. serenei,* new species, male paratype, TL 125 mm, AM P12151. (Setae omitted.) Scale: 2.5 mm.

inner longer, unarmed dorsally excepting dorsal spine above proximal exopod articulation; with minute ventral spine anterior to endopod articulation; protopod inner margin crenulate, terminal spines with small, rounded lobe on outer margin of inner spine, margin concave.

Uropod exopod proximal segment unarmed dorsally; outer margin with 7–9 (usually 8) sharp, graded, movable spines, distalmost not exceeding midlength of distal segment; distal margin with slender ventral spine; exopod distal segment longer than proximal segment; endopod unarmed dorsally, with 1 dorsal and 1 ventral carina.

Color in life.—Base color white; overall dorsal surface pale gray-green. Margin of rostral plate, dorsal carinae and gastric grooves of carapace, posterior margin of carapace and thoracic somites, SM carinae of thoracic and abdominal somites, red. A1 peduncle with alternating blue and yellow-orange banding. A2 scale blue proximally, yellow distally. Meral-carpal articulation of raptorial merus yellow. Meral depression pale yellow. IM and LT carinae of AS5–6 dark green; apices of spines red. AS2, 5 with dark rectangular median patch. Dorsal surface of telson maroon; carinae and denticulate dorsal tubercles dark green; denticles and marginal teeth white. Proximal segment of uropodal exopod dark blue; distal segment blue proximally, yellow distally. Endopod blue; distal tip yellow. No color differences were noted between the sexes.

Etymology.—This species is named for Mr. Ken Graham, NSW Fisheries, who collected much of the material used in this study.

Measurements.—Holotype: AM P42761, male, TL 139 mm, CL 26.5 mm, cornea width 7.1 mm. Paratypes: Males (n = 7), TL 92–151 mm; females (n = 2), TL 102 and 145 mm. Other material: males (n = 9) 64–151 mm; females (n = 7) TL 74–146 mm.

Remarks.—*Erugosquilla grahami,* new species, is morphologically most similar to *E. woodmasoni* (Kemp 1911) in the relatively short rostral plate and length of the prelateral lobes of the telson (subequal to or longer than margin of LT). The two species differ in the shape of the anterior margin of the ophthalmic somite (trapezoid in *E. grahami* and broadly rounded in *E. woodmasoni*), abdominal carination (*E. grahami* generally has fewer posteriorly armed lateral carinae), and the condition of the outer inferodistal angle of the raptorial merus (armed in *E. woodmasoni*). The two species have similar general coloration, including blue uropods, but may be distinguished by coloration of the A1 peduncles (red-maroon in *E. woodmasoni,* banded blue and yellow-orange in *E. grahami*). Differences between *E. grahami* and *E. serenei* are noted below, under the account of the latter species.

Both *E. woodmasoni* and *E. grahami* are known from New South Wales, but the latter is more common. Like most squillids, *E. grahami* inhabits shallow coastal waters and constructs burrows in soft level substrates. The present specimens were collected in depths of 7–73 m (but usually less than 30 m), over sandy mud and vegetated sand (*Cymodocea* and *Posidonia*).

The known distribution of *E. grahami* (i.e., Taiwan and Australia) is discontinuous, but likely reflects limited sampling effort in intermediate localities. The disjunct Australian distribution of *E. grahami* suggests that it probably occurs throughout northern Australian waters. The Taiwanese specimen agrees in almost all respects, including live coloration, with Australian material, except that the TS7 lateral process anterior lobe is sharper than in most Australian specimens.

Distribution.—Taiwan and Australia, from northern New South Wales, south to Port Jackson, and Carnarvon, Western Australia.

Erugosquilla serenei, new species
Figs. 3B, 4

Squilla massavensis.—Serène, 1951:fig. 2 [Vietnam]; 1953:507 [Vietnam]; 1954:6, 8, 54, 60–62, 87, pl. 3, figs. 5–8 [Nhatrang (12°15′N, 109°12′E) and Cauda (12°11–13′N, 109°13–16′E) bays, Vietnam]. [Not *Squilla massavensis* Kossmann 1880.]

Erugosquilla hesperia.—Manning, 1995: 24, 198, figs. 121, 122, 123a, 136a, pl. 35 [color] [Nhatrang and Cauda bays, Vietnam]. [Not *Squilla hesperia* Manning 1968.]

Material.—Holotype: MNHN-St 1940, 1 ♂, TL 125 mm, Vietnam, Oceanographic Institute of Nhatrang, opposite the laboratory, coll. R. Serène, Nov 1948.

Paratypes: USNM 266696, 1 ♂, TL 126 mm, Vietnam, coll. R. Serène, 20 May 1949; same data, USNM 266693, 1 ♀, TL 124 mm.—USNM 266695, Nhatrang Bay, 1 ♀, TL 103 mm, coll. R. Serène, 21 May 1949.—USNM 277646, 1 ♀, TL 142 mm, Oceanographic Institute of Nhatrang; AM P12151, 1 ♂, 126 mm, same locality, depth 25 m, coll. R. Serène, 23 Nov 1949; AM P51049, 1 ♀, 116 mm, same locality, coll. R. Serène, 23 Nov 1949.

Description.—Size large, TL of adults to at least 140 mm. Dorsal surface smooth, polished.

Eye large, extending to or slightly overreaching A1 peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 325–380 (holotype 349).

Ophthalmic somite anterior margin trapezoidal, with small median spinule (broken in Fig. 4A). Ocular scales separate, subtruncate.

A1 peduncle slightly shorter than CL. A1 somite dorsal processes triangular, apices acute, directed anterolaterally. A2 scale slender, length 0.7 CL.

Rostral plate appearing elongate, length and width at base subequal; lateral margins upturned, convergent anteriorly, straight; apex truncate; dorsal surface lacking MD carina.

Carapace anterior width 0.6 CL; anterolateral spines not extending beyond base of rostral plate; MD carina distinct posterior to

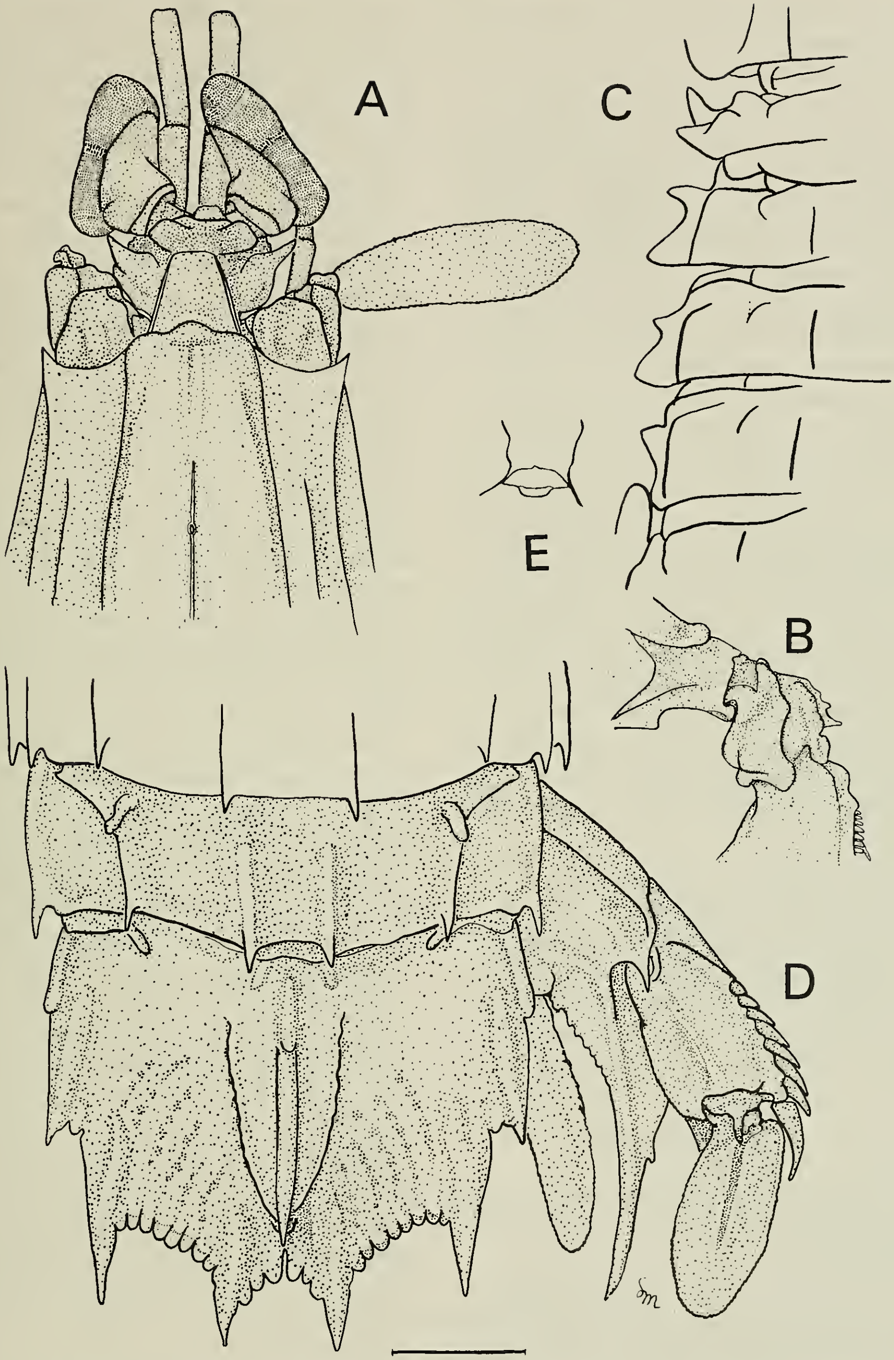

Fig. 4. *Erugosquilla serenei,* new species. A–D, female paratype, TL 103 mm, USNM 266695; E, female paratype, TL 124 mm, USNM 266693. A, Anterior part of body; B, Carpus of raptorial claw; C, Lateral processes of TS5–8; D, AS5–6, telson, and right uropod; E, anterior margin of ophthalmic somite. (Setae omitted). Scale: A–D, 5 mm; E, 2.5 mm.

dorsal pit, anterior bifurcation absent; with normal complement of carinae; posterior median projection very low.

Raptorial claw dactylus with 6 teeth, outer margin sinuous, slightly inflated, lacking basal notch or lobe; carpus dorsal carina irregularly tuberculate; propodus opposable margin evenly and finely pectinate, distal margin lacking sharp tooth; merus outer inferodistal angle a low, obtuse projection.

Mandibular palp 3-segmented. MXP1–4 each with epipod. MXP5 basal segment with low, ventrally directed spine.

TS6–8 each with SM and IM carinae, SM carinae indistinct. TS5 lateral process bilobed, anterior lobe a slender spine directed anterolaterally, posterior lobe short, triangular, apex acute, directed laterally.

TS6 lateral process bilobed, anterior lobe much shorter than posterior, slender, anterior margin convex, apex acute; posterior lobe broad, triangular, anterior margin straight, apex acute.

TS7 lateral process bilobed, anterior lobe much smaller than posterior; latter broad, triangular, anterior margin straight, apex blunt.

TS8 anterolateral margin quadrate, apex blunt; sternal keel rounded.

AS1–5 each with normal complement of carinae (SM, IM, LT, MG); SM carinae distinct, subparallel or slightly divergent posteriorly. AS6 with distinct SM, IM, and LT carinae; with minute ventrolateral spine anterior to uropod articulation. Abdominal carinae spined on following somites: SM (4) 5–6, IM (2) 3–6, LT 1–6, MG 1–5.

Male PLP1 endopod with hook process approximately half length of tube process; apex blunt.

Telson flattened, subquadrate, length and width subequal, with 3 pairs of primary marginal teeth, apices fixed; prelateral lobe shorter than margin of LT tooth; denticles SM2–3, IM7–9, LT1, rounded, each with dorsal tubercle; carinae of MG teeth at most slightly inflated in adult males; median carina interrupted proximally, armed posteriorly with apical spine overhanging 2 blunt tubercles; with single, submedian, curved, irregular carina on each side, converging posteriorly under base of median spine, and dorsolateral surface with curved rows of shallow pits; ventral surface with postanal carina.

Uropod protopod terminating in 2 slender spines, dorsally and ventrally carinate, inner longer; unarmed dorsally excepting dorsal spine above proximal exopod articulation; with minute ventrolateral spine anterior to endopod articulation; protopod inner margin crenulate, terminal spines with very small, rounded lobe on outer margin of inner spine, margin concave.

Uropodal exopod proximal segment unarmed dorsally; outer margin with 8 sharp, graded, movable spines, distalmost not extending to midlength of distal segment; distal margin with slender ventral spine; exopod distal segment subequal to proximal segment; endopod unarmed dorsally, with 1 dorsal and 1 ventral carina.

Color in life.—Basic color tan. Margin of rostral plate, dorsal carinae and gastric grooves of carapace, carinae of TS and AS, median carina of telson, and some carinae of uropod, red. A1 peduncle tan, not markedly banded; A2 scale tan. Raptorial dactylus ivory white. AS2,5 each with dusky, rectangular dorsal patch. Uropod exopod proximal segment light blue, with some white anteriorly, grading to dark blue distally, proximal segment bluish mesially, white laterally. Uropod endopod reddish mesially, tan laterally.

Etymology.—Named for the late Raoul Serène, who first recorded it from Vietnam.

Measurements.—Holotype: MNHN-St 1940, male, TL 125 mm, CL 26.2 mm, cornea width 7.5 mm. Paratypes: Males (n = 2), both TL 126 mm; females (n = 4) TL 103–142 mm.

Remarks.—Erugosquilla serenei resembles *E. grahami* and differs from *E. woodmasoni* (Kemp) in having the anterior margin of the ophthalmic somite trapezoidal in shape rather than evenly rounded and a blunt angle or lobe rather than a sharp spine at the outer inferodistal angle of the merus of the raptorial claw. *Erugosquilla serenei* differs from *E. gracilis* in having a narrower rostral plate; the prelateral lobe of the telson shorter than the LT margin; and, the antennal peduncle uniformly colored in life rather than banded with blue and yellow-orange.

Erugosquilla woodmasoni and its four congeners that have six teeth on the dactylus of the claw all also have a groove on each side of the MD carina of the telson that converges under the posterior spine of the MD carina. In *E. woodmasoni,* this groove is shallow and lacks a flanking carina or row of distinct tubercles; the groove is much more distinct in the other four species. Both *E. hesperia* and *E. massavensis* have distinct tubercles flanking this groove, one row in the former, two rows in the latter. In both of the new species the row of tubercles is replaced by an irregularly tuberculate carina.

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Key to Species of *Erugosquilla*

1. Dactylus of claw with 7 teeth; rostral plate as long as broad, apex evenly rounded .... *E. septemdentata* (Ahyong 1994) [Indonesia]
– Dactylus of claw with 6 teeth; rostral plate usually apically flattened 2
2. Telson median carina flanked by groove on each side, convergent posteriorly, with or without an irregular lateral carina, lacking distinct tubercles 3
– Telson median carina flanked by one or more rows of tubercles 5
3. Ophthalmic somite anterior margin broadly rounded, usually with apical spinule; outer inferodistal angle of raptorial merus produced to a blunt spine; A2 peduncle red-maroon in life .... *E. woodmasoni* (Kemp 1911) [western *Pacific to western Indian Ocean*]
– Ophthalmic somite anterior margin trapezoid, with apical spinule; outer inferodistal angle of raptorial merus produced to at most a blunt angle; A2 peduncle not red-maroon in life 4
4. Telson prelateral lobe subequal to or longer than margin of lateral tooth; A2 peduncle banded with blue and yellow-orange in life .... *E. grahami,* new species [Australia and Taiwan]
– Telson prelateral lobe shorter than margin of lateral tooth; antennal peduncle uniformly colored .... *E. serenei,* new species [Vietnam]
5. Rostral plate lateral margins sinuous; telson with 2 rows of tubercles flanking median carina .... *E. massavensis* (Kossmann, 1880) [Red Sea and western Mediterranean]
– Rostral plate lateral margins straight; telson with 1 row of tubercles flanking median carina .... *E. hesperia* (Manning 1968) [western Indian Ocean]

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Two new species of Macrobiotidae (Tardigrada: Eutardigrada) from the United States of America, and some taxonomic considerations of the genus *Murrayon*

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Abstract.—Two new species of eutardigrades, *Macrobiotus nelsonae* and *Murrayon stellatus,* collected in Tennessee, U.S.A., are described. *Macrobiotus hibernicus* and *Macrobiotus dianeae,* related to *M. stellatus,* are re-examined and ascribed to the genus *Murrayon* on the basis of the claw type and the presence of a ventral hook on the strengthening bar. A dichotomous key to the genus *Murrayon* is proposed.

Thulin (1928), Marcus (1936) and Ramazzotti (1962), in their systematic monographs on tardigrades, included all eutardigrades (except *Milnesium*) in the family Macrobiotidae and all those with so-called 'symmetric' claws, i.e., with respect the median plane of the leg, in the genus *Macrobiotus.* Pilato (1969a, 1969b) proposed to separate the eutardigrades in different families on the basis of the claw structure, ascribing to Macrobiotidae only the genera characterized by 'symmetric' claws, i.e., *Macrobiotus* and *Pseudodiphascon* (the latter erected as a subgenus by Ramazzotti in 1965). The status of this family remained almost unchanged until the 1980s, when new taxonomic characters, related to the bucco-pharyngeal apparatus and to the claws, were considered for the identification of the genera (Schuster et al. 1980, Bertolani 1981, Pilato 1981, Bertolani & Kristensen 1987). Today 11 genera are placed in the Macrobiotidae. Moreover, the number of known species has been increased remarkably due to a more in-depth analysis and the use of a greater number of characters. Within the genus *Macrobiotus,* for example, is the so-called '*hufelandi*' group studied by light microscopy and scanning electron microscopy (SEM) by Biserov (1990a, 1990b) and by Bertolani & Rebecchi (1993), who identified several new species within this group with so-called high intra-specific variability. Within the genus *Macrobiotus,* natural groups of species sharing similar morphology of the animals and/or of spermatozoa and eggs were identified, which led to the hypothesis of further possibilities of subdivision at the genus or subgenus level (Guidi & Rebecchi 1996).

Tardigrades from new material collected in Tennessee (U.S.A.) and comparisons with known related species have expanded our knowledge of the systematics of Macrobiotidae, one of the larger and more complex families of eutardigrades, leading to the erection of two new species and the redesignation of two other species.

Methods

Specimens from 44 samples of beech leaf litter (*Fagus grandifolia* Ehrb.) collected in fall 1995, winter 1995–1996, and spring 1996 on Roan Mountain (Southern Appalachians, Carter County, Tennessee, U.S.A.) at different altitudes (1200 m, 1500 m and 1650 m asl) were examined. Tardigrades and their eggs were preserved for SEM examinations or directly mounted in polyvinyl-lactophenol or in Hoyer's medium, or stained with acetic carmine and subsequently mounted in Faure-Berlese's mounting medium for the light microscopy (LM) observations. Light microscopy observations were done with phase contrast and differential interference contrast (DIC) under oil immersion (100×). The specimens prepared for SEM were fixed in absolute ethanol, critical point dried in liquid CO_2 and sputter-coated with gold-palladium. All the specimens were examined using a Philips SEM 500 at the 'Centro Interdipartimentale Grandi Strumenti' of the University of Modena.

As comparison material, several specimens were used: *Murrayon pullari* (Murray 1907) from Monte Rondinaio, Emilia Romagna, Italy (from Bertolani's collection); *Murrayon hastatus* (Murray 1907) from Angerfjrden, Sweden (from Kristensen's collection); *Macrobiotus hibernicus* Murray 1911 from Valtellina, Lombardia, Italy (from Pilato's collection), from Valico of Gran San Bernardo, Valle d'Aosta, Italy, from Val Piantonetto, Piemonte, Italy (both from Maucci's collection; the latter presented to him by C. Robotti) and from Godhavn, Greenland (from Kristensen's collection); *Macrobiotus dianeae* Kristensen 1982 from Unartog, Greenland (paratypes from Kristensen's collection), from Monte Rondinaio, Emilia Romagna, Italy (from Bertolani's collection); a paratype and an egg of *Macrobiotus avigliianae* Robotti 1970, and the holotype and an egg of *Macrobiotus pallarii* Maucci 1954 (both from Maucci's collection).

Macrobiotus nelsonae, new species
(Figs. 1–5, Table 1)

Etymology.—The species is dedicated to Dr. Diane R. Nelson, professor at East Tennessee State University, whose hospitality and help allowed this work.

Paratypes.—566 paratypes and 322 eggs mounted in polyvinyl-lactophenol, Hoyer's medium and Faure-Berlese (permanent slides), 3 paratypes and 3 eggs on stubs for SEM observation.

Holotype.—Adult male 786.1 μm in length, collected in January 1996, mounted in polyvinyl-lactophenol, slide labeled as 5N05a-S10 (Fig. 1A).

Type locality.—Roan Mountain (Carter County, Tennessee) on the north-facing slope at elevations between 1200 and 1650 m asl, in leaf litter from beech trees.

Diagnosis.—Animals of large size. Smooth cuticle with pores. Eye-spots anterior. Wide buccal tube; evident buccal armature, with two consistent bands of teeth and with transverse crests. Two rod-shaped macroplacoids and microplacoid. Claws of the '*hufelandi*' type, with lunulae. Eggs laid freely, with big conical reticulated processes inserted onto an areolate surface.

Description.—Length from 196.0 up to 925.4 μm. Colorless, although the largest animals may have a pink coloration. Eyespots in anterior position. Smooth cuticle, with oval cuticular pores not uniform in size and irregularly distributed, much more visible in the anterior and posterior part of the animal. In some animals a uniform and fine punctuation on the dorsal cuticle is visible, much more identifiable in recently prepared specimens (Fig. 2). Ten evident peribuccal lamellae. Buccal armature characterized by an anterior band of small teeth (mucrones), followed by a large posterior band of larger teeth, whose dimensions increase caudally (Figs. 1C, D). Three transverse crests, the dorsal ones longer than the ventral; in some animals the median ventral crest is subdivided in two or seldom into more segments of variable length. Wide buccal tube. Rounded pharyngeal bulb (ratio length/width 1.1–1.3:1) with large apophyses, two rod-shaped macroplacoids and an evident microplacoid. First macroplacoid the longest, with an evident narrowed midportion, the second with a subterminal constriction (Fig. 1B). Massive claws, of '*hufelandi*' type (Y-shaped; Figs. 1E, F), the claws of the front legs the smallest and those of the hind legs the largest. Main branch of the outer claw slightly longer than that of the inner one, both bearing

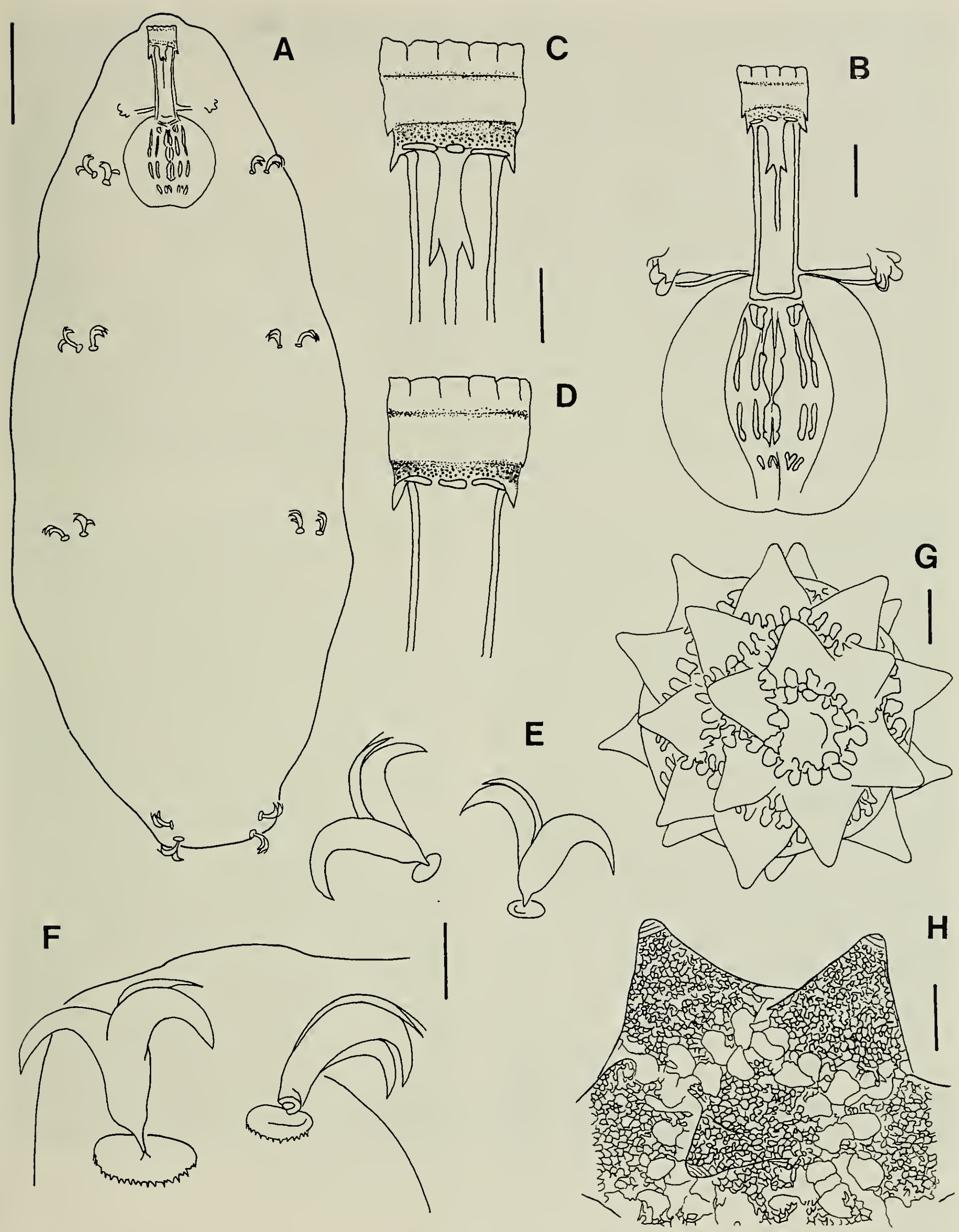
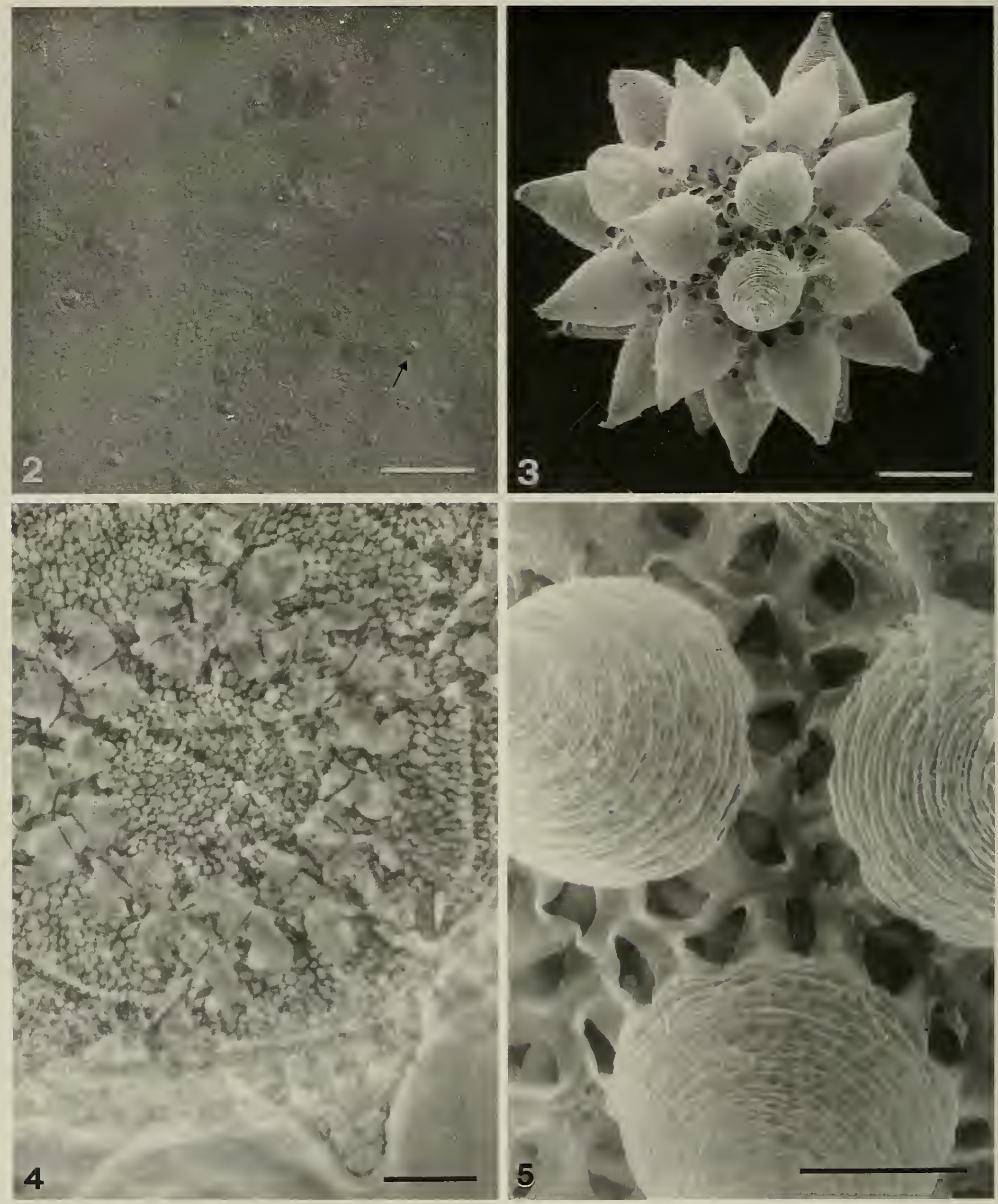


Fig. 1. Holotype of *Macrobiotus nelsonae* sp. n. A, Habitus (ventral view); B, Bucco-pharyngeal apparatus (frontal view); C, Buccal armature (ventral view); D, Buccal armature (dorsal view); E, Claws of the front legs; F, Claws of the hind legs; G, Egg. H, Particular of the egg. Scale bars, 100 μm for A; 20 μm for B, G; 10 μm for C, D, E, F, H.



Figs. 2–5. *Macrobiotus nelsonae* sp. n. 2, Dorsal cuticle with pores (arrow) and fine punctuation (DIC); 3, Egg in toto (SEM); 4, Particular of the egg (Phase contrast); 5, Particular of the egg (SEM). Scale bars, 10 μm for Figs. 2, 4, 5; 20 μm for Fig. 3.

evident accessory points. Small lunulae at the base of the claws of the first three pairs of legs. Lunulae surrounded by fine teeth in the largest animals. Lunulae of the hind claws large, even larger on the posterior claws, and with teeth of irregular dimensions in the largest animals. Three animals with modified claws on only one side of the hind legs. Two of them show a supernumerary spur (on the anterior claw in one

Table 1.—Measurements and *pt* index of the holotype* (786.1 μm in length) and nine paratypes of *M. nelsonae* sp. n.

	al	btl	btd	ssi	prl	1°pl	2°pl	ecl1°	icl1°	ecl3°	icl3°	pcl4°	acl4°
μm	embryo	42.6	5.9	34.7	16.8	9.9	5.0						
pt			13.8	81.5	39.4	23.2	13.8						
μm	230.0	33.7	5.0	27.7	14.9	7.9	5.9	7.9	6.9	8.9	7.9	9.9	8.9
pt			14.8	82.2	44.2	23.4	17.5	23.4	20.5	26.4	23.4	29.4	26.4
μm	258.7	34.0	4.0	27.0	16.8	8.9	5.9	8.9	7.9	8.9	7.9	9.9	8.9
pt			11.8	79.4	49.4	26.2	17.4	26.2	23.2	26.2	23.2	29.1	26.2
μm	437.8	46.5	6.9	37.6	26.7	14.9	10.9	10.9	9.9	11.9	9.9	12.9	11.9
pt			14.8	80.9	57.4	32.0	23.4	23.4	21.3	25.6	21.3	27.7	25.6
μm	587.1	61.4	10.9	51.5	38.6	21.8	13.9	12.9	11.9	14.9	11.9	16.8	14.9
pt			17.8	83.9	62.9	35.5	22.6	21.0	19.4	24.3	19.4	27.4	24.3
μm	626.9	57.4	10.9	48.5	36.6	21.8	12.9	12.9	11.9	15.8	12.9	17.8	16.8
pt			19.0	84.5	63.8	38.0	22.5	22.5	20.7	27.5	22.5	31.0	29.3
μm	786.1*	69.3	13.9	58.4	49.5	29.7	16.8	14.9	13.9	17.8	15.8	20.8	16.8
pt			20.1	84.3	71.4	42.9	24.2	21.5	20.1	25.7	22.8	30.0	24.2
μm	786.6	69.3	15.8	57.4	50.5	29.7	18.8	17.8	15.8	18.8	17.8	21.8	18.8
pt			22.8	82.8	69.3	42.9	27.1	25.7	22.8	27.1	25.7	31.5	27.1
μm	815.9	76.2	15.8	63.4	53.5	32.7	18.8	16.8	15.8	16.8	15.8	19.8	18.8
pt			20.7	83.2	70.2	42.9	24.7	22	20.7	22	20.7	26	24.7
μm	925.4	77.2	14.9	64.4	54.5	31.7	20.8	17.8	15.8	18.8	16.8	19.8	19.8
pt			19.3	83.4	70.6	41.1	26.9	23.1	20.5	24.6	21.8	25.6	25.6

al = animal length; btl = buccal tube length; btd = inner diameter of the buccal tube; ssi = stylet supports insertion level on the buccal tube; prl = macroplacoids row length; 1°pl = first macroplacoid length; 2°pl = second macroplacoid length; ecl = external claw length; icl = internal claw length (1° = front leg, 3° = second or third pair of legs); pcl = posterior claw length; acl = anterior claw length (4°= hind legs).

case, in the posterior one in another one); another one has a third branch on a posterior claw.

Measurements and *pt* indices (percentage ratio between the length of the considered structure and the length of the buccal tube; Pilato 1981) of the holotype and nine paratypes are reported in Table 1.

Midgut of the largest animals containing mastax of rotifers and sclerified parts of the bucco-pharyngeal apparatus of eutardigrades.

In the testis of male specimens stained with acetic carmine, spermatozoa with a particularly elongated and coiled head are visible.

Large eggs (diameter from 84.7 to 129.5 μm without processes; Figs. 1G, 3). Conical processes (height from 20.8 to 31.7 μm, diameter of the base from 20.0 to 34.7 μm) showing a reticular pattern with meshes of very irregular, variable shape and size (Figs. 1H, 4, 5). By SEM their surfaces appear annulated (Fig. 5). Top of the processes rounded and usually without reticulation but with a fine annulation, sometimes lightly notched. Each process is separated from the others by a double series of 11–12 polygonal areolations (5–6 μm in diameter) inside which no sculpture is visible (Figs. 4, 5).

Remarks.—Comparisons with the type material of *Macrobiotus pallarii* and *Macrobiotus avaglianae* confirmed the synonymy between these two species as pointed out by Pilato & Binda (1977), and indicated the close relationship between *Macrobiotus nelsonae* and *M. pallarii*. In *M. nelsonae* the average size of the animals is decidedly larger, there is a more evident microplacoid, a more complex buccal armature with a larger posterior band of teeth, a wider buccal tube, larger claws and a more posterior insertion of the stylet supports on the buccal tube. The most evident difference between *M. nelsonae* and *M. pallarii* is in the eggs.

The processes are more than twenty per hemisphere in *M. pallarii* (checked on type material) and always less than fifteen in *M. nelsonae*; they are also much longer. The areolations at the base of the processes are fewer in number in *M. pallarii* (8–9 instead of 11–12 in *M. nelsonae*) and never in a double series. In *M. nelsonae* the *pt* index seems to change with the size of the animal. Comparative studies on other species may provide further informations.

Repositories.—Holotype, 88 paratypes and 54 eggs are in R. Bertolani's collection in the Department of Animal Biology at the University of Modena; 473 paratypes and about 260 eggs in D. R. Nelson's collection in the Department of Biological Sciences of East Tennessee State University; 5 paratypes and 6 eggs are in the National Museum of Natural History, Smithsonian Institution of Washington, D.C.

Murrayon stellatus, new species
(Figs. 6–8, Table 2)

Etymology.—From *stellatus* (Latin), meaning "starry," for the star-like dots on the cuticle of the animals.

Paratypes.—6 paratypes mounted in polyvinyl-lactophenol and Hoyer's medium and 1 egg mounted in polyvinyl-lactophenol.

Holotype.—Length 234.1 μm, collected in January 1996 and mounted in Hoyer's medium, slide labelled as 5N08b-S12.

Type locality.—Roan Mountain (Carter County, Tennessee, U.S.A.), on the north-facing slope at elevations of 1500 m asl in leaf litter from beech trees.

Diagnosis.—Cuticle punctated, with evident dorsolateral bands of relatively large star-like dots. Three rod-shaped macroplacoids, microplacoid absent. Eggs laid freely, with small rod-shaped processes.

Description.—From 162.1 to 234.1 μm in length, colorless, without eye-spots. Entire cuticle has a fine punctuation; moreover, two dorsolateral bands (width about 10 μm and visible at low magnification, 5× objective) of star-like dots are also very visible (Figs. 6A, 7). They run through each side of the body and join anteriorly at the front of the animal and posteriorly just in front of the hind legs. The stars seem finer and closer together on the front of the animal and in sections above each leg, where they cover the basal portion of the dorsal surface (Fig. 7). Peribuccal lamellae evident. In these specimens the components of the buccal armature are not identifiable. Stylet supports inserted on the buccal tube at about two-thirds of its length. Shape of the strengthening bar characteristic of the genus, with a showy ventral hook. Buccal tube relatively large. Pharyngeal bulb round (ratio length/width 1.1–1.2:1), containing large apophyses and three slender rod-shaped macroplacoids (Fig. 6B). The first is the longest; the second, very close to the first, the shortest; the third shows an evident subterminal constriction. Legs long. Claws small, of '*pullari*' type (V-shaped and with a peduncle, quadrate in lateral view; Figs. 6C, D), larger on the hind legs. Main branch of the claws with evident accessory points. Small smooth lunulae at the base of each claw.

Measurements and *pt* indices of the holotype and two paratypes, compared with two paratypes of *Macrobiotus dianeae* and two specimens of *Macrobiotus hibernicus* (coll. Kristensen), are reported in Table 2.

A small broken egg was found at the type locality and attributed to this species because of its similarity with that of the related species *M. dianeae* and *M. hibernicus*. The egg has rod-shaped processes of 3–4 μm in height with a large base and a smaller head shaped like that of a nail (Fig. 6E). The processes look often curved. Some processes have a short thin spine on their heads. At some points a hyaline matrix covering the processes is visible. The processes are aligned to include wide polygonal areas, sometimes incomplete. The surfaces of these areas seem smooth.

Remarks.—*Murrayon stellatus* is similar to *Macrobiotus dianeae* and to *Macrobiotus*

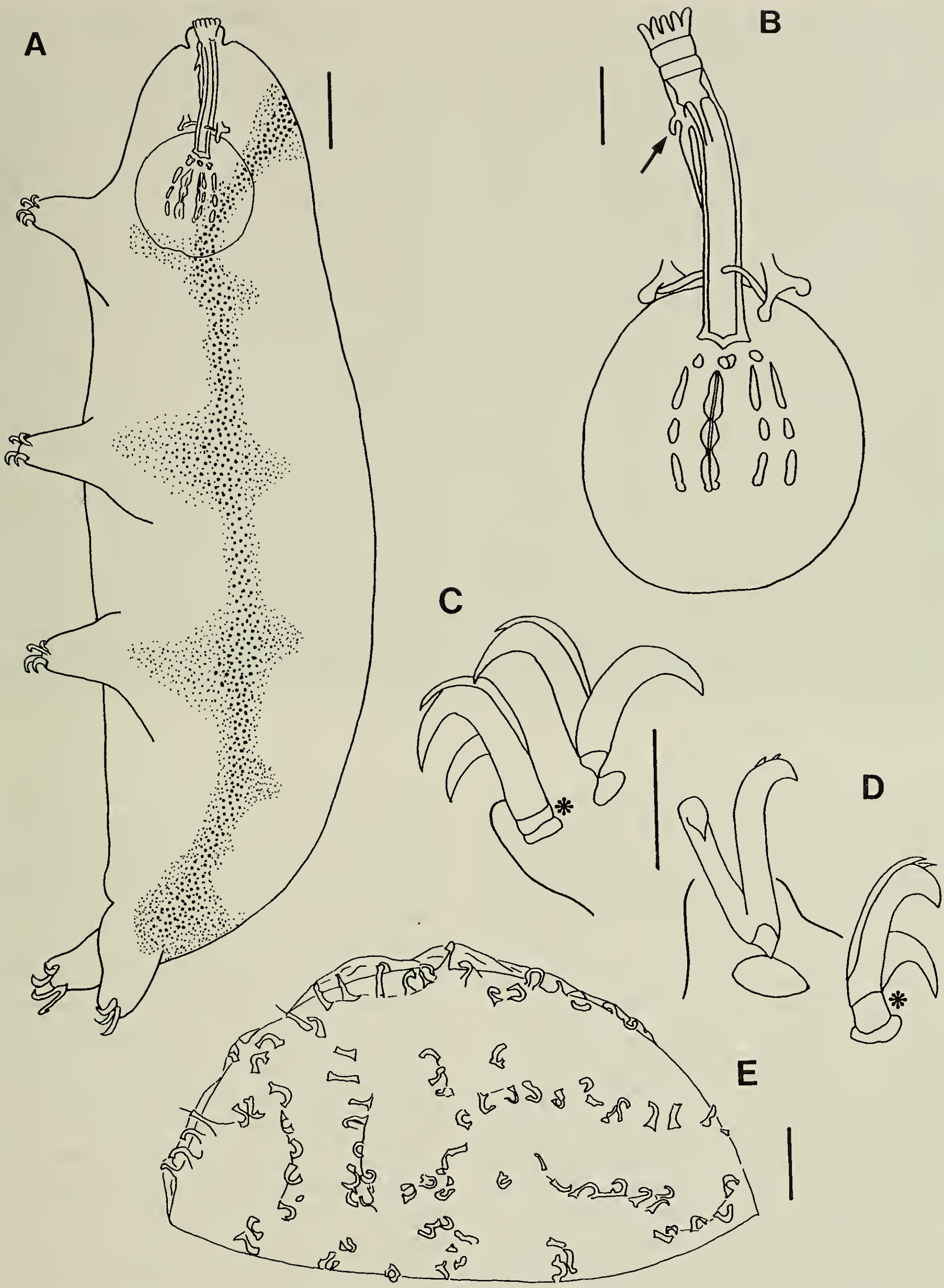


Fig. 6. Holotype of *Murrayon stellatus* sp. n. A, Habitus (lateral view); B, Bucco-pharyngeal apparatus (lateral view); C, Claws of the third pair of legs; D, Claws of the hind legs; E, Egg detail. Note in B the hook on the ventral tube (arrow) and in C and D the quadrate peduncle at the bases of the claws (asterisks). Scale bars, 20 μm for A; 10 μm for B, E; 5 μm for C, D.

Table 2.—Measurements and *pt* index of the holotype* (234.1 µm in length) and two paratypes of *M. stellatus* sp. n., two specimens of *M. hibernicus* and two paratypes of *M. dianeae.*

	al	btl	btd	ssi	prl	1°pl	2°pl	3°pl	ecl1°	icl1°	ecl3°	icl3°	pcl4°	acl4°
M. stellatus sp. n.														
µm	214.1	29.7	4.0	20.8	12.9	5.0	3.0	4.0	—	—	5.9	5.9	6.9	6.9
pt			13.5	70.0	43.4	16.8	10.1	13.5	—	—	19.9	19.9	23.2	23.2
µm	219.1	27.7	4.0	20.8	—	—	—	—	5.9	5.9	5.9	5.9	6.9	6.9
pt			14.4	75.1	—	—	—	—	21.3	21.3	21.3	21.3	24.9	24.9
µm	234.1*	29.7	3.0	20.8	13.9	5.0	3.0	4.0	5.9	5.9	5.9	5.9	6.9	6.9
pt			10.1	70.0	46.8	16.8	10.1	13.5	19.9	19.9	19.9	19.9	23.2	23.2
M. hibernicus														
µm	204.0	23.8	2.0	15.8	10.9	4.0	3.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0
pt			8.4	66.4	45.8	16.8	12.6	16.8	16.8	16.8	16.8	16.8	16.8	16.8
µm	239.0	25.7	2.0	18.8	11.9	4.0	3.0	4.0	5.0	5.0	5.0	5.0	5.0	5.0
pt			7.8	73.2	46.3	15.6	11.7	15.6	19.5	19.5	19.5	19.5	19.5	19.5
M. dianeae														
µm	204.0	24.8	2.0	16.8	11.9	4.0	3.0	4.0	4.0	4.0	4.0	4.0	—	—
pt			8.1	67.7	48.0	16.1	12.1	16.1	16.1	16.1	16.1	16.1	—	—
µm	259.0	31.7	3.0	23.8	14.9	5.0	3.0	5.0	6.9	6.9	6.9	6.9	6.9	6.9
pt			9.5	75.1	47.0	15.8	9.5	15.8	21.8	21.8	21.8	21.8	21.8	21.8

al = animal length; btl = buccal tube length; btd = inner diameter of the buccal tube; ssi = stylet supports insertion level on the buccal tube; prl = macroplacoid row length; 1°pl = first macroplacoid length; 2°pl = second macroplacoid length; 3°pl = third macroplacoid; ecl = external claw length; icl = internal claw length (1° = front leg, 3° = second or third pair of legs); pcl = posterior claw length; acl = anterior claw length (4° = hind legs).

hibernicus. The original description of *M. hibernicus* was based on an animal artificially extracted from the egg (Murray 1911). Murray described three macroplacoids of similar size, twice as long as wide, and a microplacoid, but he did not cite any cuticular sculpture. This structure was reported by Cuénot (1932), who described a punctated band of very fine grains that forms a connecting band or bridge on the dorsal surface (at a level corresponding to the pharyngeal bulb) and that continues down on the sides of the animal, running longitudinally to the caudal extremity. Cuénot added that the second macroplacoid is a little shorter than the first one and in contact with it, the third is the longest, and the microplacoid is present, but can also be absent. The attribution of the Cuénot's material to *M. hibernicus* is not certain, but very probable because of the considerable similarity of the eggs with that described by Murray (1911). The same aspect of the cuticular sculpture described by Cuénot is present in specimens of *M. hibernicus* from Val Piantonetto, Piemonte, Italy, in Mauccci's collection and from Godhavn, Greenland, in Kristensen's collection. With light microscopy *M. stellatus, M. hibernicus,* and *M. dianeae* show a similar type of cuticle. The cuticle of *M. dianeae* was studied by TEM and defined as a "'heterotardigrade type', with a mucous layer, outer laminary layer, epicuticle separated in two layers by means of pillars (rods), inner trilaminary layer and procuticle" (Kristensen 1982). Moreover, these species have very similar claws and bucco-pharyngeal apparati (see following sections: further systematic results and discussion). *Murrayon stellatus* differs from *M. dianeae* in having a more evident cuticular sculpture, very visible even with low magnification, in having a clearly rounded bulb and in having the first macroplacoid longer than the other two. Moreover the claws of *M. dianeae* are de-

Figs. 7–8. *Murrayon stellatus* sp. n. 7, Sculpture of the dorsolateral cuticle (DIC); 8, Cuticle with pillars (arrow; DIC). Scale bars, 1 μm.

cidedly smaller in animals of similar length. *M. stellatus* differs from *M. hibernicus* in the type of the punctation of the cuticle, which in *M. hibernicus* is hardly visible and only at high magnification (although dorsolateral bands are present in some observed specimens but clearly less evident than in *M. stellatus*), in having a larger buccal tube and the hind claws longer than the first three pairs. Also the egg is very similar to those of *M. hibernicus* and *M. dianeae,* but it differs from both in that the heads of the processes are smaller in diameter and also short spines are present on the processes of *M. stellatus* but absent in *M. hibernicus* and longer and very visible in *M. dianeae.*

Repositories.—Holotype, 4 paratypes and an egg are in R. Bertolani's collection in the Department of Animal Biology at the University of Modena, 2 paratypes are in D. R. Nelson's collection in the Department of Biological Sciences at East Tennessee State University; a paratype is in the National Museum of Natural History, Smithsonian Institution of Washington, D.C.

Further Systematic Results

Light microscopy observations on specimens of *Macrobiotus hibernicus* and *Macrobiotus dianeae* revealed that these two species are characterized by claws of the '*pullari*' type, i.e., V-shaped with the two branches that diverge from one another at the base, forming an acute angle, and with the typical quadrate peduncle at the base (Bertolani & Pilato 1988). Both also have an evident hook on the ventral margin of the strengthening bar of the buccal tube.

A personal communication from R. M. Kristensen on the presence of pillars in the cuticle of *Murrayon hastatus* suggests the need for further investigations on the cuticle of the genus.

Discussion

The morphological observations on *Murrayon pullari, Murrayon hastatus, Macrobiotus hibernicus* and *Macrobiotus dianeae* allow reanalysis of the systematic position of some of these species and the opportunity to define the characteristics of the genus *Murrayon.* Based on the observations of abundant material of *M. dianeae* (where claws were very visible in profile), this species had claws of the '*pullari*' type, and not of the '*hufelandi*' type with a short basal tract, as reported by Bertolani & Pilato (1988).

The presence of '*pullari*' type claws and of a ventral hook on the strengthening bar are evidence that *M. hibernicus* and *M. dianeae* should be transferred to the genus *Murrayon.* The genus *Murrayon* is therefore composed of the following 7 species: *M. pullari* (type species), *M. hastatus, Murrayon hibernicus* comb. n., *Murrayon nocentiniae* (Ramazzotti 1961), *Murrayon dianeae* comb. n., *Murrayon ovoglabellus* (Biserov 1988) and *Murrayon stellatus.*

The discovery of *M. stellatus* and the transfer of *M. hibernicus* comb. n. and *M. dianeae* comb. n. indicate that the genus *Murrayon* is not exclusively limnic, as it was previously considered.

Systematic Key to the Genus *Murrayon*

1. Cuticle superficially sculptured with more or less evident punctation (dots) 2
– Cuticle superficially smooth, without punctation 4
2. Cuticle uniformly and finely punctated, egg processes immersed in a hyaline matrix, bearing spines and delimiting polygonal areas .... *M. dianeae*
– Cuticle with two dorsolateral bands of more evident dots 3
3. Dorsolateral bands of dots very evident, egg processes with small heads, some bearing short spines on the top .... *M. stellatus*
– Dorsolateral bands of dots barely evident, egg processes without any spine .... *M. hibernicus*
4. Long thin macroplacoids, the first with a deep constriction, the second with an evident subterminal narrowing, egg with large processes covered by a hyaline matrix .... *M. hastatus*
– Short wide macroplacoids 5
5. First macroplacoid with a slight median constriction, smooth egg . . *M. ovoglabellus*
– First macroplacoid very constricted in the middle; eggs with processes separated from one to another and inserted on a smooth shell 6
6. Eggs with small, rigid, conical tubercles, with surface of the egg visible *M. pullari*
– Eggs with long conical and bent processes with aspect of large aculeus .... *M. nocentiniae*

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The genus *Perinereis* (Polychaeta: Nereididae) from Mexican littoral waters, including the description of three new species and the redescriptions of *P. anderssoni* and *P. elenacasoae*

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Abstract.—Eight species of the genus *Perinereis* were found in Mexican waters (Gulf of Mexico, Caribbean Sea and Pacific Ocean). Of these, three species are newly described: one for the Caribbean (*P. cariboea*) and two for the Mexican Pacific (*P. bajacalifornica* and *P. osoriotafalli*). *Perinereis anderssoni* is redescribed based on type material collected in Rio de Janeiro, Brazil. The previous records of this species from Mexico are referred to *P. elenacasoae.* A neotype is designated for *P. elenacasoae,* since the type material is lost, and the species is redescribed based on the neotype.

The genus *Perinereis* is characterized by the presence of conical paragnaths on both pharyngeal rings of the proboscis, except in Area VI, where either transverse long ribbon-shaped, short transverse bars, or a row of small bars occur. Bars may be so short as to appear cone-like on some species (Hutchings et al. 1991). Notopodia can be enlarged posteriorly or not modified. Only compound homogomph spinigers present in notopodia. Homogomph and heterogomph spinigers and heterogomph falcigers are present in neuropodia. The terminology of parapodial structures was taken from Fig. 1 of Hutchings & Reid (1990).

Previously, four species in this genus have been reported from littoral waters of Mexico: *P. anderssoni* Kinberg, 1866, *P. elenacasoae* Rioja, 1947, *P. monterea* (Chamberlin, 1918) and *P. villalobosi* Rioja, 1947. However, the specimens so far recorded as *P. anderssoni* from mexican shores actually belong to *P. elenacasoae.* This confusion arose from a description and illustrations by Rioja (1960: 296) of specimens from the Mexican region of the Gulf of Mexico incorrectly reported as *P. anderssoni.* For this reason, a redescription of *P. anderssoni* is undertaken, based on type material reported by Kinberg (1866) from Rio de Janeiro, Brazil. *Perinereis elenacasoae* is redescribed based on material from the type locality: Mazatlán, Sinaloa, and *P. villalobosi* is additionally described based on specimens from La Paz, Baja California Sur. *Perinereis obfuscata* Grube, 1878 was referred to *P. elenacasoae* by Salazar Vallejo (1989), based on specimens collected in western Mexico. This synonymy was found to be correct when the material deposited by Berkeley & Berkeley (1960) in the Smithsonian Institution collections (USNM) from Zihuatanejo coasts was examined by one of us (J.A.L.G).

For this study, specimens in the collections of the Natural History Museum of Los Angeles County (LACM-AHF), U.S. National Museum of Natural History, Smithsonian Institution (USNM), Naturhistoriska Rijksmuseet Stockholm (NRS), the Instituto de Ciencias del Mar y Limnologia, UNAM (CPICML) and the Universidad Autónoma de Nuevo León (UANL) were examined.

Genus *Perinereis* Kinberg, 1866

Perinereis anderssoni Kinberg, 1866

Fig. 1A–G

Perinereis anderssoni Kinberg, 1866: 175.—Hartman, 1951:47, pl. 13, Fig. 6.—Fauchald, 1977:31, Fig. 8a–b.

Material examined.—Type series consisting of 13 poorly preserved specimens collected in Rio de Janeiro, Brazil (NRS-156); other material: Punta da Cruz, Ilha de Sao Francisco, Santa Catharina, Brazil, 28 Oct 1925 (1 specimen) (USNM 24229); Juan Fernández, Chile, 8 Dec 1926 (7 specimens) (USNM 24252). Campeche: Puerto Real, Ciudad del Carmen, Mexico, M. E. Caso, coll., 31 Jul 1972 (1 specimen).

Redescription.—Best preserved specimen of type series complete with 85 setigers; 63 mm long, 4 mm wide, including parapodia, with no evident pigmentation.

Prostomium longer than wide, two pairs of eyes in trapezial arrangement. Frontal antennae short. Biarticulate palps large with conical palpostyle. Peristomium with four pairs of short tentacular cirri, longest pair extending posteriorly past first setiger (Fig. 1A).

Paragnaths of the pharyngeal areas arranged as follows: I, 4 cones in triangle; II, 13 cones in a triangle; III, 19 cones in 3 rows; IV, curved group of 27 cones; V, 3 cones in triangle; VI, short transverse bar; VII–VIII, 45 cones in 2 rows. Jaws with 5 teeth (Fig. 1B).

First two parapodia uniramous, dorsal and ventral cirri subequal (Fig. 1C). Following anterior parapodia biramous with dorsal and median notopodial ligules anteriorly rounded; neuropodial postsetal lobes truncate, superior lobe conical, inferior one rounded; ventral neuropodial ligule slender. Dorsal cirri proximally inserted. Median parapodia with dorsal and median notopodial lobes conical (Fig. 1D), neuropodial structures similar to those in anterior parapodia; dorsal cirri medially inserted. Posterior parapodia with dorsal cirri inserted medially and anteriorly, notopodial ligule enlarged; median notopodial ligule subulate; postsetal neuropodial lobes mamilliform, ventral neuropodial ligules rounded anteriorly; ventral cirri digitiform and inserted proximally (Fig. 1E).

Uniramous parapodia with supracicular homogomph spinigers, and infracicular heterogomph falcigers. Biramous parapodia with setation similar throughout body. Notopodial supracicular setae homogomph spinigers. Neuropodial supracicular setae homogomph spinigers and heterogomph falcigers; infracicular neurosetae heterogomph spinigers and falcigers. Infracicular neuropodial falcigers in anterior parapodia with distally blunt appendage (Fig. 1F); appendage in posterior parapodia slender and distally pointed (Fig. 1G).

Pygidium with terminal anus, with pair of short ventrally inserted anal cirri.

Distribution.—Amphi-American. Originally described from Rio de Janeiro, Brazil. The species is distributed in the Atlantic and Gulf of Mexico (Ciudad del Carmen, Campeche, Mexico), eastern Gulf of Mexico (Hartman, 1951) and in the Pacific, in Juan Fernandez Island (Chile).

Habitat.—Not defined in records.

Perinereis bajacalifornica, new species

Fig. 2A–F

Material examined.—Baja California Sur: Falsa Bay, La Paz, W. H. Shepherd, coll., 22 Sep 1971, (1 specimen) (USNM 48858); Balandra mangrove, La Paz, E. Amador coll., 24 Sep 1985, (1 specimen, Holotype) (USNM 180693); Zacatecas mangrove, La Paz, same collector, 12 Feb 1986 (8 specimens).

Description.—Holotype complete with 93 setigers, 40 mm long and 2.5 mm wide including parapodia. Body pale yellow, with no evident pigmentation pattern.

Prostomium pentagonal, with two pairs of eyes, anterior ones oval and slightly more separated from each other, posterior ones rounded. Pair of short cirriform antennae. Biarticulate palps with conical palpo-

Fig. 1. *Perinereis anderssoni.* A. Anterior region dorsal view; B. Everted pharynx, dorsal view from a specimen in the type group; C. 1st parapodium; D. Parapodium 39th; E. Parapodium 71th; F. Heterogomph neuropodial falciger in infracicular position from setiger 10; G. Same of setiger 65. (Scale: A, B = 1 mm; C, D, E = 100µm; F, G = 15µm).

styles. Peristomium with longest pair of tentacular cirri extending to setiger 3 (Fig. 2A).

Paragnaths arranged on pharyngeal areas as follows: I, a clump of 7 conical paragnaths; II, 11 conical paragnaths arranged in triangle; III, 15 cones in trapezial group; IV, curved group of 21 cones; V, single cone; VI, transverse, slender, ribbon-shaped bar; VII–VIII, row of 7 small cones. (Fig. 2B, C).

Anterior parapodia with notopodial and neuropodial lobes and ligules conical, subequal; dorsal cirri stout not longer than dorsal ligules (Fig. 2D). Median parapodia with notopodial dorsal ligules slightly longer than other lobes; dorsal cirri similar to those of anterior parapodia and proximally inserted. Posterior parapodia with notopodial dorsal ligules conspicuously longer, distally conical and dorsally pigmented; dorsal cirri slender, medially inserted, not longer than the dorsal ligules. Notopodial median ligules conical. Neuropodial postsetal lobes rounded, ventral ligules digitiform, slightly longer than neuropodial postsetal lobes. Ventral cirri slender (Fig. 2E).

Supracicular homogomph spinigers in notopodia. Supracicular homogomph spinigers and heterogomph falcigers in neuropodia, but only homogomph spinigers in anterior parapodia. Neuropodial infracicular setae consisting of single homogomph spiniger and some hetrogomph falcigers; latter with 9–10 teeth on margin (Fig. 2F).

Pygidium with two short slender anal cirri; anus terminal.

Discussion.—*Perinereis bajacalifornica,* n. sp., belongs to the group of species in which a ribbon-shaped transverse bar is present in Area VI of the proboscis and notopodial lobes are enlarged on posterior setigers. In their revision, Hutchings et al. (1991) included 16 species in this group: *P. amblyodonta* (Schmarda 1861) and *P. barbara* (Monro 1926) from Australia, *P. anderssoni* Kinberg, 1866 and *P. pontoni* Kinberg, 1866 from Brazil, *P. elenacasoae* Rioja, 1947, from western Mexico, *P. falklandica* Ramsay, 1914, for the Falkland islands, *P. longidonta* Rozbaczylo & Castilla, 1973 from Chile, *P. macropus* (Claparède 1870) from the Mediterranean Sea, *P. malayana* (Horst 1889), *P. nigropunctata* (Horst 1889) and *P. tobeloana* (Augener 1933) from the Malay Archipielago, *P. obfuscata* (Grube 1878) and *P. sululana* (Horst 1924) from the Philippines, and *P. pseudocavifrons* Fauvel, 1930 from New Caledonia. *Perinereis bajacalifornica,* n. sp., differs from the other species in this group by having a single row of seven small cones on pharyngeal areas VII–VIII. In the other species of the group, a variable number of conical paragnaths, arranged in 2–4 rows and varying in numbers from 18 to 101, is present.

Perinereis elenacasoae, described from western Mexico, is biogeographically the most closely related species to *P. bajacalifornica,* n. sp. These species can be differenciated from each other and from other species in the group mainly by the arrangement of their paragnaths.

Etymology.—The specific name is derived from the name of the State of Baja California Sur, Mexico.

Distribution.—This species is only known from the mangrove areas in La Paz, Baja California Sur, Mexico.

Habitat.—In sediment trapped among mangroves.

Perinereis cariboea, new species
Fig. 3A–E

Material examined.—Quintana Roo: Ascención Bay, Punta Pajaros, V. Solís-Weiss, coll. 6 Oct 1983 (Holotype, USNM 180694). Yucatan: Cerritos Island, S. I. Salazar Vallejo, coll. 18 Jan 1991 (6 specimens).

Description.—Holotype complete with 53 setigers, 35 mm long, 1.5 mm wide, green with strongly pigmented prostomium.

Pharynx not everted in specimens. Analysis performed by dissection.

Prostomium pentagonal, with dorsal groove, with two pairs of rounded eyes in quadrate arrangement. Pair of short digitiform frontal antennae. Biarticulate palps globose, with small, conical palpostyles. Peristomium with four pairs of tentacular cirri, anterior pair extending posteriorly to setiger 4 (Fig. 3A).

Paragnaths arranged on pharyngeal areas as follows: I, 2 cones; II, 8 cones in 2 rows; III, oval group of 7 cones; IV, triangular

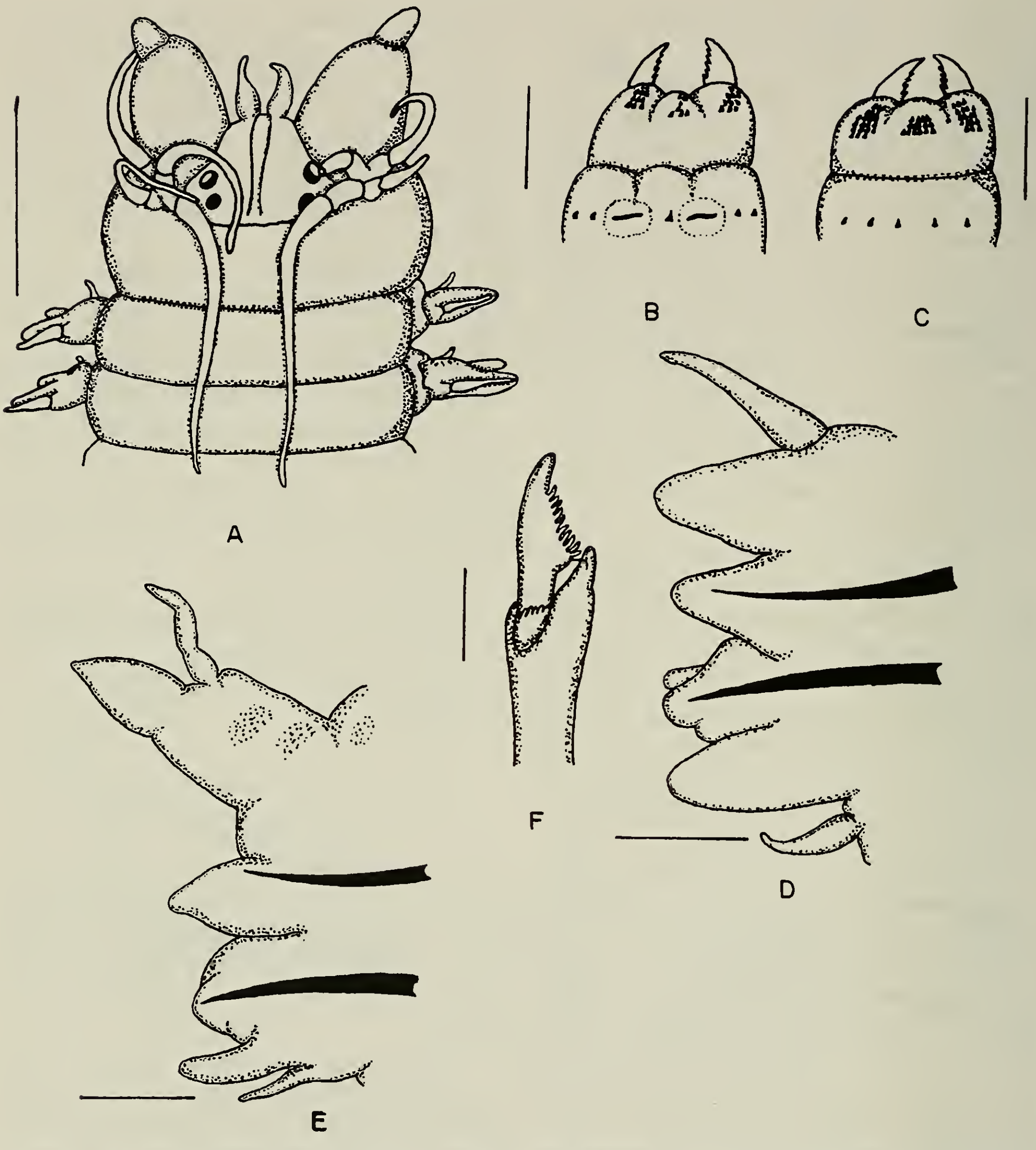

Fig. 2. *Perinereis bajacalifornica,* n. sp. A. Anterior end, dorsal view; B. Pharynx in dorsal view; C. Pharynx in ventral view; D. Parapodium 10th; E. Parapodium 80th; F. Heterogomph neuropodial falciger in supracicular position from setiger 80. (Scale: A, B, C = 0.5 mm; D, E = 150μm; F = 10μm).

group of 12 cones; V, no paragnaths; VI, 2 transverse flattened bars, VII–VIII, 11 cones in 2 rows.

Anterior notopodia with dorsal and ventral ligules conical, neuropodial postsetal lobes rounded, ventral ligules enlarged; dorsal cirri inserted proximally, stouter than the ventral cirri (Fig. 3B). Median parapodia with notopodial dorsal ligules proximally enlarged, median ligules, neuropodial postsetal lobes and ventral ligules rounded; dorsal cirri inserted medially (Fig. 3C). Posterior parapodia with notopodial dorsal ligules enlarged; median ligules, neuropodial postsetal lobes and ventral ligules similar to those of median parapodia. Dorsal

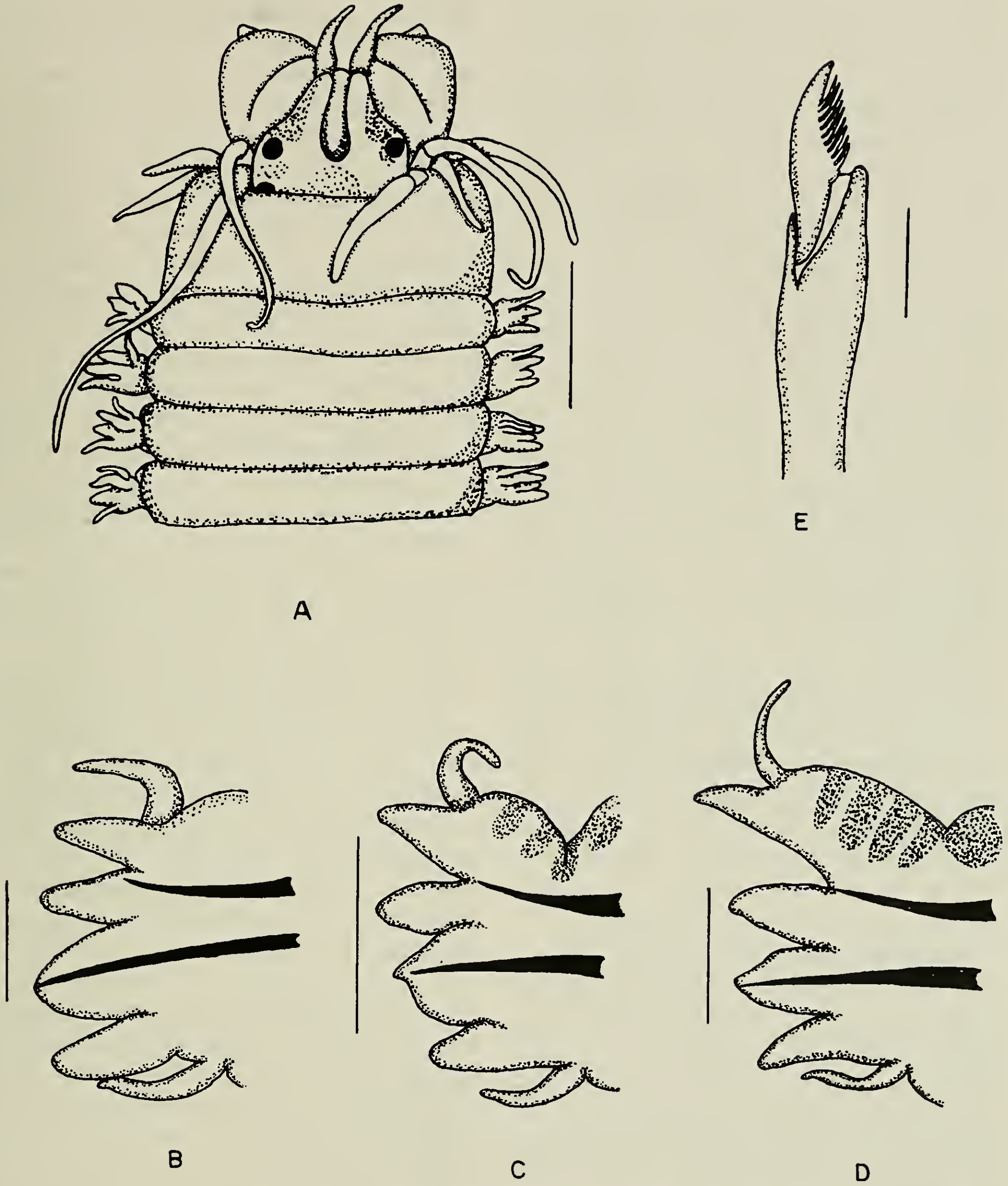

Fig. 3. *Perinereis cariboea,* n. sp. A. Anterior end, dorsal view; B. Parapodium 10th; C. Parapodium 30th; D. Parapodium 50th; E. Heterogomph neuropodial falciger in supracicular position from setiger 30. (Scale: A = 0.5 mm; B, C, D = 100μm; E = 8μm).

cirri inserted near distal margin of dorsal ligules (Fig. 3D).

Setation similar throughout body as follows: notosetae all homogomph spinigers; supracicular neurosetae homogomph spinigers and heterogomph falcigers; infracicular neurosetae heterogomph, represented by single spiniger and 4 falcigers (Fig. 3E).

Pygidium with a pair of short anal cirri; anus termino-dorsal.

Discussion.—*Perinereis cariboea,* n. sp., belongs to the group of species in which two transverse flattened bars are present in area VI of the proboscis and notopodial dorsal ligules are enlarged posteriorly. Only two other species are known in this group: *P. mochimaensis* Liñero-Arana, 1983 described from Venezuela, and *P. osoriotafalli,* n. sp, herein described. These species can be differentiated from each other by the ornamentation of pharyngeal areas I, V and VII–VIII. In *P. cariboea,* n. sp., two small cones in a row are present on area I, area V lacks paragnaths, and 11 cones in two rows are present on areas VII–VIII. In *P. mochimaensis,* 11 cones in a triangle are present on area I, two cones are present on area V and 32 cones in two rows are present on areas VII–VIII. In *P. osoriotafalli,* n. sp., four cones are present on area I in trapezial arrangement, one cone is present on area V, and eight cones in a row are present on areas VII–VIII.

Etymology.—The specific name is derived from the name of the Caribbean Sea.

Distribution.—Mexican Caribbean; only known from two localities: Concepción Bay, Quintana Roo State and Cerritos Island, Yucatan.

Habitat.—Among algae attached to rocks in the intertidal zone.

Perinereis elenacasoae Rioja, 1947
Figs. 4A–E, 5A–D

Perinereis elenacasoi Rioja, 1947: 531, Figs. 8–17.

Perinereis elenacasoae Salazar Vallejo, 1989:50

Perinereis obfuscata Berkeley & Berkeley, 1960:359

Perinereis anderssoni Rioja, 1960:295. Figs. 12–15.

Material examined.—Baja California Sur: La Paz Bay, W. M. Shepherd, coll., Aug 1976 (10 specimens); Caimancito beach, La Paz Bay, J. A. de León-González, coll., 12 Oct 1987 (2 specimens). Sonora: Peñasco Harbor, in front of shrimp farm, 5 May 1981, same collector (2 specimens); same locality, M. Silva, coll., 7 Jan 1985 (1 specimen); same locality, Norse beach, V. A. Gallardo, coll. no date (6 specimens). Sinaloa: Mazatlán, Est. 14309, Reef of southern lighthouse island, E. Y. Dawson, coll., 12 Jul 1946 (1 specimen); same locality and collector, Est. 14308, north Olas Atlas lighthouse, 12 Dec 1946 (3 specimens); same locality and collector, Est. 14311, 2 miles north of Mazatlán, 6 Jul 1952 (1 specimen); same locality, Cerritos beach, J. A. de León-González, coll., 15 May 1981 (Neotype, USNM 180695) and 6 specimens; Mazatlán area, collector unknown, 1986 (8 specimens); same locality, Casa del Marino, collector unknown, 1986 (16 specimens); same locality, Chivos Island, collector unknown, 1986 (10 specimens). Nayarit: Larga Island, Marietas Islands, C. López Rivas, coll., 17 Dec 1994 (1); same, 13 Feb 1995 (5 specimens). Jalisco: Barra de Navidad, Est. 14310, E. Y. Dawson, coll., 25 Dec 1946 (3 specimens). Guerrero: Acapulco Harbor, San Lorenzo reef, Est. 1552-46, E. Y. Dawson, coll., 9 Apr 1946, (4 specimens). Oaxaca: Salina Cruz, collector unknown, 27 May 1951 (1 specimen). Veracruz: Veracruz Harbor, Playa Norte reef, E. Rioja, coll., Jan 1960 (12 specimens); Boca del Rio, north jetty, M. L. Jones, coll., 8 Aug 1962 (60 specimens); Tuxpam, north rocky area, H. González, coll., 25 May 1978 (3 specimens); same locality, G. Góngora-Garza, coll., 05 Jun 1984 (3 specimens); Barra de Cazones, Pulpo point, J. A. de León-González, coll., 1 Jun 1985 (9 specimens); same, 15 Jun. 1985 (37 specimens); same, 31 Oct 1991 (93 specimens); Barra of Tamiahua, north rocky area, J. A. de León-González, coll., 5 May 1985 (1 specimen); same locality, G. Guajardo, coll., 25 May 1991 (3 specimens); same, 8 Jun 1991 (4 specimens). Campeche: Puerto Real, Ciudad del Cármen, M. E. Caso, coll., 31 Jul 1972 (1 specimen). Quintana Roo: Smithsonian-Bredin Expedition IV: Mujeres Island, stn. 29-60, 31 Mar 1960 (1 specimen); Espiritu Santo Bay, stn. 41-60, 6 Apr 1960 (3 specimens); Allen Point, Ascención Bay, stn. 45-60, 07

Apr 1960 (2 specimens), Nicchehabin reef, Ascención Bay, stn. 67-60, 13 Apr 1960 (3 specimens); same, stn. 72-60, 14 Apr 1960 (1 specimen); same, stn. 91-60, 18 Apr 1960 (1 specimen); Ascención Bay, V. Solís-Weiss, coll., 6 Oct 1983 (1 specimen); Cozumel Island, same collector, 10 Oct 1983 (2 specimens).

Epitokous material examined.—Guerrero: Zihuatanejo, W. L. Klawe, coll., 6 Sep 1958 (1 female), (USNM 33496).

Description of the Neotype.—Specimen complete with 72 setigers, 34 mm long and 2 mm wide including parapodia; color pale yellow, vestigial dark pigmentation in anterior region.

Prostomium pentagonal, two pairs of eyes in quadrate arrangement. Frontal antennae stout, digitiform. Biarticulate palps slender with globose palpostyles. Peristomium with four pairs of relatively short tentacular cirri, longest pair extending posteriorly to second setiger (Fig. 4A).

Pharynx not everted in specimens. Analysis performed by dissection.

Pharynx with paragnaths arranged on pharyngeal areas as follows: I, group of 11 cones; II, 25 cones in trapezial arrangement; III, oval group of 25; IV, curved group of 16–17 cones in 4 rows; V, single cone; VI, transverse flattened, ribbon-shaped bar; VII–VIII, 37 cones in 2 rows.

Anterior parapodia with notopodial dorsal and median ligules distally rounded, neuropodial postsetal lobes less developed; dorsal and ventral cirri subequal (Fig. 4B). Median parapodia with notopodial and neuropodial lobes and ligules conical, neuropodial dorsal ligules longer (Fig. 4C); dorsal and ventral cirri similar to those of anterior segments. Posterior parapodia notopodial dorsal ligules enlarged, dorsal cirri medially inserted; median ligule and neuropodial postsetal lobes distally conical, ventral ligule digitiform; ventral cirri inserted proximally, with posterior protusion (Fig. 4D).

Setation similar throughout body. Notopodia with homogomph spinigers. Supracicular neurosetae homogomph spinigers and stout heterogomph falcigers with anterior slender tooth directed downward (Fig. 4E); infracicular neurosetae heterogomph spinigers and slender heterogomph falcigers.

Pygidium with a pair of short anal cirri inserted ventrally. Anus terminal.

Epitokous female.—Best preserved specimen with 43 setigers, 14 mm long and 2.5 mm wide without parapodia.

Prostomium longer than wide with a frontal median dorsal groove. Pair of small digitiform antennae, 2 pairs of large eyes in quadrate arrangement. Peristomium with 4 pairs of tentacular cirri, longer ones extending posteriorly to setiger 3 (Fig. 5A).

Body divided into moderately modified anterior region and heteronereidid region; anterior region with modified, proximally stout dorsal cirri in first 5 setigers (Fig. 5B); parapodia similar to those of atokous specimens from setiger 6 to 17. Parapodia of heteronereidid region compressed, flattened antero-posteriorly; dorsal cirri without evident crenulation. Natatory lamellae associated with parapodial lobes and ligules and with proximal region of dorsal and ventral cirri (Fig. 5C, D). Normal setae replaced by natatory setae with broad, paddle-shaped appendages.

Discussion.—*Perinereis elenacasoae* Rioja, 1947, was originally described from Mazatlán, (Sinaloa State) shores; unfortunately the type material, as well as all the other types described by Enrique Rioja, have been lost. Based on Article 75 of the International Code of Zoological Nomenclature, in this paper a Neotype for this species, collected in the type locality: Mazatlán, Sinaloa, is designated.

Distribution.—Amphi-American. Mexican Pacific from Puerto Peñasco, Sonora (Gulf of California), to Salina Cruz (Oaxaca); Atlantic Ocean from Gulf of Mexico and Caribbean Sea south to Brazil. This is the first record for the species from the western Atlantic.

Habitat.—On rocky substrates, among rhizoids of algae attached to rocks, and coral substrates.

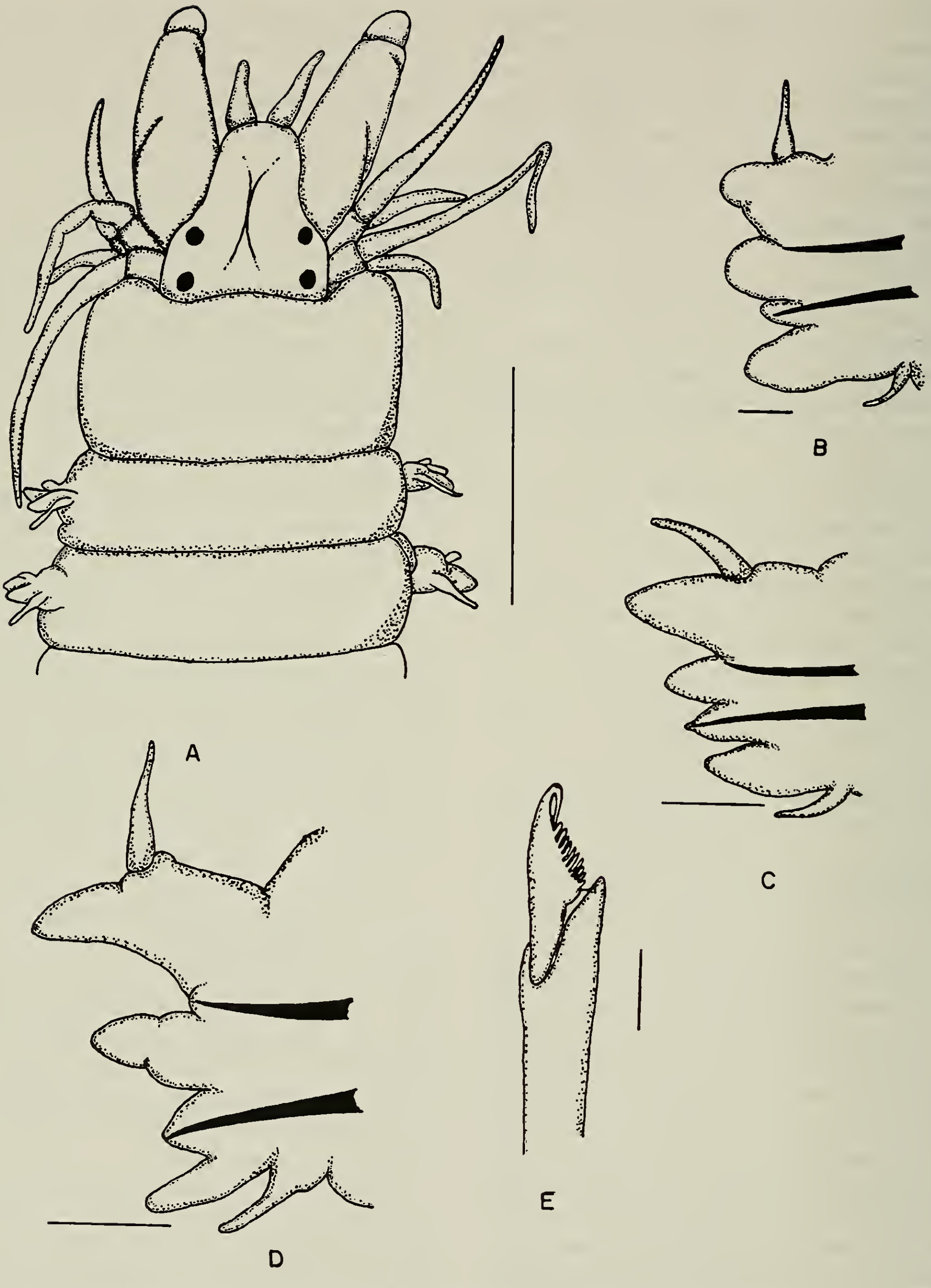

Fig. 4. *Perinereis elenacasoae.* A. Anterior end, dorsal view; B. Parapodium 10th; C. Parapodium 31th; D. Parapodium 50th; E. Heterogomph neuropodial falciger in supracicular position from setiger 50. (Scale: A = 1 mm; B, C, D = 150μm; E = 10μm).

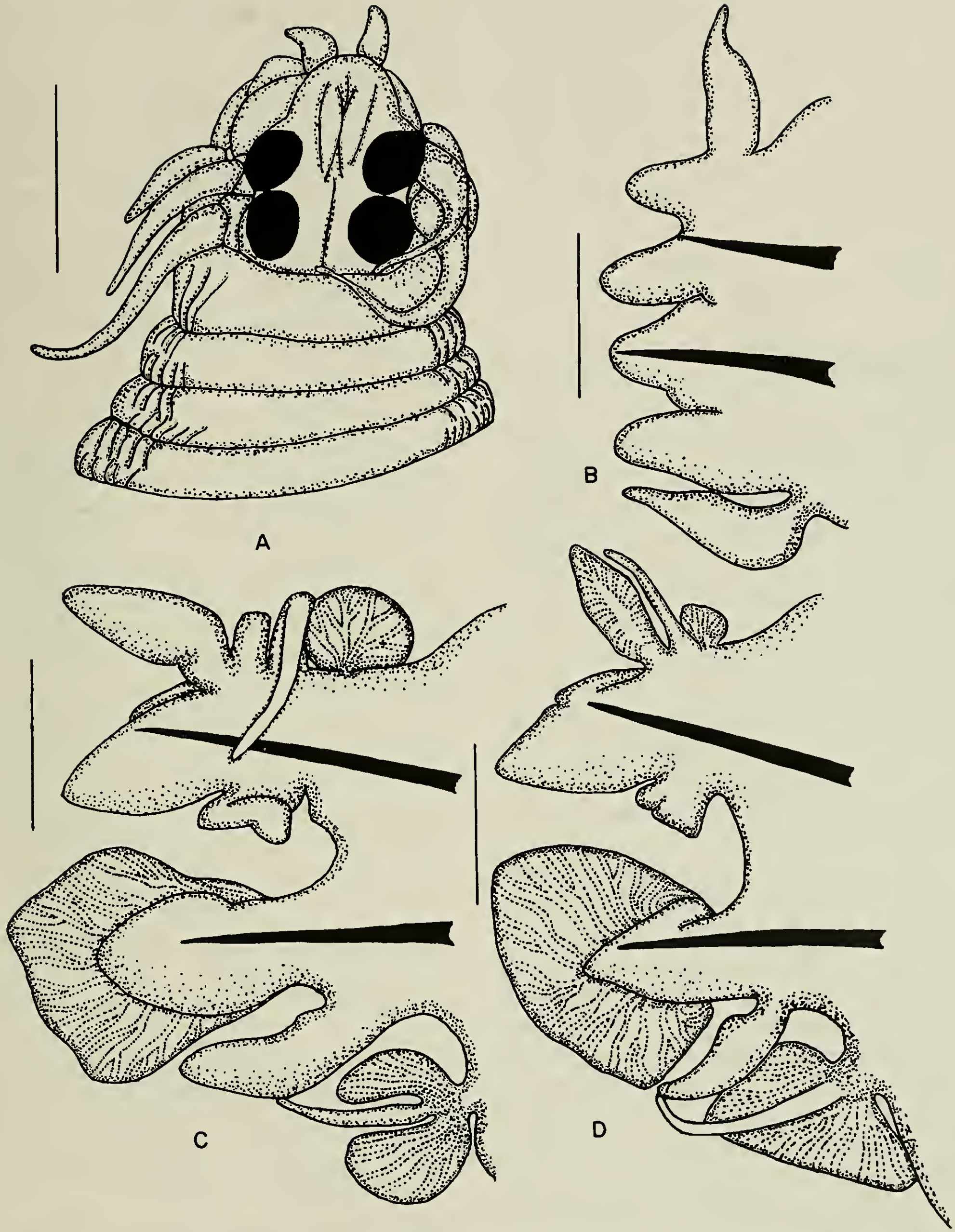

Fig. 5. *Perinereis elenacasoae* (epitoke). A. Anterior end, dorsal view (parapodia omitted); B. Parapodium 4th; C. Parapodium 30th; D. Parapodium 40th. (Scale: A = 1 mm; B, C, D = 100μm).

Perinereis floridana Ehlers, 1868
Figs. 6A–E, 7A–E

Perinereis floridana Ehlers, 1868: 503.—Salazar Vallejo & Jimenez-Cueto, 1996–1997: 367.

Material examined.—Campeche: Alacranes reef East, V. Solís-Weiss, coll., 28 Oct 1990 (7 specimens); same, 23 Mar 1991 (45 specimens); Alacranes reef West, same collector, 23 Mar 1991 (3 specimens); Arenas

Cay, Southwest, same collector, 21 Mar 1991 (8 specimens); Arenas Cay North, same collector 17 Mar 1991 (4 specimens). Quintana Roo: Mujeres Island, stn. 21-60, Smithsonian-Bredin Expedition IV, 30 Mar 1960 (1 specimen); Ascención Bay, stn. 67-60, same expedition, 13 Apr 1960 (2 specimens).

Epitokous material.—Key Largo, Florida, USA, J. Ross, coll., 20 Dec 1950, (1 female).

Diagnosis.—Best preserved specimen incomplete, 50 mm long, 3 mm wide including parapodia, with 73 setigers.

Prostomium longer than wide, two pairs of small eyes in quadrate arrangement. Frontal antennae cirriform. Palps biarticulate, palpostyles conical. Peristomium with longest pair of tentacular cirri extending posteriorly to setiger 4 (Fig. 6A).

Pharynx not everted in specimens. Analysis performed by dissection.

Pharynx with paragnaths arranged on pharyngeal areas as follows: I, 2 cones; II, 9 cones in 2 rows; III, oval group of 16 cones; IV, long curved group of 18; V, single cone; VI, short transverse bar; VII–VIII, 24 cones in 2 rows.

First two parapodia uniramous, following ones biramous. Anterior biramous parapodia with notopodial dorsal ligules slender distally; notopodial median ligules distally truncate; neuropodial postsetal lobes rounded, ventral ligules subulate. Dorsal and ventral cirri subequal (Fig. 6B). Median and posterior parapodia with notopodial ligules, neuropodial postsetal lobes and neuropodial ventral ligules all triangular. Notopodial dorsal ligules not enlarged; dorsal cirri inserted medially, ventral cirri inserted proximally (Fig. 6C, D).

Setation similar throughout body: notopodial supracicular setae homogomph spinigers; neuropodial supracicular setae homogomph spinigers and heterogomph falcigers, infracicular neurosetae heterogomph spinigers and falcigers; latter with slender appendage (Fig. 6E).

Epitokous female.—Specimen light yellow, 32 mm long and 4 mm wide, with 97 setigers.

Prostomium as long as wide, with pair of slender cirriform antennae and two pairs of large, highly modified eyes; biarticulate palps with rounded palpostyles. Peristomium with longest pair of tentacular cirri extending to setiger 5 (Fig. 7A).

Body divided into moderately modified anterior region and highly modified heteronereidid region; first five setigers of anterior region with modified dorsal and ventral cirri (Fig. 7B); parapodia similar to those of atokous specimens from setigers 6 to 18 (Fig. 7C). Parapodia of heteronereidid region highly modified with lamellae associated with parapodial lobes, as well as with ventral and dorsal cirri; lamellae trilobed and associated with ventral cirri in median parapodia (Fig. 7D), appearing bilobed in posterior region (Fig. 7E); normal setae replaced by natatory setae with broad paddle-shaped appendages.

Distribution.—Western Atlantic: Gulf of Mexico and Caribbean Sea. Reported in Mexico from Quintana Roo.

Habitat.—Associated with coral rubble.

Perinereis monterea (Chamberlin, 1918)
Fig. 8A–F

Nereis (*Neanthes*) *monterea* Chamberlin, 1918: 474.

Nereis spinifera Treadwell, 1929: 5, figs. 15–20.

Perinereis monterea Berkeley & Berkeley, 1958: 403.–Hartman, 1968: 557.—Banse & Hobson, 1974: 71, Fig. 18n.—Kudenov, 1979: 118.—Salazar Vallejo, 1985: 108, Fig. 33 a–e.

Material examined.—Baja California: Ensenada Harbor, Todos Santos Bay, S. I. Salazar Vallejo, coll., 15 Apr 1983 (6 specimens). Baja California Sur: Isla Margarita, stn. 159, M. Cárdenas, coll., 12. Jun 1948, (3 specimens) (USNM 24727). Sonora: Puerto Peñasco, La Cholla bay, R. Dougherty, coll., Oct 1976 (2 specimens).

Diagnosis.—Best preserved specimen

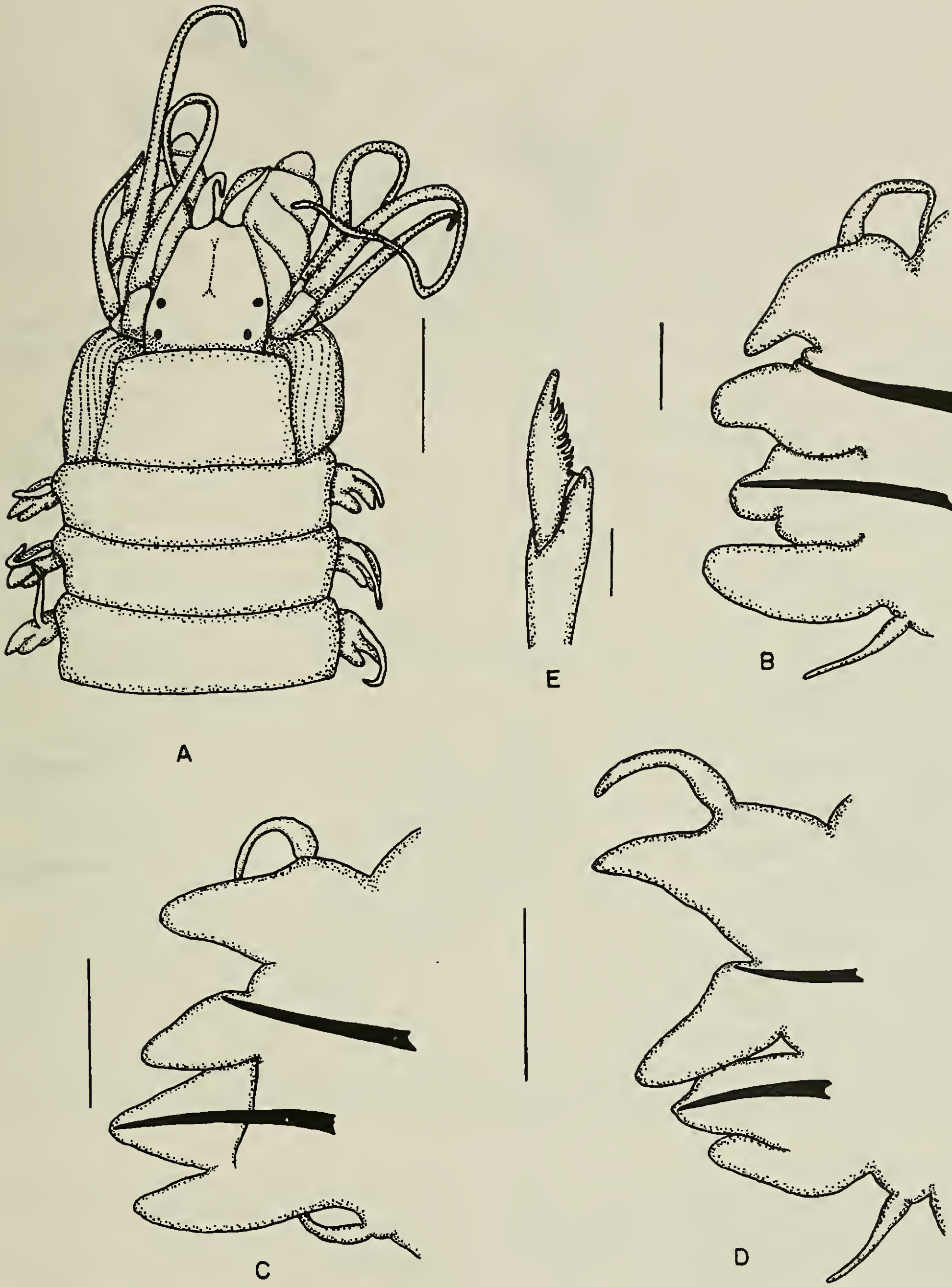

Fig. 6. *Perinereis floridana.* A. Anterior end, dorsal view; B. Parapodium 10; C. Parapodium 30; D. Parapodium 70; E. Heterogomph neuropodial falciger in supracicular position from setiger 30. (Scale: A: 1 mm; B, C, D = 100μm; E = 10μm).

Fig. 7. *Perinereis floridana* (epitoke). A. Anterior end, dorsal view (parapodia omitted); B. Parapodium 3th; C. Parapodium 10th; D. Parapodium 30th; E. Parapodium 60 th. (Scale: A = 1 mm; B, C, D, E = 150μm).

complete, 65 mm long and 2.5 mm wide including parapodia, with 116 setigers, reddish with densely pigmented dorsal region.

Prostomium pentagonal, longer than wide, with two pairs of eyes in rectangular arrangement. Frontal antennae digitiform. Biarticulate palps with globose palpostyles (Fig. 8A). Peristomium with short tentacular cirri, longest pair extending posteriorly to first setiger, lower pair short and stout.

Pharynx not everted in specimens. Analysis performed by dissection.

Paragnaths arranged on pharyngeal areas as follows: I, single large cone; II, oval group of 19 cones; III, oval group of 51 cones in 5 rows; IV, long curved group of 60 cones, and 2 small proximal bars; V, single large cone; VI, single short, cone-shaped bar; VII–VIII, 40 cones in 4 rows, additional row of 5 cones in midventral region.

Anterior parapodia with dorsal and ventral notopodial ligules distally rounded, superior lobes short, digitiform; neuropodia with postsetal lobe truncate, superior lobe short, inferior lobe quadrate, ventral ligule similar in length to notopodial dorsal ligule; dorsal cirri medially inserted, ventral cirri proximally inserted (Fig. 8B). Notopodial dorsal ligules enlarged on median and posterior parapodia, dorsal cirri inserted anteriorly and medially. Neuropodial ventral ligules reduced to rounded lobes on middle segments, even more reduced posteriorly (Fig. 8C, D).

Notosetae homogomph spinigers on all parapodia. Anterior neuropodia with supracicular neurosetae homogomph spinigers and heterogomph falcigers, latter with slender, distally pointed appendage (Fig. 8E); infracicular neurosetae including only heterogomph falcigers. Median and posterior parapodia with supracicular homogomph spinigers and heterogomph falcigers; latter with anteriorly rounded appendage (Fig. 8F); infracicular neurosetae heterogomph spinigers and falcigers.

Pygidium with terminal anus, pair of slender anal cirri inserted lateral to anal opening.

Distribution.—Temperate to tropical waters of northeastern Pacific Ocean: Canada through State of Guerrero, Mexico.

Habitat.—Reported herein from under tests of barnacle *Tetraclita squamosa* Darwin, 1854 in Puerto Peñasco, La Cholla Bay, Sonora; not defined in other records.

Perinereis osoriotafalli, new species
Fig. 9 A–F

Material examined.—Sonora: Guaymas, San Francisco Inlet, E. Y. Dawson and F. Durham, colls., 18 Mar 1946 (1 specimen); Guaymas, las playas road, in front of Las Palmas, B. Burch, coll., 13 Feb 1953 (2 specimens); Puerto Peñasco, La Cholla Bay, stn. V-1, V. A. Gallardo, coll., (1 specimen). Sinaloa: Topolobampo, Los Patos Island, B. F. Osorio-Tafall, coll., 15 May 1961 (Holotype, USNSM 180696) and 3 specimens; same, J. Reddell, coll., 24 Nov 1968 (6 specimens).

Description.—Holotype 42 mm long, 5 mm wide including setae, complete with 86 setigers; color pale yellow, no evident pigmentation pattern.

Prostomium subpentagonal, longer than wide; two pairs of black rounded eyes in quadrate arrangement, anterior ones more widely separated. Pair of short digitiform antennae; palps biarticulate, palpostyles small, not everted. Peristomium with anterior pair of tentacular cirri, extending posteriorly to setiger 4, posterior pair appearing segmented proximally. (Fig. 9A).

Pharynx not everted in specimens. Analysis performed by dissection.

Pharynx with brown, calcified jaws, with three stout teeth present on the interior margin. Paragnaths arranged on pharyngeal areas as follows: I, 4 cones in diamond-shaped group; II, small group of 12 cones; III, oval group of 17 cones; IV, elongate group of 23 cones; V, single cone; VI, 2 transverse, ribbon-shaped bars; VII–VIII, 8 cones in single row.

Notopodial and neuropodial ligules rounded to conical on anterior parapodia; dorsal cirri digitiform, proximally enlarged, inserted on the median posterior region of notopodial dorsal ligules; ventral cirri cirriform, proximally inserted on neuropodial ventral ligule (Fig. 9B). Notopodial dorsal ligules enlarged on median and posterior parapodia, dorsal cirri inserted on middle distal part of dorsal ligules, relatively smaller than on anterior parapodia; ventral cirri increasing considerably in size towards posterior end (Fig. 9C, D).

Setation of anterior setigers as follows: supracicular notosetae homogomph spinigers, with finely serrated appendages; supracicular neurosetae homogomph spinigers similar to those in notopodia, and heterogomph falcigers; latter with distally rounded appendage denticulate on inner margin; infracicular neurosetae hetero-

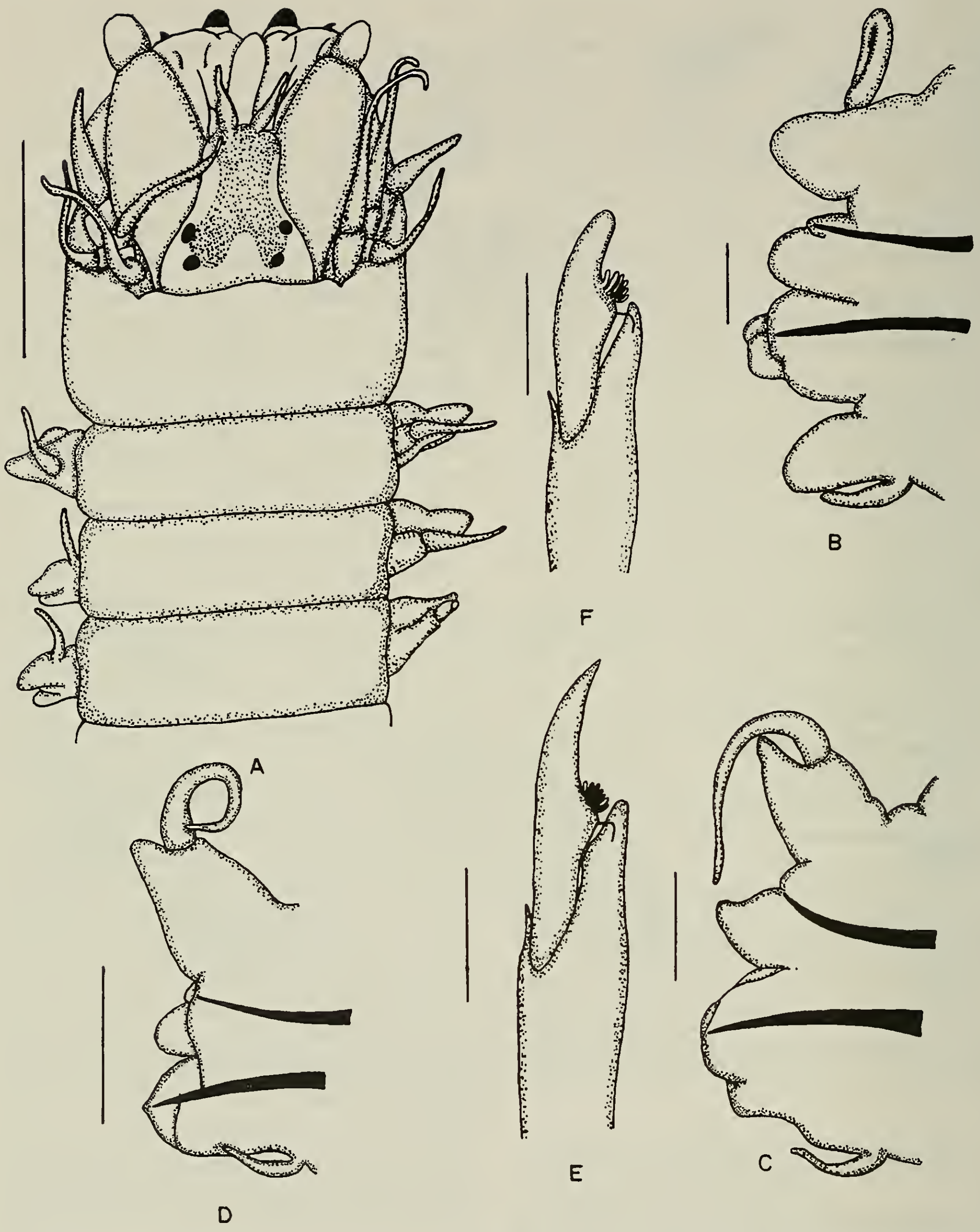

Fig. 8. *Perinereis monterea.* A. Anterior end, dorsal view; B. Parapodium 9th; C. Parapodium 40th; D. Parapodium 99th; E. Heterogomph neuropodial falciger in supracicular position from setiger 9; F. Same from setiger 99. (Scale: A = 1 mm; B, C, D = 150μm; E, F = 15μm).

gomph falcigers, similar to supracicular falcigers, but smaller (Fig. 9F). Median and posterior parapodia with setation similar to that of anterior parapodia, with similar spinigers and falcigers (Fig. 9E), except for the presence of one pair of infracicular heterogomph neuropodial spinigers with finely serrated appendage.

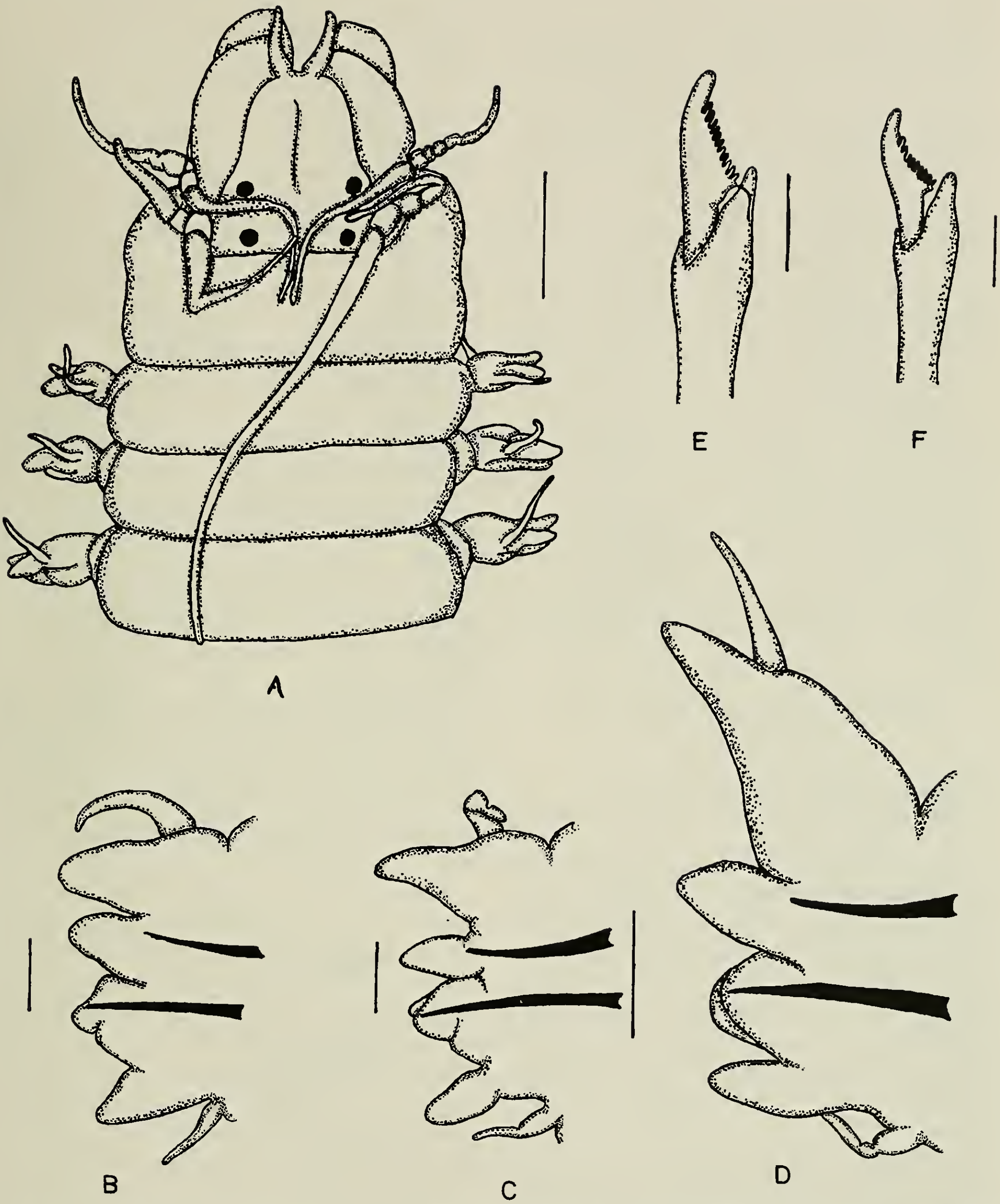

Fig. 9. *Perinereis osoriotaffali,* n. sp. A. Anterior end, dorsal view; B. Parapodium 10th; C. Parapodium 40th; D. Parapodium 80th; E. Heterogomph neuropodial falciger in infracicular position from setiger 10; F. Same from setiger 80. (Scale: A = 1 mm; B, C, D = 150µm; E, F = 8µm).

Pygidium with terminal anus, with pair of short anal cirri.

Discussion.—The new species is included along with *P. cariboea,* n. sp., in a group that previously included only *P. mochimaensis* Liñero-Arana 1983. This species group is characterized by having two transverse bars on Area VI and enlarged notopodial dorsal ligules on posterior parapodia. *Perinereis osoriotafalli*, n. sp., can be differentiated from *P. cariboea*, n. sp. and *P. mochimaensis* by its pharynx ornamentation, especially on area VII–VIII. *Perinereis osoriotafalli* has eight cones present in one row on area VII–VIII, whereas in the other two species, the cones on area VII–VIII are arranged in two rows. *Perinereis mochimaensis* has 32 cones on area VII–VIII, whereas in *P. cariboea* only 11 cones are present in this region of the proboscis.

Etymology.—This species is named in honor of B. F. Osorio Tafall, a close aide of Dr. E. Rioja, who collected the material upon which this species is described.

Distribution.—Gulf of California: From Puerto Peñasco to Los Patos Island, Ohuira Bay, in front of Topolobampo Harbor.

Habitat.—Among algae on rocky substrate.

Perinereis villalobosi Rioja, 1947
Fig. 10 A–E

Perinereis villalobosi Rioja, 1947: 532, figs. 18–22.—Salazar Vallejo, 1989: 50.

Material examined.—Baja California: Ensenada, Punta Banda, S. I. Salazar Vallejo, coll., 7 Mar 1982 (1 specimen); Rincon de Ballenas, V. Díaz Castañeda, coll., 20 Mar 1996 (4 specimens). Baja California Sur: La Paz, "El Comitán" beach, 1 km north of Centro de Investigaciones Biológicas del Noroeste building, J. A. de León-González, coll., 1 Dec 1986 (12 specimens).

Description.—Best preserved specimen 100 mm long and 4 mm wide including parapodia, incomplete with 120 setigers. Anterior region with diffuse dark pigmentaton with no evident pattern.

Prostomium as long as wide, with two pairs of eyes in trapezial arrangement, anterior ones lensed; frontal antennae measuring half length of prostomium; palps globose, with conical palpostyles. Peristomium as long as first two setigers; with longer tentacular cirri extending posteriorly to setiger 3 (Fig. 10A).

Pharynx not everted in specimens. Analysis performed by dissection.

Paragnaths arranged on pharyngeal areas as follows: I, single cone; II, right side with 33 cones, left side with 24, both groups in triangular arrangement; III, 63 cones in 5 rows; IV, curved group of 74 cones; V, single large cone; VI, single short, transverse bar; VII–VIII, 42 cones in 2 rows, but 1 row with 3 cones on each side.

First two parapodia uniramous. Other anterior parapodia with rounded ligules; dorsal and ventral cirri well developed, dorsal ones better developed (Fig. 10B). On median and posterior parapodia notopodial dorsal ligules enlarged and median ligules conical. Neuropodial postsetal lobes mamilliform, neuropodial ventral ligules capitate; dorsal cirri subdistally inserted, ventral cirri proximally inserted (Fig. 10C, D).

All notosetae homogomph spinigers with slender, finely serrated appendage. Supracicular neurosetae homogomph spinigers and heterogomph falcigers (Fig. 10E). Infracicular heterogomph spinigers and falcigers.

Discussion.—*Perinereis villalobosi* was described from Mazatlán, Sinaloa state, shores, from a single epitokous specimen. Hutchings et al. (1991), placed this species in their group "1A," characterized by the presence of a transverse bar on Area VI and the notopodial dorsal ligule not greatly enlarged on middle and posterior segments. However, the transformation of posterior parapodia during the epitokous phase is such that it does not allow for the correct determination of the degree of enlargement of that ligule. The specimens reported in this study are referred to *P. villalobosi* due to their having the pharyngeal ornamentation typical of the species. Since the notopodial dorsal ligules are greatly enlarged, the species would belong to group "1B" of Hutchings et al. (1991).

Distribution.—Eastern Pacific Ocean. Re-

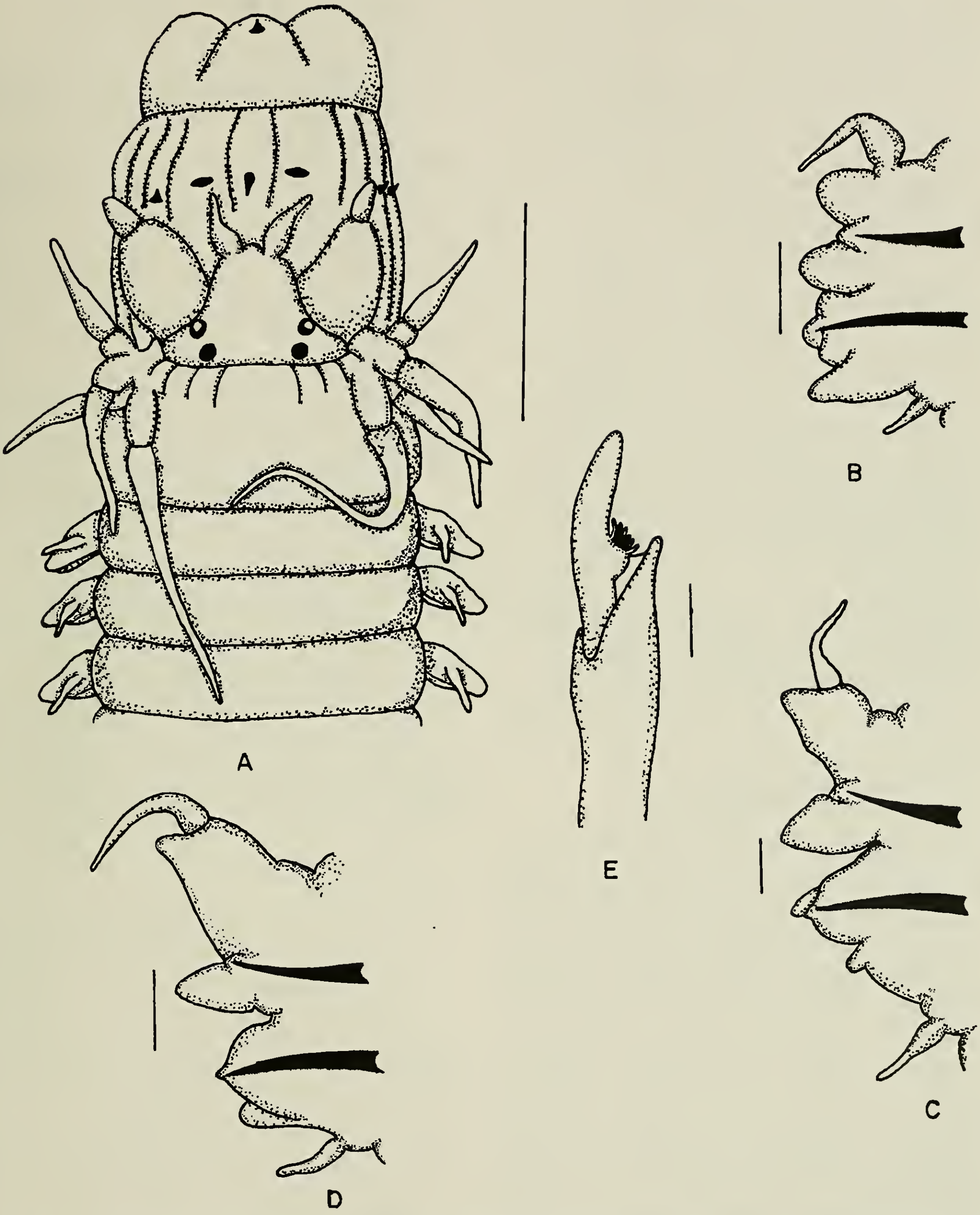

Fig. 10. *Perinereis villalobosi.* A. Anterior end, dorsal view; B. Parapodium 10th; C. Parapodium 49th; D. Parapodium 100th; E. Heterogomph neuropodial falciger in supracicular position from setiger 49. (Scale: A = 0.5 mm; B, C, D = 150μm; E = 10μm).

ported from the western coast of Baja California south to Mazatlán, Sinaloa, Mexico.

Habitat.—In galleries in sandy rocks in supralittoral zone (found after fragmentation of rocks).

Key to the Species of *Perinereis* from Mexican Shores

1. Notopodial dorsal ligules enlarged 2
– Notopodial dorsal ligules not enlarged.

- Two cones in a row present on area I, short bar on Area VI .... *P. floridana*

2. No bars on area IV 3
- Two small basal bars on area IV in addition to cones, short cone-shaped bar on area VI .... *P. monterea*

3. Single bar on area VI 4
- Two bars on area VI 7

4. Bar of area VI short 5
- Bar of area VI long and slender, ribbon-shaped 6

5. Areas I and V each with single cone.. .... *P. villalobosi*
- Area I with 4 cones; area V with 3 cones .... *P. anderssoni*

6. Area I with 7 cones; area VII–VIII with single row of 7 cones .. *P. bajacalifornica*
- Area I with 11 cones; area VII–VIII with 37 cones in two rows ... *P. elenaocasoae*

7. Two cones on area I, no paragnaths on areas V; 11 cones in 2 rows on areas VII–VIII .... *P. cariboea*
- Four cones in a diamond-shaped arrangement on area I; single cone on area V; eight cones in single row on area VII–VIII .... *P. osoriotafalli*

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We would like to thank K. Fauchald, and L. Ward (USNM) for their help in making available for examination the material under their care. Special thanks are also due to Leslie Harris, (LACM-AHF), for kindly allowing us to examine the specimens from the AHF collections. Thanks are due to S. I. Salazar Vallejo who loaned us some material from the Mexican Caribbean area, to V. Diaz Castañeda who sent us the specimens of *P. villalobosi* from Rincón de Ballenas, Baja California; and to K. Sindemark (NRS), who sent us material of *P. anderssoni.* We also thank the two anonymous reviewers whose comments greatly improved the manuscript.

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Streblospio gynobranchiata, a new spionid polychaete species (Annelida: Polychaeta) from Florida and the Gulf of Mexico with an analysis of phylogenetic relationships within the genus *Streblospio*

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Abstract.—*Streblospio gynobranchiata,* a new species of spionid polychaete, is described from Florida and the Gulf of Mexico. This species is distinguished by the presence of strap-like branchiae, beneath which larvae are brooded, in the genital body region of the females. Data from experimental crosses conducted in the laboratory are presented that indicate incipient reproductive isolation between *S. gynobranchiata* from Florida and *S. benedicti* from North Carolina and California. The spermatophores produced by males of *S. gynobranchiata* and *S. benedicti* are described for the first time. Morphological, developmental, and reproductive characteristics are used in combination to construct a cladogram that suggests possible phylogenetic relationships between known species in the genus *Streblospio.*

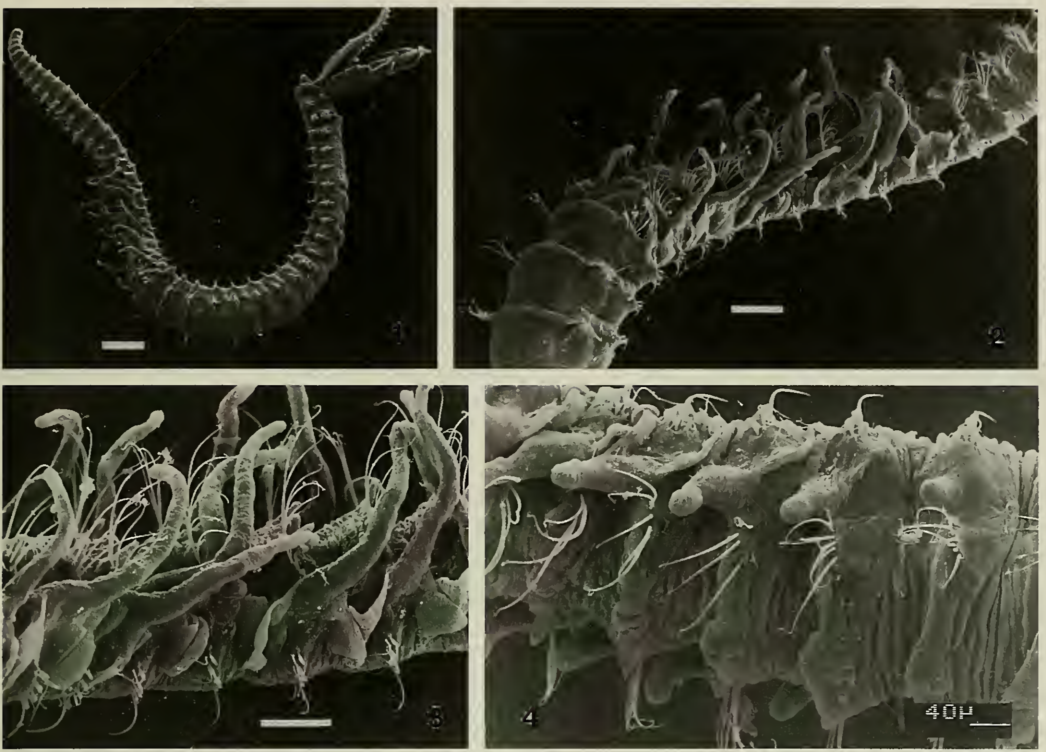
Genus *Streblospio* Webster, 1879

Diagnosis.—The genus *Streblospio* was established by Webster (1879) based upon material from New Jersey. Distinguishing features of the genus include: conical, rounded prostomium with 2–4 pairs of eyes and with or without a small nuchal tentacle; peristomium fused with the first setiger and forming a U-shaped envelope around the prostomium laterally and ventrally; one pair of palps and one pair of branchiae on the peristomium; a dorsal collar across the dorsum of setiger 2; notosetae all capillary, neurosetae include capillaries, multidentate hooded hooks and ventral sabre setae; and pygidium simple, with ventral lappets or without appendages.

Streblospio gynobranchiata, new species
Figs. 1–13

Type material.—Holotype: adult female (USNM 178822), length 8.4 mm, Tampa Bay, Florida; Courtney Campbell Causeway (west): depth 1 m, muddy sand, 27 Jul 1989. Paratypes: 17 males (USNM 178824), 8 females (USNM 178823), same collection data as holotype.

Additional material prepared for scanning electron microscopy (SEM): Stub #1 (USNM 178825)—4 anterior ends, collected 22 Jun 1987, Hillsborough River, Tampa, Florida, at the University of Tampa, depth 2 m, muddy sand; Stub #2 (USNM 178826)—2 adults, collected 23 Mar 1987, same as Stub #1; Stub #3 (USNM 178827)—4 anterior ends, collected 4 Aug 1988, same coll. data as holotype; Stub #5 (USNM 178828)—4 anterior ends, same coll. data as Stub #3; Stub #7 (USNM 178829)—4 adults, coll. 26 Mar 1987, same coll. data as holotype; Stub #8 (USNM 178830)—5 adult females, coll. 2 May 1987, same coll. data as holotype; Stub #9 (USNM 178831)—5 adults, same coll. data as Stub #8; Stub #10 (USNM 178832)—6 adults, same coll. data as Stub #8; Stub #11 (USNM 178833)—3 adults, coll. 1 Apr 1987, same coll. data as holotype.



Figs. 1–4. *Streblospio gynobranchiata,* new species (USNM 178830): 1, whole female with characteristic brood structures; 2, posterior dorsal portion of female showing strap-like brood structures; 3, lateral view of brood structures in female; 4, dorsal view of most anterior brood structures and notosetae. Scales = 200 μm for 1; 100 μm for 2, 3.

Other material examined.—Massachusetts: Provincetown, coll. H. E. Webster, type (USNM 415), 6 specimens + 3 fragments; San Francisco Bay, Berkeley Beach, coll. O. Hartman, 27 Jul 1934, (USNM 20220) 8 paratypes; New Jersey, Little Egg Inlet, coll. 17 Apr 1972, (USNM 71677) 8 specimens, (USNM 71678) 22 specimens; SEM preparations: Box #7, Stub #4—1 anterior end, Stub #6—3 anterior ends, coll. Bogue Sound, North Carolina, coll. L. Levin; Cultured material: Sebastian River, Florida, 29 Mar 1993; Copano Bay, Texas, 18 Oct 1983; Godineaux, Trinidad 3 Apr 1984; Ballast Point, Tampa Bay, Florida 6 Jun 1984.

Distribution.—*Streblospio gynobranchiata* has been collected from the east and west coasts of Florida, Texas, and Trinidad. The type locality is Tampa Bay, Florida in the subtidal estuarine sediments of the Hillsborough River adjacent to the University of Tampa in downtown Tampa.

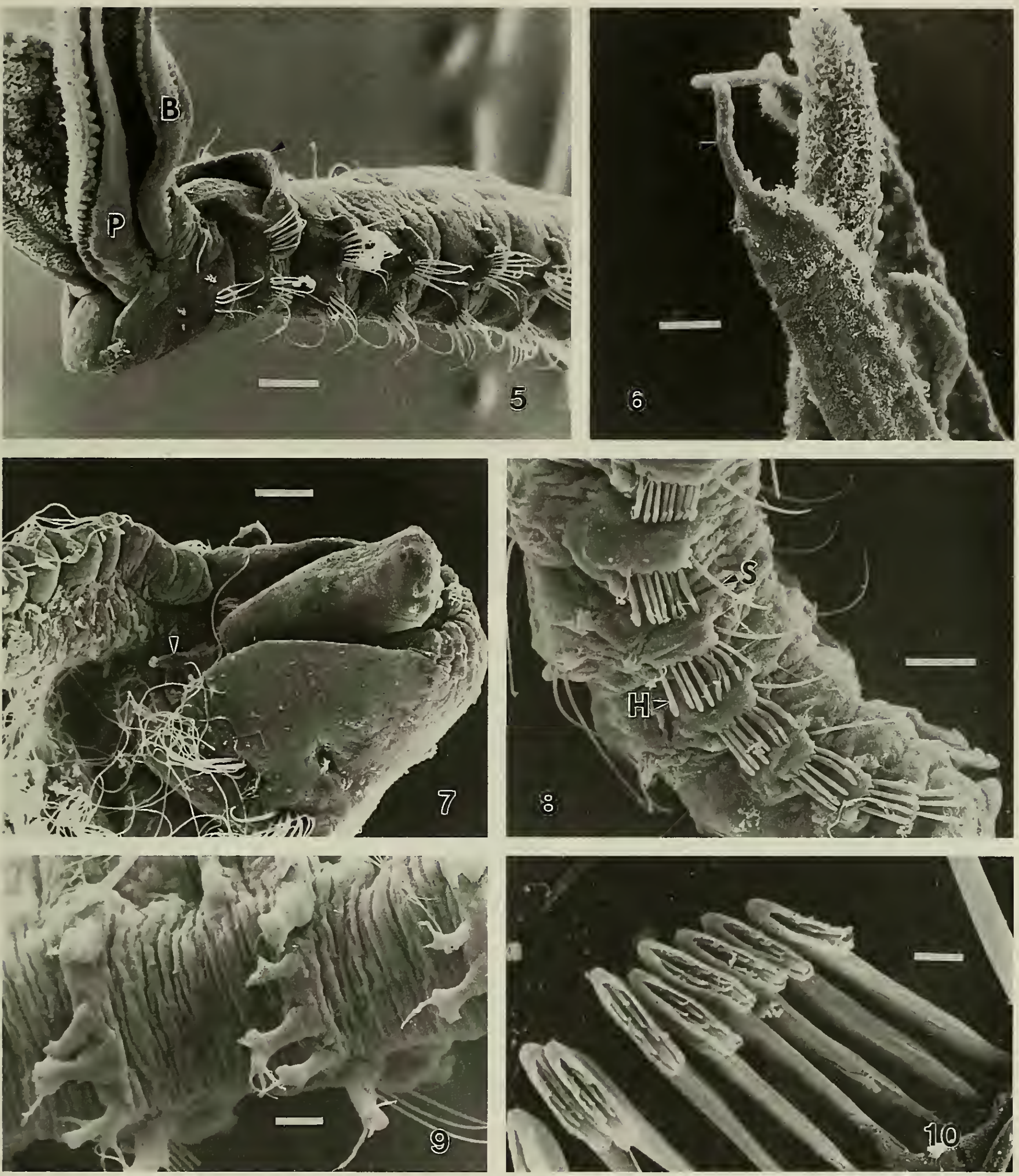
Etymology.—The specific name, *gynobranchiata,* refers to the branchiate brood structures found in mature females of this species. The prefix is from the Greek, *gyne,* meaning woman or female plus the suffix from the Greek, *branchia,* refering to "gills."

Description.—Prostomium elongate and rounded anteriorly, flanked laterally by peristomial ridges leading to ventral mouth. One pair of palps located lateral to prostomium and median to peristomial ridges. Palps short; about same length as adjacent branchiae and densely ciliated on frontal surfaces (Figs. 1, 5). One pair of thick, ciliated branchiae inserted just posterior to palps. These branchiae with distal digitiform appendage terminally (Fig. 6). Small conical nuchal tentacle present between branchiae (Fig. 7). Nuchal tentacle difficult to see without removing branchiae.

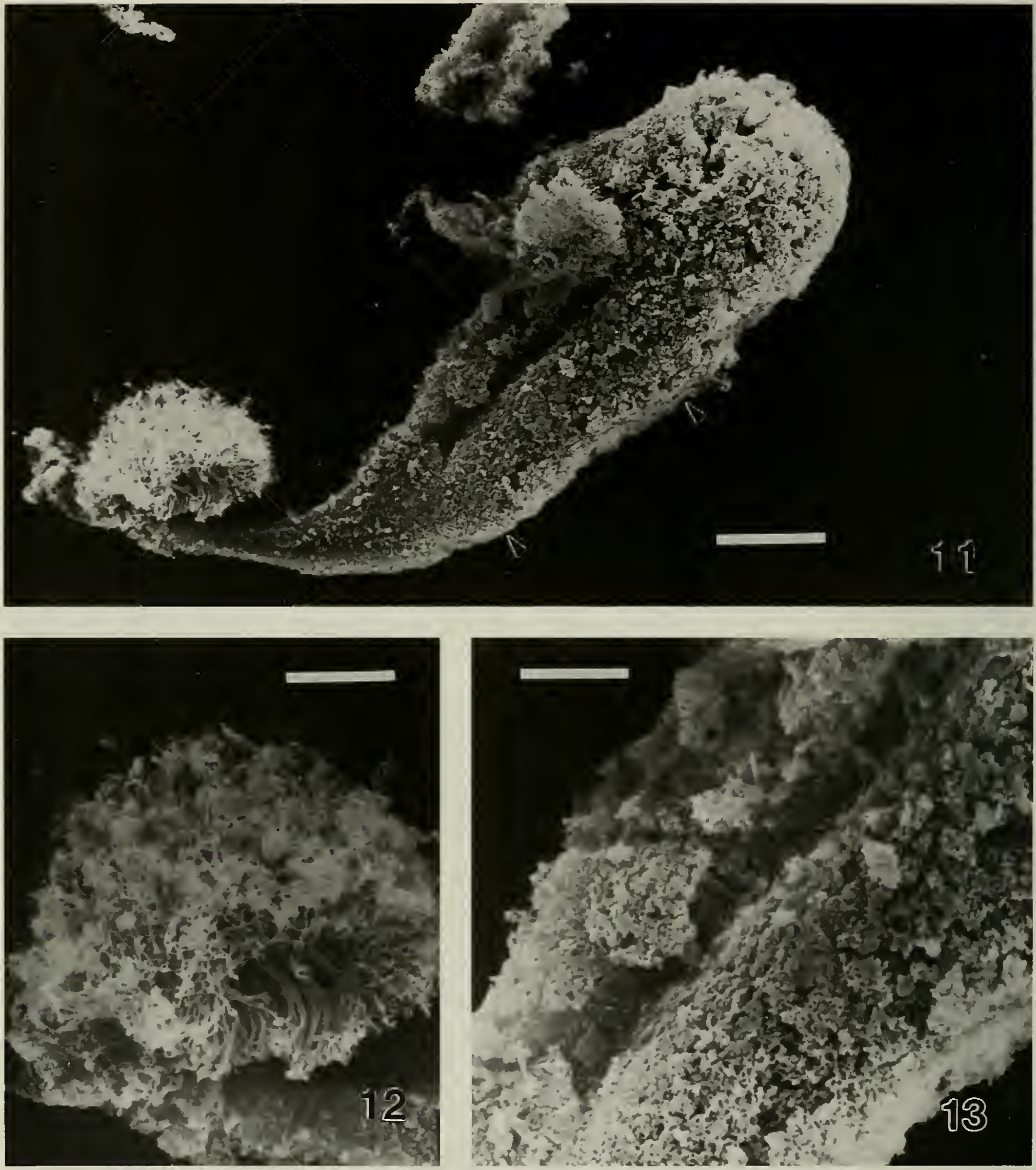
Notopodium of setiger 1 with 1–3 capillary setae and no postsetal lobe (Fig. 5). First neuropodium with 3–6 capillary setae and flap-like postsetal lobe. Second notopodium with 6–12 capillary setae and broad, postsetal lobe continuous with dorsal hood that extends across dorsum connecting left and right notopodia. Anterior margin of hood flares upward and forms opening into dorsal pouch that extends posteriorly to end of third setiger (Fig. 5). Second neuropodium with 6–8 capillary setae and broad flap-like postsetal lobe. Notopodia of females situated along lateral sides of body anterior to branchiate region but shifted dorsally throughout branchiate region (setigers 20–35) and on posterior setigers. Notosetae in branchiate and posterior body regions longer than anterior notosetae. Notopodial lobes flap-like through anterior one-half of body, becoming digitiform and shifted dorsally toward posterior. Neurosetae capillary in setigers 1–6. Ventralmost capillary seta in neuropodia 3–6 stouter than others and curving ventrally under body. Neuropodial hooded hooks and sabre setae beginning on setiger 7 and continuing to end of body (Figs. 8, 10). Hooded hooks accompanied by 1–3 small anterior capillary setae to near end of body. Single inferior sabre seta present in each neuropodium from setiger 7 to end of body (Fig. 8). Hooded hooks number 2–4 in setiger 7 to 6–8 near end of body; each hook with three or four pairs of small teeth in addition to main unpaired tooth (Fig. 10). Neuropodial lobes flap-like on setigers 1–6, decreasing in size posteriorly.

Brood structures present on females from about setiger 20 to about 35 (24–35 in holotype), small in anterior and posterior regions, reaching maximum size in middle of range (Figs. 1–4). Largest pouches composed of broad semicircular fold arising laterally between noto- and neuropodium and extending dorsally as thin digitiform appendage resembling a branchium. Developing larvae loosely held between branchiae by brooding females. Posterior to branchiate region on females are dorsal, segmentally arranged extensions of epidermis forming branched, ciliated appendages in rows between left and right notopodia (Fig. 9). Three or four of these extensions present on posterior setigers to near end of body. Cilia on these epidermal extensions arranged in discrete tufts.

Males of *Streblospio gynobranchiata* produce spermatophores in laboratory cultures in the presence or absence of females. These spermatophores are composed of a sickle-shaped proximal piece and a distal sperm ball (Fig. 11). The proximal piece is divided into two regions: a thick coarsely granular region (0.28 mm long and 0.12 mm wide) further from the sperm ball and a curved, conical, tapering region (0.24 mm long and 0.08 mm wide at widest point) leading to and attached to the sperm ball. The former, thick region has a groove down one side that ends at the junction between it and the conical region (Figs. 11, 13). The conical region is smoother than the thick region. The sperm ball measures 0.51 mm in diameter and is spherical in shape (Fig. 12). The dimensions of the spermatophore components vary with the size of the worm producing them, with larger worms releasing larger spermatophores. In cross-section, the material making up the thick and conical regions of the spermatophore appears to be composed of fibrous material of unknown composition. The sperm ball is surrounded by a thin layer of this fibrous material. Only mature sperm are found inside the sperm ball. These sperm are oriented parallel to each other and closely packed inside the sperm ball with their tails extending in a single direction. In fresh spermatophores, the sperm tails have a refringent color in reflected light and move in slow synchronous beating motions. Spermatophores of the same general structure as



Figs. 5–10. *Streblospio gynobranchiata,* new species (5, 9, USNM 178829; 6, USNM 178831; 7, USNM 178828; 8, 10, USNM 178830): 5, lateral view of anterior end with branchia (B), palp (P), and hood (arrow) visible; 6, distal tip of branchium showing finger-like extension (arrow): 7, lateral view of anterior end with right palp and branchium removed to expose the nuchal antenna (arrow); 8, lateral view of posterior setigers showing hooded hooks (H) and sabre setae (S), sabre setae are ventral to the hooded hooks; 9, dorsal view of female posterior to brood structures showing segmental epidermal extensions with tufts of cilia; 10, hooded hooks from posterior setiger showing pairs of small teeth distal to the main tooth. Scales = 100 μm for 5; 50 μm for 6, 7; 25 μm for 8, 9; 5 μm for 10.



Figs. 11–13. *Streblospio gynobranchiata,* new species: 11, whole spermatophore as released by male; arrows indicate region enlarged in Fig. 13; 12, sperm ball attached to end of spermatophore; 13, central portion of spermatophore (region between arrows in Fig. 11) showing central groove and texture of material of spermatophore. Scales = 100 μm for 11; 25 μm for 12, 13.

described above were produced in laboratory cultures of *S. benedicti* from North Carolina and Los Angeles. The mature sperm of *S. gynobranchiata* are greatly elongate with a mean head length (nucleus plus acrosome) of 41.15 μm (n = 150).

Biology.—*Streblospio gynobranchiata* is found in estuarine to marine conditions in shallow-water sediment. Worms may form dense assemblages of tubes in stressed or disturbed habitats. Larval development is planktotrophic with brooding to the three-setiger stage followed by release into the plankton and settlement at about 9–12 setigers. Females that are forced to leave their tubes while brooding may drop their embryos prematurely. Male worms produce spermatophores (described above) that are incorporated into ventrally located seminal receptacles in the females. Site of fertilization and transport of mature oocytes into brood structures have not been observed.

Remarks.—In Webster's (1879) original description of *Streblospio benedicti,* reference is made to the genital pouches in females: "On one specimen the middle third of the dorsum was covered by a very thin, transparent, raised membrane." (Webster 1879: 121). Webster (1879) did not use the term "pouches" to describe these female structures; however, examination of worms from Little Egg Inlet, New Jersey (USNM 71678) revealed brood pouches on females similar to those typically seen in worms from North Carolina and California. Webster (1879) did not mention what have been called "sabre setae" in the neuropodium from setiger 7 to the end of the body nor did he describe the pairs of small teeth located above the main tooth on neuropodial hooded hooks. He refers to the hooded hook morphology as: ". . . they have four terminal teeth, the outer one being shortest . . ." (Webster 1879: 121). Examination of the material from New Jersey (USNM 71678) by SEM revealed that sabre setae begin in setiger 7 and continue to near the end of the body and that the neuropodial hooded hooks have 3 or 4 pairs of small teeth in addition to the main unpaired tooth. The morphological and reproductive characteristics of the species in the genus *Streblospio* are summarized in Table 1.

Levin (1984) reported that *Streblospio benedicti* displayed different patterns of larval development over its range with some populations producing lecithotrophic larvae and others producing planktotrophic larvae. Planktotrophic and lecithotrophic populations were shown to be interfertile but females from interpopulational crosses tended to produce larvae characteristic of their original population. The production of different larval types was not affected by temperature or food availability in populations of *S. benedicti* from North Carolina (Levin & Creed 1986), although *S. benedicti* from Narragansett Bay increased brood sizes in response to elevated nutrient levels in mesocosm studies (Levin 1986). The demographic consequences of planktotrophy versus lecithotrophy in *S. benedicti* have been addressed by Levin, et al. (1987), Levin & Huggett (1990) and Levin & Bridges (1994). A genetic basis for this polymorphism in *S. benedicti* was demonstrated by Levin et al. (1991).

Buchanan (1890) described a species, *Streblospio shrubsolii* (originally *Hekaterobranchus shrubsolii*) from Sheppey, England, that differed from *S. benedicti* by lacking a median nuchal tentacle (conical papilla or cirrus) on the first segment, lacking the conical dorsal cirri on posterior setigers, and lacking thoracic nephridia. Additional features of *S. shrubsolii* that distinguish it from *S. benedicti* include: the first appearance of hooded hooks on setiger 8; the apparent lack of ventral sabre setae; the two-lobed dorsal hood on setiger 2; and the 2 rows of small teeth on hooded hooks. Subsequent examinations of this species revealed differences in egg diameter, location of the first gametogenic setiger, larval development, brood structures on females, and isozyme frequencies. According to Cazaux (1985) and our unpublished observations (LAL), *S. shrubsolii* from France exhibit mature ova 200–230 μm in diameter, with one large larva brooded between transverse ridges on each segment. Development is direct in this species. In an examination of four enzyme systems (PHI, MDG-2, ADH, and IDH), individuals of *Streblospio shrubsolii* ($n = 12$) were fixed for completely different isozymes than planktotrophic individuals ($n = 8$–70) and leci-

Table 1.—Morphological and reproductive characteristics of described species of *Streblospio.*

Character	*Streblospio gynobranchiata* new species	*Streblospio benedicti* Webster 1879	*Streblospio shrubsolii* Buchanan 1890	*Streblospio benedicti japonica* Imajima 1990
Body length (mm)	8.4	6–12	6–10	7
No. of segments	70	70	48	48
Pairs of eyes	2–3	2–3	2–4	2
Nuchal antenna on 1st segment	present	present	absent	present
Branchial pairs	1	1	1	1
Start of hooded hooks (setiger)	7	6/7/8/9	8	7
No. hooks per ramus				
anterior	3–4	3–5	2–3	5–6
posterior	8–10	8–12	5	?
Dorsal collar	one piece	one piece	2 lobes	one piece
Brood structures	branchiate	pouches	transverse, mid-segmental ridges	?
First saber seta	7	7	?	3
Rows of small teeth on hooded hooks	3–4	3–4	2	5 pairs
Pygidium	simple	simple or lobed	simple	2 lappets
Egg diameter (μm)	70–90	70–90 (planktotrophic) 100–220 (lecithotrophic)	200–230	?
Larval development	planktotrophic	planktotrophic and lecithotrophic	Direct	?
Larval swimming setae	yes	yes (planktotrophic) no (lecithotrophic)	no	?
Number of larvae per brood	100–200	200–400 (planktotrophic) 30–70 (lecithotrophic)	?	?
Sperm head length (μm)	41.15	47.81	?	?

thotrophic individuals (n = 10–60) of *S. benedicti.*

Studies of oogenesis in *Streblospio* have revealed differences in yolk bodies that appear to vary with species and developmental mode. The size of yolk granules and relative proportion of heterosynthetically-derived yolk differs between planktotrophic and lecithotrophic forms of *S. benedicti* (Eckelbarger 1980, 1986). Preliminary ultrastructural studies suggest that average yolk body diameter in *S. shrubsolii* (6.8 μm) is greater than that in *S. gynobranchiata* (3.2 μm) from Fort Pierce, or from planktotrophic (2.6–3.2 μm) or lecithotrophic (3.2–5.3 μm) *S. benedicti.* The mature egg of *S. shrubsolii* contains large quantities of lipid droplets not evident in the other species, as well as a different morphology of the egg envelope (K. Eckelbarger, pers. comm.). These differences suggest interspecific divergence in female gamete morphology similar to that reported for sibling species of *Capitella* (Eckelbarger & Grassle 1983).

Horst (1909) described an additional species of *Streblospio* (*S. dekhuyzeni*) from Zuide Zee, France that had two types of capillary notosetae and more hooded hooks per ramus than *S. shrubsolii.* These differences were minor enough to lead most taxonomists to consider *S. dekhuyzeni* and *S. shrubsolii* synonyms (Fonseca-Genevois & Cazaux 1987).

Hartman (1936) described *Streblospio lutincola* from several locations along the central California coast. She (pg. 46) considered this new species to differ from *S. benedicti* in having a "... much smaller ventral peristomial fold, and its much larger prostomium." *Streblospio lutincola* was later synonymized with *S. benedicti* (Hartman 1944).

Foster (1971) proposed a synonymy of all previously described species making the genus *Streblospio* monotypic. In a note at the end of her treatment of the genus (pg. 115), she mentions a population of *Streblospio* collected from Maracaibo estuary that has branchiate brood structures in females. This appears to be the first mention of *S. gynobranchiata* in the literature.

While *Streblospio gynobranchiata* generally possesses a more southerly distribution than the other described species of *Streblospio,* it has been reported in the same geographical regions as *S. benedicti.* For example, lecithotrophic *S. benedicti* have been collected from Big Slough in Aransas Bay, Texas and *S. gynobranchiata* from an attached estuarine system, Copano Bay, Texas. Planktotrophic *S. benedicti* from Fort Pierce, Florida were collected within a few km of the Sebastian River system where *S. gynobranchiata* occurs. It is unknown whether these patterns of distribution are natural or the result of anthropogenic transport since *Streblospio* may be transported in ship ballast water from one location to another (Carlton 1975).

Imajima (1990) described a new subspecies (*Streblospio benedicti japonica*) from the Yatsu tidelands, Japan. This new form differs from *S. benedicti* in having ventral sabre setae beginning on setiger 3 and by having 5 pairs of small teeth in addition to the main unpaired tooth on the hooded hooks.

The mean length of the sperm (acrosome + nucleus + middlepiece) from spermatophores is significantly different ($P < 0.001$) between *Streblospio gynobranchiata* (41.15 μm ± 4.22, $n = 150$) from Tampa Bay and *S. benedicti* (47.81 μm ± 2.83, $n = 150$) from Los Angeles. The location of the first gametogenic setiger in males of *S. gynobranchiata* (15.66 ± 9.98, $n = 35$) is not significantly different from that of planktotrophs of *S. benedicti* from Fort Pierce (9.0 ± 2.28, $n = 6$).

In females of *Streblospio gynobranchiata,* the location of the first gametogenic setiger is significantly different from that of *S. benedicti* (planktotrophs and lecithotrophs), and *S. shrubsolii* (Table 2). In addition, the percent gametogenic setigers, the location of the first brood structure, and the total number of brood structures is significantly different between *S. gynobranchiata* and *S. benedicti* (Table 2).

Reproductive isolation has been reported between *Streblospio gynobranchiata* from Tampa Bay, Florida and *S. benedicti* from North Carolina and from Los Angeles, California (Rice 1991). Experimental crosses between populations were undertaken with worms that had been raised in isolation until sexual maturity then paired with a mate from an exotic population (experimental) or from the same population (control) and monitored for production of larvae. Females from unsuccessful interpopulational crosses were subsequently paired with males from their own population to ensure female fertility. In 28 reciprocal crosses between Tampa Bay and North Carolina worms, 26 crosses produced no offspring (see Rice 1991, table 11). In six crosses between Tampa Bay females and Los Angeles males, no offspring were produced.

In a separate series of experimental crosses, we were able to successfully cross *Streblospio gynobranchiata* from Copano Bay, Texas with lecithotrophic *S. benedicti* from Big Slough, Texas. We also found larval production in limited crosses between females of *S. gynobranchiata* from Tampa Bay and males (planktotrophic) of *S. benedicti* from Tar Landing, North Carolina, indicating that reproductive isolation between these two (or more) species is not complete.

In an experimental cross between one

Table 2.—Reproductive characteristics of mature females of *Streblospio* species. Underlined mean values are not significantly different ($P > 0.05$).

Characteristic	*S. benedicti* (planktotrophs)	*S. benedicti* (lecithotrophs)	*S. gynobranchiata*	*S. shrubsolii*	Analysis of Variance
Total setigers					
mean	47.8	45.0	46.6	51.3	F = 1.502
std. dev.	6.4	10.7	11.8	6.5	*P* = 0.2146
number	68	97	79	6	
First gametogenic setiger					
mean	10.5	12.7	7.7	19	F = 217.2
std. dev.	1.1	1.3	2.0	1.1	*P* = 0.0001
number	71	80	78	6	
% gametogenic setigers					
mean	38.3	34.6	45.4	—	F = 12.7
std. dev.	8.7	6.8	8.7	—	*P* = 0.0001
number	6	18	61	—	
First pouch/branchium					
mean	21.2	21.6	20.0	—	F = 7.46
std. dev.	2.2	1.9	3.6	—	*P* = 0.0007
number	69	94	66	—	
Total pouches/paired branchiae					
mean	9.6	8.4	14.5	—	F = 16.97
std. dev.	2.7	2.7	11.5	—	*P* = 0.0001
number	69	92	66	—	

male of *S. gynobranchiata* from Copano Bay, Texas and one female of *S. shrubsolii* from Sully Island, Wales, larvae were produced after 12 days but were misshapen and did not survive. In two experimental crosses between males of *S. gynobranchiata* from Trinidad and planktotrophic females of *S. benedicti* from North Carolina, no larvae were produced. These results suggest that reproductive isolation is incipient between *S. gynobranchiata* and *S. benedicti* and between *S. gynobranchiata* and *S. shrubsolii.* Reproductive compatibility between populations is generally considered to be a pleisiomorphic characteristic, whereas loss of reproductive potential between closely related taxa can be considered an apomorphic characteristic. Considering the degree of morphological differentiation (Tables 1, 2) in addition to the differences in geographic range and reproductive isolation, it seem certain that *S. gynobranchiata* represents a new and distinct species.

At present, there appear to be at least four species of *Streblospio* that can be distinguished based upon morphological characteristics (Table 1). *Streblospio gynobranchiata* differs from *S. benedicti* in its more southern distribution, the presence of branchiate brood structures on females, the presence of posterior dorsal ciliated appendages in females, gamete distribution in females, and mature sperm dimensions. *Streblospio gynobranchiata* differs from *S. shrubsolii* in the distribution of hooded hooks (beginning on setiger 7 in the former species and setiger 8 in the latter), the incomplete dorsal collar in the latter species, and the absence of a prostomial nuchal tentacle in the latter species. *Streblospio gynobranchiata* differs from *S. benedicti japonica* in the distribution of ventral sabre setae (beginning on setiger 3 in the latter species) and in the number of paired small teeth on the hooded hooks [see Ohwada & Nishino (1991) for a discussion of variability in this character]. In addition to the differences in standard morphological characteristics between *S. gynobranchiata* and the other described species in the genus, there are also differences in gamete morphology, gamete distribution (Table 2), modes of larval development, and reproductive compatibility.

Phylogenetic relationships.—The four species of *Streblospio* were analyzed for phylogenetic relationships using the cladistic programs, MacClade 3.01 (Maddison & Maddison 1992) and PAUP 3.1.1 (Swofford 1993). A character matrix consisting of 16 morphological and reproductive characteristics was constructed from literature reports and personal observations (Appendix 1). All characters were unweighted and unordered. The three most parsimonious trees found via an exhaustive search (Fig. 14A, B, C) all consist of 30 steps (consistency index = 0.933, retention index = 0.714) and were rooted using *Paraprionospio pinnata* and *Spiophanes kroyeri* as the designated outgroups. The strict consensus tree (Fig. 14D) groups *S. gynobranchiata* and *S. benedicti* as a clade with *S. benedicti japonica* and *S. shrubsolii* joining as a polytomy. More information is needed concerning the characteristics of these latter two species in order to resolve this node. A bootstrap analysis of 100 replicates in PAUP using tree-bisection-reconnection branch swapping, MULPARS activated, zero-length branches collapsed, and multistate characters interpreted as polymorphism, resulted in the values listed on the branches in Fig. 14D.

Sigvaldadóttir et al. (1997) presented a cladistic analysis of the genera within the Spionidae based upon 25 morphological characters. Analysis of generic characteristics, including variation between species within a genus, resulted in a large number of most parsimonious trees (13305) and contributed little to our understanding of spionid relations. A second analysis using only type species as generic representatives produced more informative results with four equally parsimonious trees. In the consensus tree derived from these four trees, *Streblospio benedicti* is grouped as the most plesiomorphic member of a clade including *Aurospio dibranchiata, Orthoprionospio cirriformia, Paraprionospio pinnata, Prionospio banyulensis, Prionospio steensrtupi,* and *Laubieriellus grasslei.* Sigvaldadóttir et al. (1997) point out that many characteristics of spionid genera are missing or incorrectly reported in the literature and that resolution of spionid phylogeny will likely require re-examination of species and development of new characters. Incomplete literature reports and polymorphic characters within species hampered resolution in the present study also. Four characters are coded as missing in the *Streblospio* data matrix for *S. benedicti japonica* since these four characters were not included in the description of the species by Imajima (1990). Knowledge of these characters would likely help to resolve the polytomy in the *Streblospio* consensus tree.

The study of variation within the genus *Streblospio* emphasizes the value of considering reproductive characters along with standard morphological traits when distinguishing traits within a polychaete genus. Eckelbarger and Grassle (1984) demonstrated a similar situation in which sibling species of *Capitella* are distinguished primarily by reproductive features. Characters such as strap-like branchiae in the genital region of females, the position and number of gametogenic setigers, and mature sperm dimensions distinguish *S. gynobranchiata* from other species of *Streblospio* (Table 1). In mature specimens, reproductive characters like brood structures are more readily observed than setal or ciliation patterns. Unfortunately, immature specimens of different species of *Streblospio* appear similar in overt morphology and care must be taken with identification in regions where more than one species is likely to occur (e.g., southern USA, Europe). We expect that additional sibling species of *Streblos-*

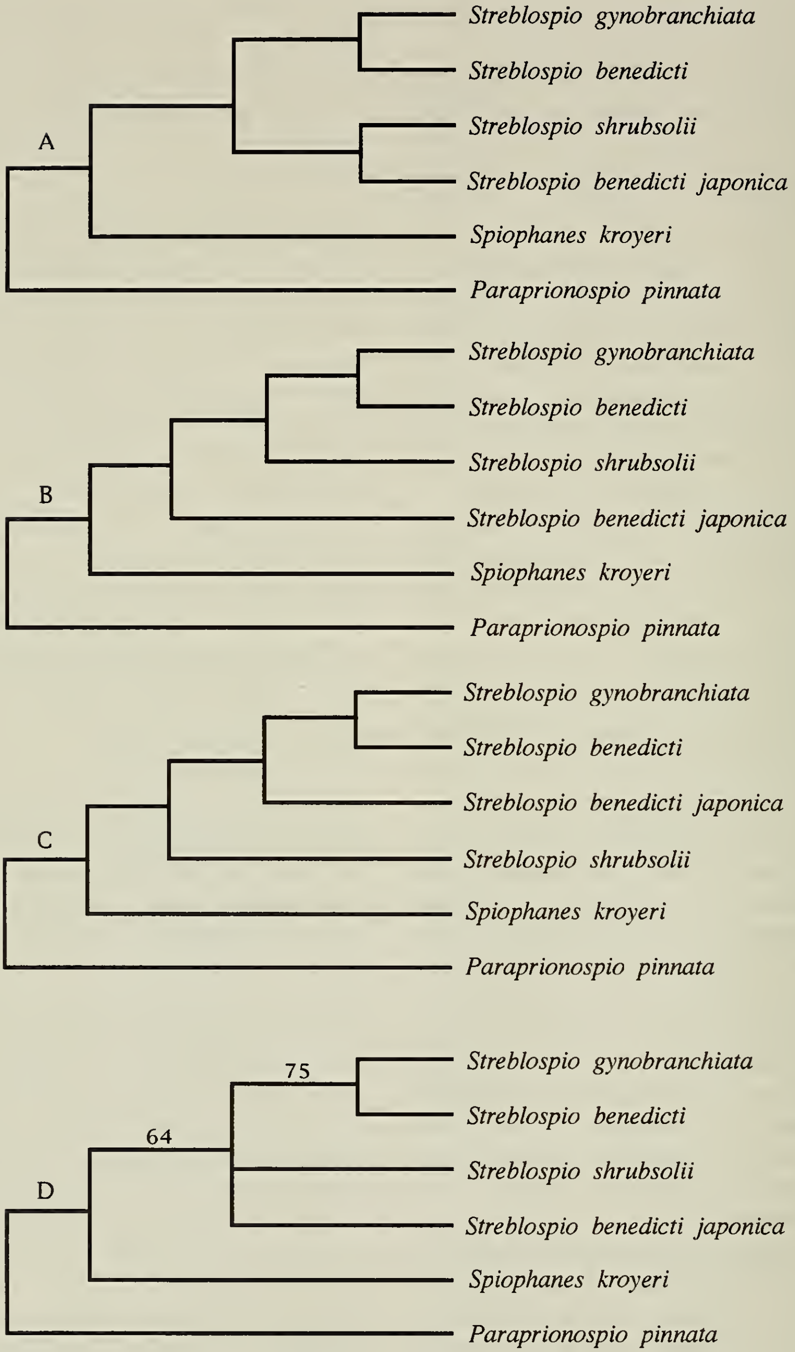


Fig. 14. A, B, C, three most parsimonious trees for the four species in the genus *Streblospio*. Each tree is 30 steps; D, strict consensus tree with bootstrap values listed on branches.

Table 3.—Character code data matrix.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
S. gynobranchiata	1	1	0	1	0	1	1	2	1	1	2	1	0	0	1	1
S. benedicti	1	1	0	1	0	1	1	2	1	0	2	1	0	0/1	1	1
S. shrubsolii	0	1	1	2	0	0	1	1	1	2	?	0	0	2	1	1
S. benedicti japonica	0	1	0	1	0	?	1	2	1	?	0	2	1	?	1	1
Paraprionospio pinnata	1	0	1	3	1	2	0	0	0	2	3	0	2	0	1	1
Spiophanes kroyeri	0	1	0	4	2	1	0	0	2	2	1	?	2	?	0	0

pio will emerge as reproductive, genetic, and morphological characters of populations around the world are examined in greater detail.

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Appendix 1.—Character codes for phylogenetic analysis of *Streblospio* species (and Table 3).

1. *Total number of segments*
0: <50
1: >70
2. *Membrane on palps*
0: present
1: absent
3. *Nuchal antenna*
0: present
1: absent
4. *First hooded hook*
0: 6th setiger
1: 7th setiger
2: 8th setiger
3: 9th setiger
4: 15th setiger
5. *Pairs of Branchiae*
0: 1 pair
1: 3 pair
2: none
6. *Hooks per posterior ramus*
0: 5
1: 8–12
2: >12
7. *Notopodial hooks*
0: present
1: absent
8. *Dorsal collar at setiger 2*
0: absent
1: 2 lobes
2: 1 lobe
9. *Anterior postsetal lamella*
0: auricular
1: semicircular
2: pointed
10. *Brood structures*
0: pouches
1: branchiae
2: none
11. *First sabre seta*
0: 3rd setiger
1: 4th setiger
2: 7th setiger
3: 9th setiger
12. *Small teeth on hooded hooks*
0: 2 pair
1: 3 or 4 pairs
2: 5 pairs
13. *Pygidium*
0: simple
1: ventral lappets
2: lobes and cirri
14. *Larval development*
0: planktotrophic
1: lecithotrophic
2: direct
15. *Body regions*
0: distinct
1: graded
16. *Neurosetal spines*
0: present
1: absent

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Capitellids (Polychaeta: Capitellidae) from the continental shelf of the Gulf of California, México, with the description of a new species, *Notomastus angelicae*

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Abstract.—In this study 11 species of capitellids in 6 genera are recorded from the continental shelf of the Gulf of California. The genus *Notomastus* is represented by 5 species, among them *Notomastus angelicae* is described.

The Gulf of California is located approximately between 21°–32°N and 107°–114°W, in the northwestern region of Mexico. Shaped as a semiclosed basin, it has only one opening connecting it to the Pacific Ocean at its southern end. Due to its geographic location and the fact that several water masses are known to penetrate it (subarctic, tropical and subtropical) it is one of the most ecologically complex systems in Mexico. A large variety of habitats for the fauna (which can be locally highly diversified) can be found there. The polychaetes and, in particular, the capitellid family is no exception to this: 28 species in 13 genera have been recorded so far in the continental shelf of the Gulf in addition to six species from deep waters. Among these, 10 species in six genera were identified for this study, in addition to the new species, *Notomastus angelicae,* herein described.

Capitellids are among the most common and widely distributed families of polychaetes worldwide. Found mainly in soft bottoms, they can occur in a large variety of sedimentary types and from intertidal to abyssal depths (Ewing 1984a). However, despite the relatively large number of species so far recorded in this family for the Gulf of California, our benthic studies of the region indicate that this is not an abundant family in the area (Hernández-Alcántara 1992).

Capitellids are known to be morphologically relatively simple organisms which is partly why their correct taxonomic identification is difficult. They were the first polychaetes identified, Fabricius being the first to record in 1780 the species *Capitella capitata* (as *Lumbricus capitatus*). Since then, approximately 140 species in 36 genera have been described (Ewing 1984a). In the Gulf of California, the first record for this family was published by Fauvel (1943) who reported *Dasybranchus caducus* for San José Island (Baja California Sur). From the 34 species recorded so far, 12 have been originally described for the Gulf of California: *Notomastus lobatus* Hartman 1947, *N. sonorae* Kudenov 1975, *N. angelicae* n.sp., *Dasybranchus parplatyceps* Kudenov 1975, and *D. platyceps* Hartman 1947, in the continental shelf and *Notomastus abyssalis* Fauchald 1972, *N. cinctus* Fauchald 1972, *Leiochrides hemipodus* Hartman 1960, *Neoheteromastus lineus* Hartman 1960, *Neomediomastus glabrus* (Hartman 1960), *Neonotomastus glabrus* Fauchald 1972, and *Notodasus magnus* Fauchald 1972, in deep waters. This relatively high species richness can be partly explained both by considering the geographic situation of the Gulf of California, which allows the confluence of tropical, subtropical and temperate waters, as well as its extended littorals with contrasting environmental conditions.

Material and Methods

The specimens were collected on board R/V *El Puma* (UNAM) as part of the institutional "CORTES" project in March 1985. A Smith-McIntyre grab was used to collect the sediment which was then sieved through a 0.5 mm sieve. Following fixation with 10% formalin, the organisms were separated, identified and preserved in 70% ethanol.

The holotype of *N. angelicae* as well as some paratypes were deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) collection. Additional paratypes are deposited in Natural History Museum of Los Angeles County (LACM), Australian Museum (AM), British Natural History Museum (BNHM), and in the Polychaete Collection of the Instituto de Ciencias del Mar y Limnología, UNAM (CP-ICMyL), where the other identified species are also deposited.

The habitat data for each species are abbreviated as follows: D = depth in meters, T = temperature in °C, S = salinity in ‰, OM = organic matter content in the sediments in %, and DO = dissolved oxygen in ml/l.

Results

In this study, 428 capitellids (11 species in six genera) were collected and identified from the continental shelf of the Gulf of California.

Decamastus nudus Thomassin, 1970

Decamastus nudus Thomassin, 1970:81, figs. 6a–c.

Material examined.—21 specimens: Rocas Consag, 30°59.4′N, 114°04.1′W, sta. 39, 106.4 m, silty sands, 16 Mar 1985 (1 specimen). North Tiburón Island; 29°23.3′N, 112°30.7′W, sta. 26, 71.9 m, fine sands, 14 Mar 1985 (7 specimens). San Miguel Cape, 28°08.0′N, 112°45.8′W, sta. 20, 54.1 m, fine sands, 13 Mar 1985 (10 specimens). Santa María Bay; 25°02.4′N, 108°31.7′W, sta. 3, 32 m, fine sands, 10 Mar 1985 (3 specimens).

Habitat.—Coarse substrates, coralline sands next to marine phanerogam meadows (Thomassin 1970). In this study it was collected in fine and silty sands; D = 32.0–106.4; T = 13.2–14.4; S = 35.04–35.35; OM = 1.5–5.7; DO = 1.02–3.25.

Distribution.—Southwestern Madagascar (Thomassin 1970). North of Sonora, west of Santa María Bay, Sinaloa, and north of Santa Rosalía, Baja California Sur.

Leiocapitella glabra Hartman, 1947

Leiocapitella glabra Hartman, 1947:438, pl. 54, figs. 1–3.—Ewing, 1984a:14.45, figs. 14.39, 14.40 a–d.—not Day, 1973: 100 type Ewing, 1984a.

Material examined.—59 specimens: Rocas Consag, 30°59.4′N, 114°04.1′W, sta. 39, 106.4 m, silty sands 16 Mar 1985 (6 specimens). Tepoca Cape, 30°02.4′N, 112°55.4′W, sta. 44, 104.1 m, silty sands, 17 Mar 1985 (4 specimens). Punta Arboleda, 26°46.6′N, 110°06.7′W, sta. 14, 92 m, medium sands, 12 Mar 1985 (10 specimens). Santa Inés Bay, 26°59.4′N, 111°53.5′W, sta. 49B, 68.8 m, 19 Mar 1985 (26 specimens). Santa Inés Bay, 26°59.6′N, 111°50.4′W, sta. 49A, 100 m, fine sands, 19 Mar 1985 (13 specimens).

Habitat.—53 to 100 m (Hartman 1947), silty clay sediments (Ewing 1984a). In this study it was collected in fine, medium and silty sands; D = 68.6–106.4; T = 13.2–14.2; S = 35.09–35.26; OM = 3.0–7.2; DO = 0.92–2.40.

Distribution.—Northern Gulf of Mexico (Ewing 1984a). Southern California; in the Gulf of California it has been reported in the Baja California eastern shores (Hartman 1947). Continental shelf of northern and southern Sonora, and west of Santa Inés Bay, Baja California Sur.

Leiochrides hemipodus Hartman, 1960

Leiochrides hemipodus Hartman, 1960:136; 1963:22; 1969:381, fig. 1.—Fauchald, 1972:242–243.

Material examined.—1 specimen: Punta Arboleda, 26°46.6′N, 110°06.7′W, sta. 14, 92 m, medium sands, 12 Mar 1985 (1 specimen).

Habitat.—Abyssal basins and canyons in muddy greenish sediments, with siliceous sponges (Hartman 1969). In this study it was collected in medium sands; D = 92.0; T = 13.6; S = 35.09; OM = 5.3; DO = 0.92.

Distribution.—Southern California (Hartman 1969). In the Mexican Pacific, it has been collected in deep waters in front of Jalisco and Baja California (Hartman 1963), and Baja California Sur coasts (Fauchald 1972). Punta Arboleda, Sonora, coasts.

Mastobranchus ?variabilis Ewing, 1984

Mastobranchus sp. A.—Ewing, 1984a: 14.35, figs. 14.29, 14.30a–f.

Mastobranchus variabilis Ewing, 1984b: 793–796, figs. 1a–d.

Material examined.—6 specimens: El Fuerte River, 25°42.1′N, 109°30.6′W, sta. 51, 49.5 m, silty sands 20 Mar 1985 (2 specimens). María Madre Island, 21°38.2′N, 106°31.9′W, sta. 62C, fine sands, 22 Mar 1985 (4 specimens).

Remarks.—The specimens analyzed are incomplete with a maximum of 41 setigers, which makes it impossible to confirm the presence of branchiae. According to the original description, they should be present in the middle-posterior region of the abdomen as eversible "groups" of 5–8 cirriform filaments emerging from the posterior region of the notopodial uncinigers. The presence of capillary setae accompanying hooded hooks in most of the abdominal segments also could not be ascertained. However, the two other described species which belong to this genus, *M. trinchesii* Eisig 1887 and *M. loii* Gallardo 1968, have a biramous first setiger, among other major differences with the specimens collected here. This led us to name the organisms as *M. ?variabilis.*

Habitat.—9.7 to 58 m, in sands (Ewing 1984b). In this study it was collected in fine and silty sands; D = 29.7–49.5; T = 14.8–22.1; S = 35.10–35.15; OM = 4.2–7.2; DO = 1.80–5.29.

Distribution.—Alabama and Florida, northern Gulf of Mexico, North Carolina shores (Ewing 1984b). West of El Fuerte River, Sinaloa, and María Madre Island, Nayarit.

Mediomastus californiensis Hartman, 1944

Mediomastus californiensis Hartman, 1944: 264, pl. 6, figs. 64–65; 1947:408, pl. 46, figs. 3–4; 1969:387, figs. 1–4.—Day, 1973:99.—Hutchings & Rainer, 1979: 779.—Hobson & Banse, 1981:66.—Ewing, 1984a:14.14, figs. 14.9, 14.10a–c.

Material examined.—2 specimens: Tepoca Cape, 30°08.6′N, 112°08.6′W, sta. 43, 68.8 m, silty sands 17 Mar 1985 (1 specimen). Punta Willard, 30°11.5′N, 114°31.7′W, sta. 34, 32.9 m, sandy silty clay, 15 Mar 1985 (1 specimen).

Habitat.—Intertidal to 517 m, commonly found in fine, muddy sands (Ewing 1984a). In this study it was collected in silty sands and muds; D = 32.9–68.8; T = 15.1–15.2; S = 35.38–35.45; OM = 6.9–8.9; DO = 3.03–4.30.

Distribution.—Central and southern California (Hartman 1969); from North Carolina to Florida; northern Gulf of Mexico, Australia (Ewing 1984a). Baja California coasts (Hartman 1963), Baja California Sur (De León-González 1994), Sinaloa (Salazar-Vallejo 1981, Van Der Heiden & Hendrickx 1982, Arias-González 1984), and Jalisco (Varela-Hernández 1993). Northern Gulf of California.

Notomastus americanus Day, 1973

Notomastus americanus Day, 1973:100, figs. 131–n.—Ewing, 1984a:14.31, figs. 14.25,14.26a–d.

Material examined.—61 specimens: Rocas Consag, 30°59.4′N, 114°04.1′W, sta. 39, 106.4 m, silty sands, 16 Mar 1985 (12 specimens). Tepoca Cape, 30°02.4′N, 112°55.4′W, sta. 44, 104.1 m, silty sands, 17 Mar 1985 (8 specimens). Punta Willard, 30°11.5′N, 114°31.7′W, sta. 34, 32.9 m, sandy silty clay, 15 Mar 1985 (1 specimen). Punta Arboleda, 26°51.1′N, 110°06.5′W, sta. 15, 49.8 m, 12 Mar 1985 (13 specimens). Punta Arboleda, 26°46.6′N, 110°06.7′W, sta. 14, 92 m, medium sands, 12 Mar 1985 (1 specimen). El Fuerte River, 25°42.1′N, 109°30.6′W, sta. 51, 49.5 m, silty sands, 20 Mar 1985 (2 specimens). El Fuerte River, 25°46.8′N, 109°35.4′W, sta. 50, 97.0 m, silty sands, 20 Mar 1985 (4 specimens). Santa Inés Bay, 26°59.6′N, 111°50.4′W, sta. 49A, 100 m, fine sands, 19 Mar 1985 (3 specimens). Punta San Marcial, 25°58.6′N, 111°06.9′W, sta. 10, 39 m, very fine sands, 11 Mar 1985 (4 specimens). Santa María Bay; 25°02.4′N, 108°31.7′W, sta. 3, 32 m, fine sands 10 Mar 1985 (1 specimen). Santa María Bay; 24°56.9′N, 108°41.8′W, sta. 4, 79 m, silty sands, 10 Mar 1985 (4 specimens). María Madre Island, 21°38.2′N, 106°31.9′W, sta. 62C, fine sands, 22 Mar 1985 (8 specimens).

Remarks.—In small specimens, sometimes we observed a mixture of hooks and acicular setae in the neuropodia of setiger 10, as Ewing (1984a) noted. In the same fashion, in some small organisms, the same feature can be observed but in the neuropodia of eleventh setiger.

Habitat.—35 to 100 m, in fine to very fine sands to coarse sands (Ewing 1984a). In this study, it was collected in fine, medium and silty sands, and muds; D = 29.7–106.4; T = 13.2–22.1; S = 34.99–35.51; OM = 3.0–7.2; DO = 0.80–5.29.

Distribution.—North Carolina (Day 1973); northern Gulf of Mexico (Ewing 1984a). In the mexican Pacific it has been reported from the Jalisco coasts (Varela-Hernández 1993), upper Gulf of California, southern Sonora, northern Sinaloa, and central Baja California Sur.

Notomastus hemipodus Hartman, 1945

Notomastus (Clistomastus) hemipodus Hartman, 1945:38; 1947:424, pl. 48, figs. 1–5; 1951:103, pl. 24, figs. 1–3; 1969: 393, figs. 1–5.

Notomastus hemipodus.—Day, 1973: 100.—Ewing, 1984a:14.28, figs. 14.23, 14.24a–d.

Material examined.—63 specimens: Rocas Consag, 31°16.1′N, 114°21.7′W, sta. 37, 30.3 m, fine sands, 16 Mar 1985 (11 specimens). Rocas Consag, 30°59.4′N, 114°04.1′W, sta. 39, 106.4 m, silty sands, 16 Mar 1985 (5 specimens). Punta Willard, 30°11.5′N, 114°31.7′W, sta. 34, 32.9 m, sandy silty clay, 15 Mar 1985 (2 specimens). Punta Arboleda, 26°53.2′N, 110°04.1′W, sta. 16, 22.2 m, fine sands, 12 Mar 1985 (3 specimens). Punta Arboleda, 26°51.1′N, 110°06.5′W, sta. 15, 49.8 m, 12 Mar 1985 (20 specimens). Santa Inés Bay, 26°59.6′N, 111°50.4′W, sta. 49A, 100 m, fine sands, 19 Mar 1985 (7 specimens). Punta San Marcial, 25°58.6′N, 111°06.9′W, sta. 10, 39 m, very fine sands, 11 Mar 1985 (13 specimens). Santa María Bay; 24°56.9′N, 108°41.8′W, sta. 4, 79 m, silty sands, 10 Mar 1985 (2 specimens).

Habitat.—Intertidal to 120 m, in muds and muddy sands (Ewing 1984a). At 30 m and 30°C, 0.31% organic carbon, in sandy muds (González-Ortiz 1994). In this study it was collected in fine, medium and silty sands and muds; D = 22.2–106.4; T = 13.2–17.5; S = 35.00–35.51; OM = 2.4–6.9; DO = 0.80–5.40.

Distribution.—North Carolina (Day 1973); northern Gulf of Mexico (Ewing 1984a); southern California (Hartman 1969). In the mexican Pacific it has been collected in the Jalisco coasts (Varela-Hernández 1993), and the Gulf of Tehuantepec (González-Ortiz 1994). Northern and central Gulf of California.

Notomastus latericeus Sars, 1851

Notomastus latericeus.—Fauvel, 1927:143, figs. 49a–h.—Day, 1967:599, figs. 28.2a–

d.—Gallardo, 1968:120, pl. 53, fig. 13.—Thomassin, 1970:83, figs. 8a–e.—Ewing, 1984a:14.26, figs. 14.29, 14.20a–e.

Material examined.—20 specimens: Tepoca Cape, 30°02.4′N, 112°55.4′W, sta. 44, 104.1 m, silty sands, 17 Mar 1985 (5 specimens). Punta Willard, 30°11.5′N, 114°31.7′W, sta. 34, 32.4 m, sandy silty clay, 15 Mar 1985 (1 specimen). Estero Tastiota, 28°17.8′N, 111°37.1′W, sta. 47, 36.9 m, 18 Mar 1985 (1 specimen). Punta Arboleda, 26°51.1′N, 110°06.5′W, sta. 15, 49.8 m, 12 Mar 1985 (3 specimens). Santa Inés Bay, 26°59.4′N, 111°53.5′W, sta. 49B, 68.8 m, 19 Mar 1985 (1 specimen). Santa María Bay; 25°02.4′N, 108°31.7′W, sta. 3, 32 m, fine sands, 10 Mar 1985 (6 specimens). Banco Gorda, 23°06.6′N, 109°24.3W, sta. 56, 101 m, fine sands, 21 Mar 1985 (3 specimens).

Habitat.—Intertidal to 4360 m; in very different kinds of sediments (Ewing 1984a). In this study it was collected in fine and silty sands and muds; D = 32.0–104.1; T = 13.7–15.1; S = 34.80–35.38; OM = 5.7–7.2; DO = 1.02–4.30.

Distribution.—Cosmopolitan (Ewing 1984a). Sonora coasts, northern Sinaloa, and northern and southern coasts of Baja California.

Notomastus lineatus Claparede, 1870

Notomastus (Clistomastus) lineatus Claparéde, 1870:18, pl. 17, fig. 4.—Hartman, 1947:419, pl. 46, figs. 1–2; 1969:395, figs. 1–5.

Notomastus lineatus.—Fauvel, 1927:145, figs. 51a–i.—Hobson and Banse, 1981:66.—Ewing, 1984a:14.24, figs. 14.17, 14.18a–e.

Material examined.—51 specimens: Tepoca Cape, 30°12.2′N, 112°46.9′W, sta. 42, 29.9 m, fine sands, 17 Mar 1985 (18 specimens). El Fuerte River, 25°39.9′N, 109°30.6′W, sta. 51, 49.5 m, silty sands, 20 Mar 1985 (1 specimen). San Miguel Cape, 28°10.4′N, 112°48.1′W, sta. 19, 30.4 m, coarse sands, 13 Mar 1985 (14 specimens). San Miguel Cape, 28°08.0′N, 112°45.8′W, sta. 20, 54.1 m, fine sands, 13 Mar 1985 (3 specimens). Santa Inés Bay, 26°59.2′N, 111°58.3′W, sta. 49C, 28.9 m, very fine sands, 19 Mar 1985 (1 specimen). Punta San Marcial, 25°33.4′N, 110°59.8′W, sta. 8, 52 m, fine sands, 11 Mar 1985 (2 specimens). Punta San Marcial, 25°47.8′N, 111°03.8′W, sta. 9, 77.5 m, fine sands, 11 Mar 1985 (1 specimen). Banco Gorda, 23°08.7′N, 109°28.3′W, sta. 55, 32.5 m, fine sands, 21 Mar 1985 (11 specimens).

Habitat.—Shallow subtidal to 298 m, in fine to coarse sands, sandy gravel and coral rubble (Ewing 1984a). In this study it was collected in fine, medium and coarse sands; D = 28.9–77.5; T = 13.6–21.3; S = 34.70–35.54; OM = 1.8–7.2; DO = 1.80–5.11.

Distribution.—Mediterranean Sea (Fauvel 1927); northern Gulf of Mexico (Ewing 1984a); Panama, Antarctic Ocean, from Canada to California (Hartman 1969). In the Mexican Pacific, reported from Todos los Santos Bay, Baja California Sur (Salazar-Vallejo 1985), and in Sinaloa coasts (Van Der Heiden & Hendrickx 1982). Mainly present in Baja California Sur littorals.

Notomastus tenuis Moore, 1909

Notomastus (Clistomastus) tenuis.—Hartman, 1947:420, pl. 47, figs. 1–5; 1969:397, figs. 1–5.

Notomastus tenuis.—Hobson & Banse, 1981:66.

Notomastus ? tenuis.—Ewing, 1984a:14–26, figs. 14.21, 14.22a–e.

Material examined.—100 specimens: Rocas Consag, 31°08.3′N, 114°13.3′W, sta. 38, 71.9 m, 16 Mar 1985 (4 specimens). Estero Tastiota, 28°16.4′N, 111°36.6′W, sta. 48, 60.2 m, fine sands, 18 Mar 1985 (5 specimens). Punta Arboleda, 26°46.6′N, 110°06.7′W, sta. 14, 92 m, medium sands, 12 Mar 1985 (5 specimens). El Fuerte River, 25°39.9′N, 109°28.6′W, sta. 52, 28.6 m, silty sands, 20 Mar 1985 (5 specimens). El

Fuerte River, 25°42.1′N, 109°30.6′W, sta. 51, 49.5 m, silty sands, 20 Mar 1985 (8 specimens). El Fuerte River, 25°46.8′N, 109°35.4′W, sta. 50, 97 m, silty sands, 20 Mar 1985 (5 specimens). San Miguel Cape, 28°07.7′N, 112°42.1′W, sta. 21, 104.1 m, 13 Mar 1985 (2 specimens). Santa Inés Bay, 26°59.2′N, 111°58.3′W, sta. 49C, 28.9 m, very fine sands, 19 Mar 1985 (5 specimens). Santa María Bay; 25°02.4′N, 108°31.7′W, sta. 3, 32 m, fine sands, 10 Mar 1985 (5 specimens). Santa María Bay; 24°54.6′N, 108°45.3′W, sta. 5, 120 m, silty sands, 10 Mar 1985 (2 specimens). Punta Mita, 20°53.9′N, 105°27.5′W, sta. 61, 50.4 m, fine sands, 23 Mar 1985 (6 specimens). María Madre Island, 21°38.2′N, 106°31.9′W, sta. 62C, 29.7 m, fine sands, 22 Mar 1985 (48 specimens).

Habitat.—Intertidal to depths of 379 m, in muddy and sandy substrates (Hartman 1969). In this study it was collected in fine, medium and silty sands; D = 28.6–120.0; T = 12.9–22.1; S = 34.92–35.45; OM = 3.6–7.2; DO = 0.54–5.40.

Distribution.—From Canada to California (Hartman 1969); northern Gulf of Mexico? (Ewing 1984a). In the Mexican Pacific, collected in the littorals of Baja California Sur (Rioja 1962, De León-González 1994), Sinaloa (Salazar-Vallejo 1981, Van Der Heiden & Hendrickx 1982), and in deeper zones from Baja California, Baja California Sur, Nayarit, and Jalisco (Fauchald 1972). It is found practically along the entire continental shelf of the Gulf of California.

Notomastus angelicae, new species

Figs. 1a–d, 2, 3

Material examined.—44 specimens, Location: littoral, west of El Fuerte River, Sinaloa, México (25°39′54″N, 109°28′36″W), at a depth of 28.6 m. Holotype (USNM: 180697) and 5 paratypes (USNM: 180698); 5 paratypes (LACM-AHF-POLY-1902); 5 paratypes (A.M.: W24586); 5 paratypes (BNHM.: 1998.786-790); and 23 paratypes (CP-ICMyL: POP-17-001).

Description.—Holotype incomplete with 48 setigers, 15 mm long and 0.75 mm wide. Thorax length 3 mm. Paratypes with 21 to 40 setigers (mean = 29.48 ± 5.43), 7.5 to 13 mm total length (mean = 10.0 ± 2.12), and 0.75 to 1 mm width (mean = 0.76 ± 0.12).

Color of preserved specimens yellowish to light brown. Thorax slightly enlarged in first four to five setigers (Fig. 1a); epithelial surface clearly areolated as rhomboids in first four setigers (Fig. 2), following setigers smooth except for segmental biannulation. Inferior region of thorax from setigers 1–11 enlarged (Fig. 1b), as a consequence a middle longitudinal groove appears to be present. Abdominal epithelium smooth.

Prostomium short, a small triangular terminal palpode and two elongate ocular patches in posterior region (Fig. 1a). Peristomial ring achaetous, almost twice as long as following setigers. Eversible pharynx papillose.

Anterior thoracic notopodia dorsolateral, from setiger 7 widely separated. First setiger biramous. Only capillary setae in first ten setigers (10–20 per fascicle); last thoracic segment (setiger 11) with capillary setae in notopodia and only hooded multidentate hooks (14–16) in neuropodia (Figs. 1c, 3).

Nephridial apertures located in segmental groove between each thoracic segment. Lateral organs present on all thoracic segments between noto- and neuropodium (Fig. 3). Transition from thorax to abdomen is apparent by size changes in segments, the presence of a hump-like protuberance in each segment and notopodial hooded hooks (Fig. 1a). Only multidentate hooded hooks in abdominal tori (Fig. 1d). Length of tori and hook number increase in neuropodia and disminish in notopodia towards posterior region. No branchiae.

Abdomen with a large rounded dorsotransverse hump-like structure (Fig. 1e). Initially, tori located in middle part of segments but migrating gradually towards pos-

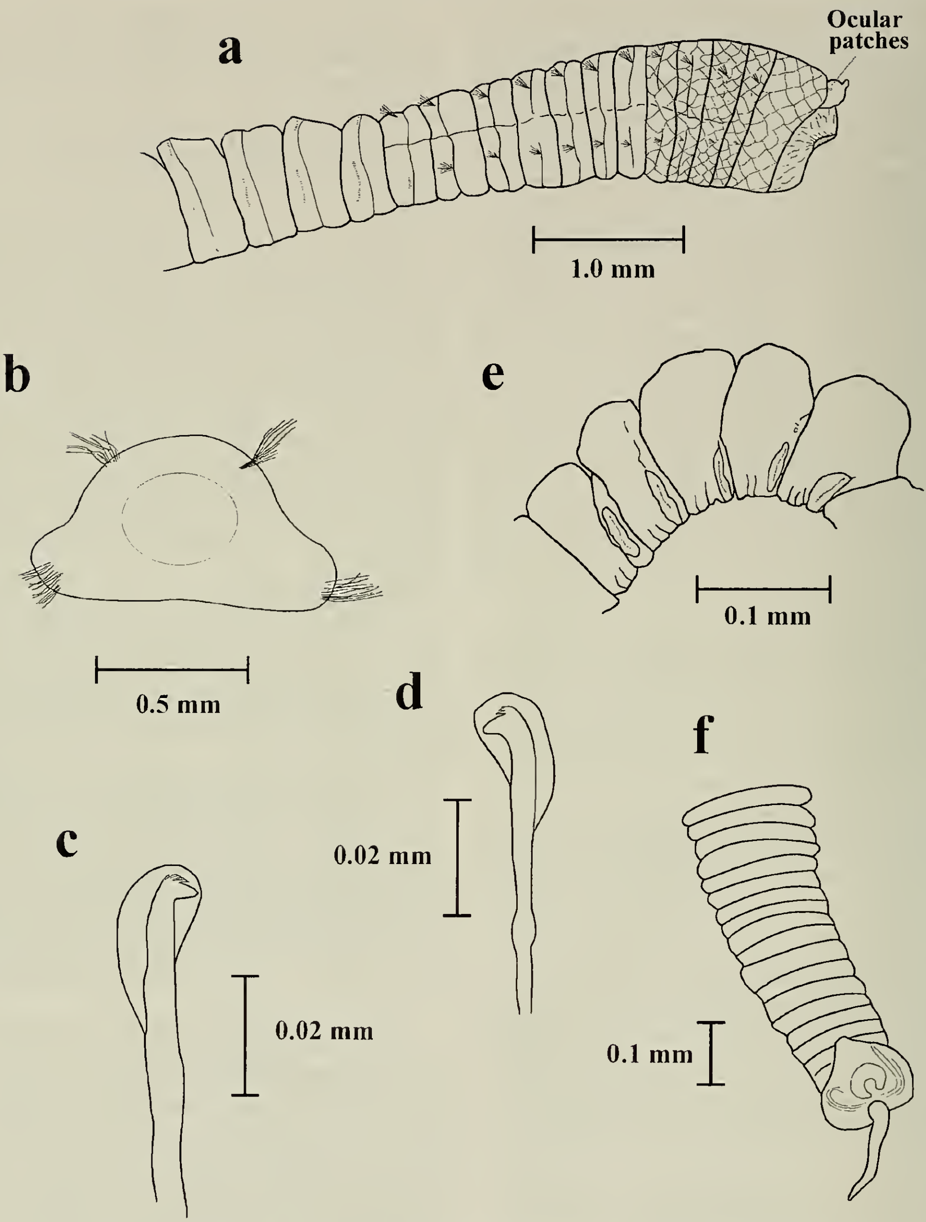

Fig. 1. *Notomastus angelicae,* new species: a, thoracic and anterior abdminal region, lateral view; b, transverse section of fourth setiger; c, thoracic multidentate hooded hook; d, abdominal multidentate hooded hook; e, midabdominal segments, lateral view; f, pygidium of a regenerating organism.

terior region of the segment until they almost reach the intersegmental line.

Pygidium unknown in all but one specimen with 23 setigers well developed and a posterior regenerating region of 44 segments with a pygidium. However, due to regeneration the shape could be somewhat atypical: it is tube-like with terminal part heart-shaped and a median digitiform cirrus (Fig. 1f).

Habitat.—Specimens found at 28.6 m, in silty sands, 35.19 ‰ salinity, 16.8°C tem-

Fig. 2. SEM Prostomium and anterior thoracic region (peristomium) from *Notomastus angelicae.*

perature, 5.4 ml/l dissolved oxygen and 3.6% of organic matter.

Distribution.—*Notomastus angelicae* is only present in the eastern coasts of the Gulf of California, west of El Fuerte River, Sinaloa.

Etymology.—The species is named after Angélica Hernández Huitrón, niece of one of us (P H-A).

Gender.—Feminine.

Remarks.—Ewing (1984b) indicates that in the genus *Notomastus,* as well as in other capitellid genera, during setal development the thoracic hooks are gradually replaced by capillary setae in the middle-posterior region of thoracic neuropodia.

As organisms reach adulthood, in some neuropodia a mixture of capillary setae and hooks appear; this arrangement is only present in one specimen analyzed with hooded hooks in setiger 10; the other 43 specimens only have hooks in neuropodia of setíger 11.

Genus *Notomastus* Sars, 1851 was emended by Ewing (1982) to include capitellids with 11 thoracic setigers with only capillary setae on both rami or with neuropodial hooks in last 1–3 thoracic setigers. *Notomastus angelicae* differs from most species in the genus by having hooks in one thoracic neuropodium instead of only capillary setae in both thoracic rami. From the species with hooks in one or two thoracic neuropodia, none presents a prostomial palpode, and from those, *N. precocis* Hartman, 1960, *N. teres* Hartman, 1965, *N. mossambicus* (Thomassin 1970), *N. americanus* Day, 1973 and *Notomastus* sp. A Ewing,

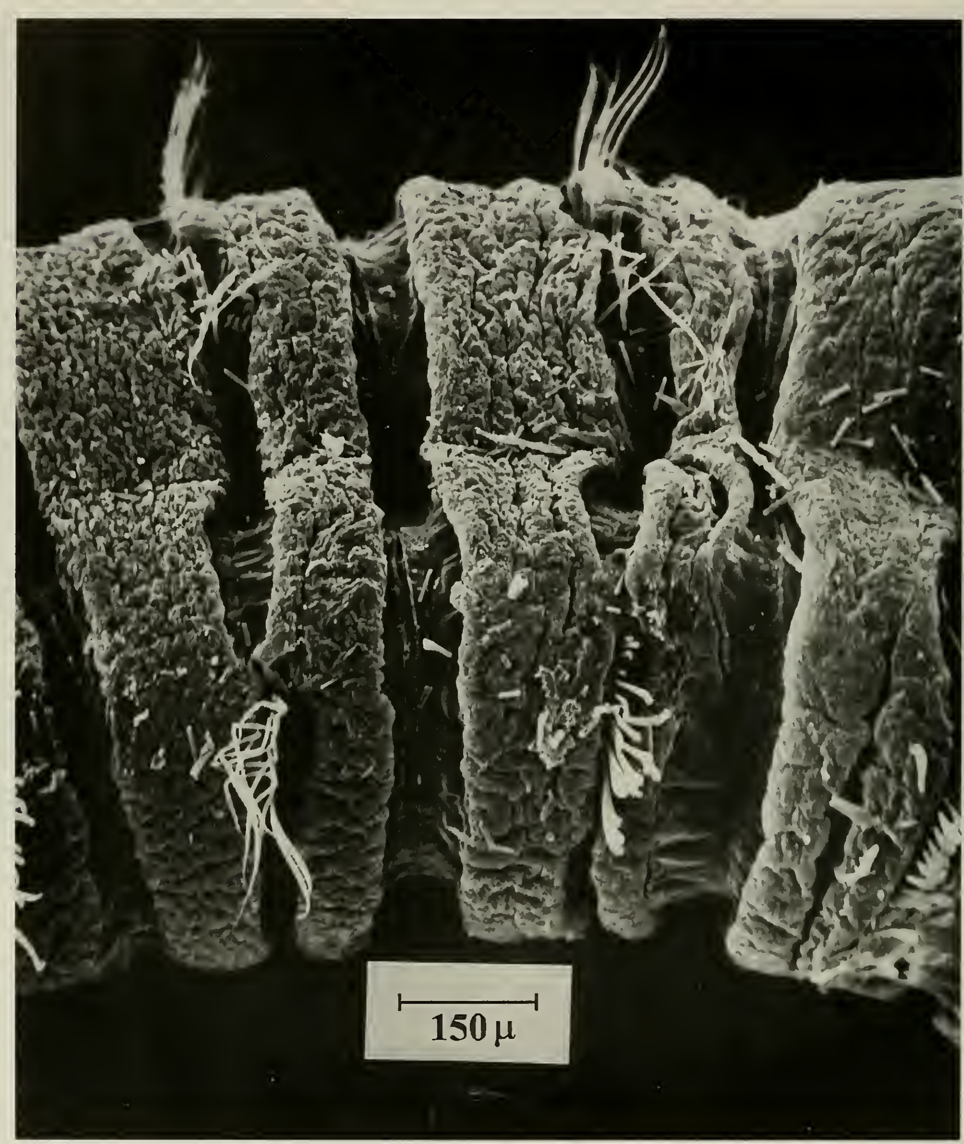

Fig. 3. SEM Setigers 10 and 11, lateral view from *Notomastus angelicae.*

1984, all have only notopodia in first setiger (Table 1).

Notomastus daueri Ewing, 1982, described from the northern Gulf of Mexico, is the only species in the genus with hooks in some thoracic neuropodia and first setiger complete. *Notomastus angelicae* differs from it basically by the presence of the prostomial palpode, ocular spots, the abdominal neuropodial shape and the well defined areolated area in the anterior thoracic region. The only species of the group with branchiae is *N. daueri*; however, these structures could not be seen here since the specimens are incomplete.

Key to the Capitellids from the Gulf of California

1. Thorax with ten setigers 2
– Thorax with more than ten setigers .. 3
2. Thoracic setigers with capillary setae

only; first setiger incomplete, with notosetae only .... *Decamastus nudus*

– Setigers 1–4 with capillary setae; first setiger complete, with noto- and neurosetae ...... *Mediomastus californiensis*

3. Thorax with 11 setigers 4

– Thorax with more than 11 setigers .. 10

4. Thoracic setigers with capillary setae only; abdominal notopodia with mixed fascicles of capillary setae and hooded hooks; first setiger incomplete .... *Mastobranchus ?variabilis*

– Thoracic setigers with capillary setae only in both rami or with hooks only in neuropodia of last 1–3 setigers; abdominal setigers with hooded hooks only 5

5. First setiger complete 6

– First setiger incomplete 8

6. Last thoracic segment with capillary setae only in both rami 7

– Last thoracic segment with capillary setae only in notopodia and hooded hooks only in neuropodia .... *Notomastus angelicae*

7. Nephridial apertures restricted to thorax; thoracic segments uniannulate ... . *Notomastus lineatus*

– Nephridial apertures restricted to abdomen; thoracic segments biannulate .... *Notomastus latericeus*

8. All thoracic setigers with capillary setae only 9

– Last thoracic neuropodia with hooded hooks only ..... *Notomastus americanus*

9. Prostomium with long ocular patches .... *Notomastus tenuis*

– Prostomium with pair of minute (often inconspicuous) eyespots .... *Notomastus hemipodus*

10. Thorax with 12 setigers, all thoracic setigers with capillary setae only; first setiger incomplete .. *Leiochrides hemipodus*

– Thorax with 14 setigers; setigers 1–13 with capillary setae only in both rami, last thoracic setiger with capillary setae only in notopodia and hooded hooks only in neuropodia; first setiger incomplete .... *Leiocapitella glabra*

Acknowledgements

We would like to thank especially Dr. Kristian Fauchald for his help in the revi-

Table 1.—Morphological characters commonly used to differentiate the species of *Notomastus* with hooks in some thoracic notopodia.

Character	*N. daueri* Ewing 1982	*N. precocis* Hartman 1960	*N. teres* Hartman 1965	*N. mossambicus* (Thomassin 1970)	*N. americanus* Day 1973	*Notomastus* sp. A Ewing 1994	*N. angelicae,* new species
Prostomial palpode	Absent	Absent	Absent	Absent	Absent	Absent	Present
Eyes or ocular spots	Absent	Absent	Absent	Present	Present	Present	Present
First setiger	Biramous	Uniramous	Uniramous	Uniramous	Uniramous	Uniramous	Biramous
Anterior thoracic epithelium	Finely areolated	Plain	Plain	Areolated	Plain	Plain	Areolated
Hooded hooks	Neuropodium 11	Neuropodium 9–11	Neuropodium 10–11	*Neuropodium 11	*Neuropodium 11	*Neuropodium 10–11	Neuropodium 11
Branchiae	Present (around setiger 60)	Absent	Absent	Absent	Absent	Absent	?

* In juveniles of these species hooded hooks or a mixture of capillary setae and hooks in setigers 9–11 can be present.

sion of the new species as well as his constant interest and help in our projects. Thanks are also due to M. Sc. Yolanda Homelas for the electron microscope photographs.

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Phytoplankton composition within the tidal freshwater region of the James River, Virginia

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Abstract.—Based on a 10.5 year data set, 271 taxa were identified at a single tidal freshwater station in the James River. The mean monthly concentrations of major algal categories, total biomass and productivity are given. Diatom maxima were associated with peak periods of river discharge, with chlorophytes, cyanobacteria, and autotrophic picoplankton abundance and productivity greater during reduced river flow and more stable water conditions.

Within the tidal stretch of estuarine rivers, there is a unique and little studied region dominated by freshwater plankton, yet it is subjected to daily tidal influence and the occasional intrusion of estuarine species. These waters are referred to as tidal fresh. The channel divisions between freshwater, tidal fresh, and oligohaline sections of a river are not constant, but will move longitudinally within the river basin in response to changes in the amount of river flow and tidal influence. During a period of drought, the range of the tidal fresh area moves farther upstream, whereas, during the seasonal rains, it would extend farther downstream. The abundance of tidal fresh algae in this region has been associated to hydrodynamic events in the river, with cell concentrations inversely related to freshwater input and directly related to the water's residency time (Jackson et al. 1987, Schuchardt & Schirmer 1991, Jones et al. 1992). Other major environmental factors influencing abundance in this region include turbidity, nutrients, tidal cycles, and light availability (Cole et al. 1982, Cloern et al. 1983, Cloern 1987, Haas et al. 1981, Jones 1991). The extent of dominance by freshwater algae downstream varies within different estuaries, but the downstream flora will be dominated by estuarine species (Haerte et al. 1969, Forester 1973, Jackson et al. 1987, Marshall & Alden 1990). In tidal freshwater (<0.5 ppt), the algae are mainly composed of chlorophytes, cyanobacteria, and diatoms (Forester 1973, Opute 1990, Marshall 1994), with diatoms often predominating (Haertel et al. 1969, Jackson et al. 1987, Schuchardt & Schirmer 1991). Diatoms are more common during periods of high river discharge in contrast to chlorophytes, cyanobacteria, and phytoflagellates, which are more dominant during low river discharge (Farrell 1994, Schmidt 1994).

The James River is a major tributary of the Chesapeake Bay, with a drainage basin of 26,440 km^2, a length of 545 km and a mean monthly discharge rate of approximately 7100 ft^3 sec^{-1} (Belval et al. 1995). Within the southern Chesapeake Bay tributaries, several studies have compared phytoplankton spatial and temporal distribution within the tidal fresh and saline sections of these rivers (Marshall & Alden 1990, Marshall & Affronti 1992, Marshall 1994). These studies indicate the transport of estuarine species upstream via sub-surface waters and the transition to estuarine species dominance downstream. Marshall and

Alden (1990) recognized two distinct and dominant assemblages within the tidal James River. These were tidal fresh and oligo-mesohaline populations. The tidal freshwater group was dominated by the centric diatoms *Skeletonema potamos, Cyclotella striata,* and several *Aulacoseira* spp. Estuarine diatoms became dominant downstream. These included *Skeletonema costatum, Leptocylindrus minimus,* and *Cyclotella caspia* (*C. choctawhatcheeana*). In the James River, Filardo and Dunstan (1985) reported productivity in the lower saline regions was inversely correlated to river discharge. They noted inverse relationships between phytoplankton abundance in the oligohaline reach of the river to phytoplankton biomass downstream, suggesting this region may control nutrient availability downstream. Other studies within Chesapeake Bay tributaries have indicated phytoplankton development may become nutrient limited in spring due to reduced phosphorus and silicon levels, and in late summer as nitrogen levels decrease (Anderson 1986, Webb 1988). Based on a 5-year study of the James River, Belval et al. (1995) reported median annual concentrations near the fall line of total nitrogen (TN) and total phosphorus (TP) as 0.74 and 0.15 mg l^{-1}, respectively. The median value for dissolved orthophosphate was 0.04 mg l^{-1}. They found total nitrogen, total phosphorus, and total suspended solids (TSS) directly related to increase river discharge, and dissolved orthophosphate increased with periods of reduced river flow (and summer). Mean annual productivity for the tidal freshwater station (TF5.5) in the James River was reported by Marshall & Nesius (1993) as 279.9 gC m^2 yr^{-1}, with higher values noted downstream. Using a 5-year data set for the station in this study (TF5.5), they gave mean water concentrations for the following parameters (in mg l^{-1}: Si (5.8), O_2 (8.5), TP (0.16), TN (0.89), and TSS (30.3), and a mean pH of 7.5. In the tidal freshwater section of the Potomac River, Jones (1991) associated high photosynthesis rates during cyanobacteria blooms to increased pH (>9) and the release of sediment phosphorus into the water column, which may then stimulate more productivity.

The objectives of this study are to: 1) identify phytoplankton taxa at a tidal freshwater station in the James River, and 2) present the mean monthly concentration levels for the dominant phytoplankton categories in this region. This information will come from a 10.5-year data base at this station.

Methods

Phytoplankton composition and abundance were determined from a vertical series from surface to bottom of monthly composite water samples taken from July 1986 through December 1996 at Station TF5.5 in the James River as part of the Chesapeake Bay Plankton Monitoring Program (Marshall & Alden 1990). The station is located above the turbidity maximum zone (37°18′46″N, 77°13′59″W), with mean water depth of 10.6 m, and a tidal range of <1 m (Marshall 1994). Monthly 500 ml sub-samples were taken for analysis using a modified Utermöhl method to settle, siphon, and concentrate the water sample into settling chambers for microscope analysis (Marshall & Alden 1990). Identification and cell abundance for each sample were based on a minimum microscope count of 200 cells, using a minimum of 10 random fields examined at both 315× and 500×, in addition to having the entire bottom of the settling chamber scanned at 125× for larger, less abundant cells that may be missed in the random field counts. The autotrophic picoplankton component and productivity values are based on a 7.5 year data set derived from monthly samples taken from July 1989 through December 1996. The autotrophic picoplankton were distinguished from heterotrophic cells using epifluorescence microscopy (Marshall 1995), with ^{14}C productivity measurements taken

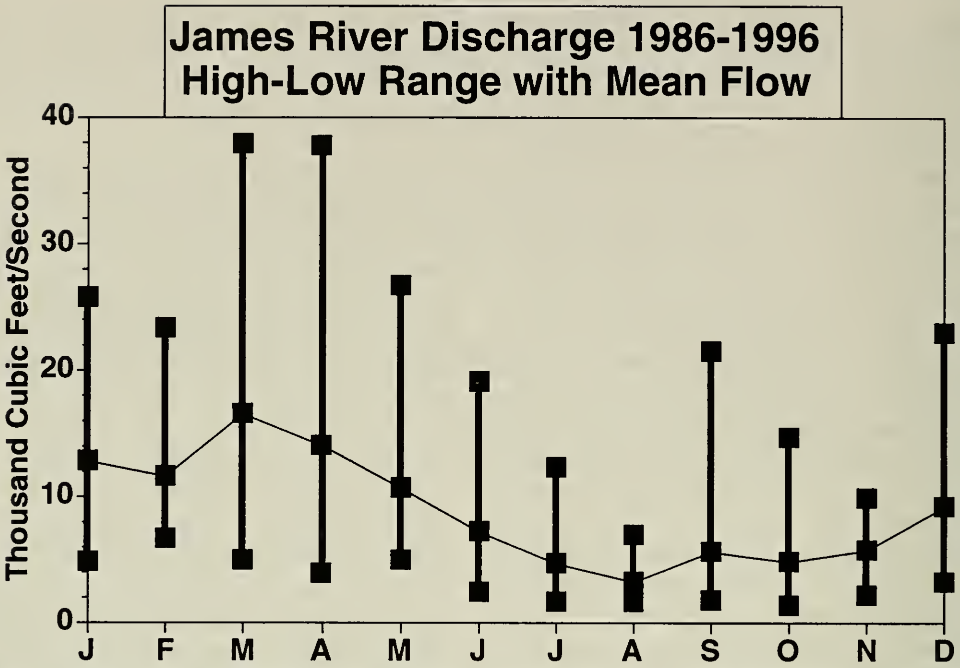

Fig. 1. High-low and mean monthly river discharge rates in the James River (fall line values), 1986 through 1996.

as described by Marshall and Nesius (1993). A 12-month set of samples from 1995 were also re-examined for further species identification using both light and scanning electron microscopy. Biomass was calculated from cell volume measurements as cell carbon (Smayda 1978). Reference to seasons uses December, January and February as winter, followed by the sequential 3-month periods for spring, summer, and fall. Water discharge rates were provided through the information data bank of the U.S. Geological Survey.

Results

The tidal fresh station (TF5.5) maintained <0.5 ppt salinity during this study. A total of 271 taxa were identified within the following categories: Bacillariophyceae (78), Chlorophyceae (94), cyanobacteria (36), Xanthophyceae (19), Euglenophyceae (15), Dinophyceae (13), Chrysophyceae (9), and Cryptophyceae (7). The autotrophic picoplankton were collectively compiled as a composite group, but consisted mainly of single-celled cyanobacteria, but these are not included in the cyanobacteria concentrations given in Fig. 4.

The pattern of river discharge in the James river is maximum flow in spring, reduced discharge during summer, and an increase during fall and winter (Fig. 1). The greatest monthly ranges for flow occurred during the period of spring rains in March and April, and least during summer. During the 10.5-year study, annual mean monthly flows ranged from 4495 (1988) to 13,192 (1996) ft^3 sec^{-1}. Many of the high monthly ranges represented extreme, and not common occurrences; therefore the mean flow rate is considered here more typical for each month. The most consistent and least variable months of flow were July and August. During these months the salinity gradients would move farther upstream and more stratified water column conditions would exist in the river, in contrast to the high discharge periods of spring. Consid-

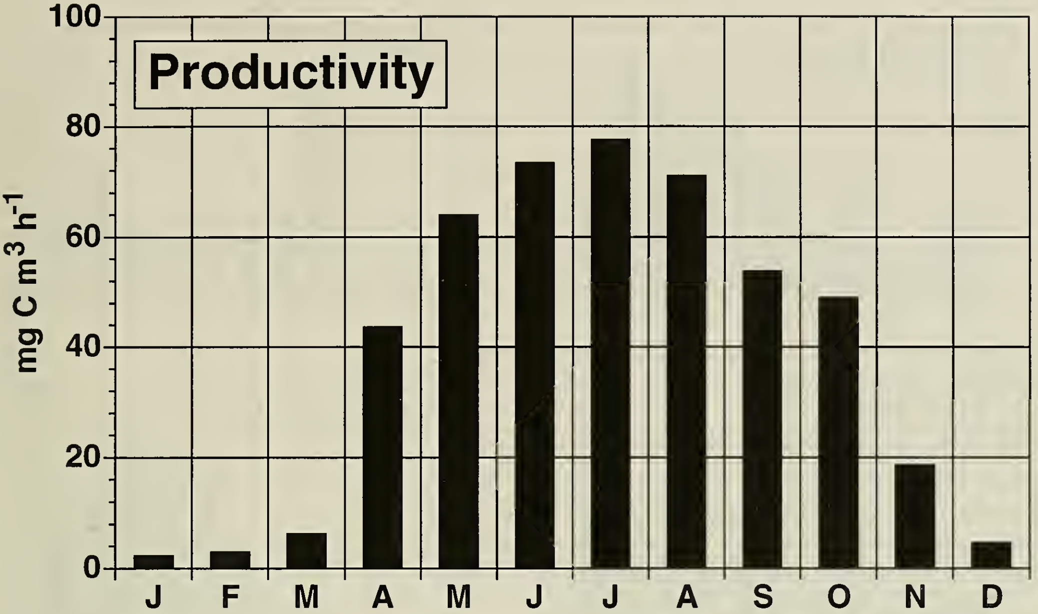

Fig. 2. Mean monthly productivity rates at the tidal freshwater station (TF5.5) from July 1989 through December 1996.

erable variability in the amount and timing of river discharge occurred, which influenced the residency time and period of development for phytoplankton in the water column.

The mean monthly productivity for this site is given in Fig. 2. The period of highest productivity occurred between mid-spring (April) and continued into mid-fall (October). These values decreased into winter. The lowest production levels were in January at 2.3 mgC m^3 hr^{-1} (Fig. 2). In summer, they reached 71–77 mgC m^3 hr^{-1}. This period coincided with maximum development of the total phytoplankton and autotrophic picoplankton components. The spring and fall pulses were dominated by diatoms, whereas the summer months contained a diverse assemblage of phytoplankton that contributed to this productivity.

The phytoplankton composition was dominated by freshwater diatoms, chlorophytes, cyanobacteria, and cryptomonads. Maximum total phytoplankton abundance occurred during April (64×10^6 cells 1^{-1}) and from July through October ($79–109 \times 10^6$ cells 1^{-1}), after which came a sharp decrease into winter (Figs. 3, 4). The spring development was a product of the diatom pulse, whereas a combination of chlorophytes, diatoms, and cyanobacteria were mainly responsible for the summer and fall growth. The mean monthly biomass pattern was similar to phytoplankton concentrations, having greater biomass occurring in spring and from mid-summer through fall (Fig. 3). In addition to the primary categories responsible for the cellular abundance mentioned above, the biomass levels were enhanced by euglenophytes during their peak time of development in July and August (Fig. 4).

Bacillariophyceae.—The lowest diatom concentrations (3×10^6 cells 1^{-1}) were in winter and early spring (Fig. 3). Cell numbers increased with peak abundance occurring during the spring pulse (April and May), when mean concentrations reached 41×10^6 cells 1^{-1}. The maximum diatom development also coincided with the peak discharge period of April. There were reduced diatom concentrations in summer,

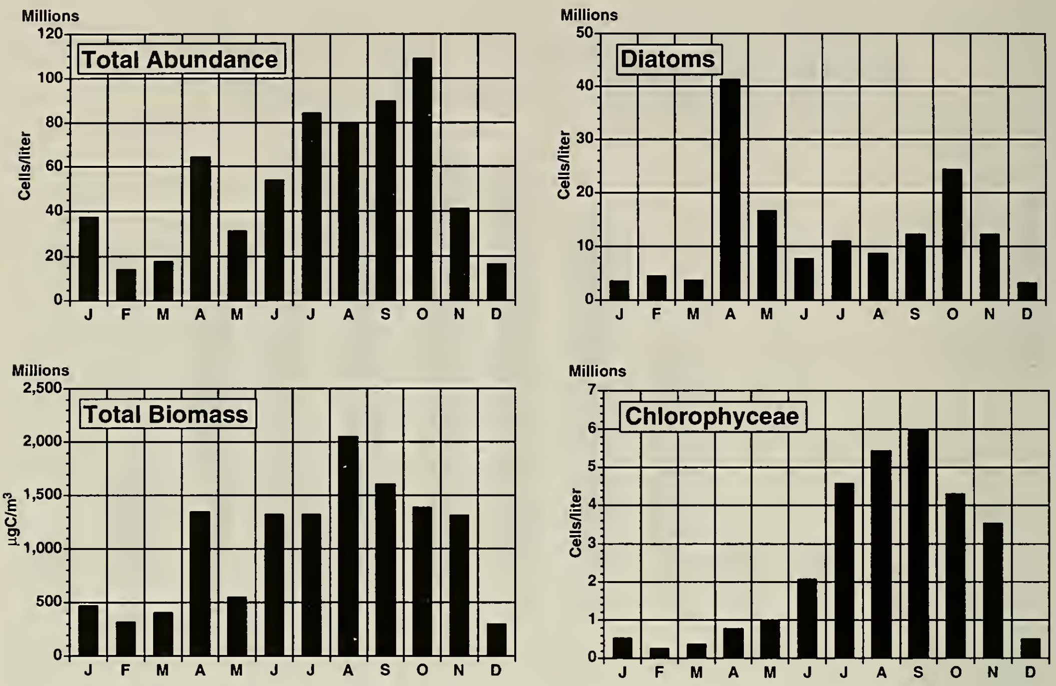

Fig. 3. Mean monthly abundance for total phytoplankton, diatoms, and chlorophytes, and the mean monthly phytoplankton biomass at the tidal freshwater station, (TF5.5), July 1986–December 1996.

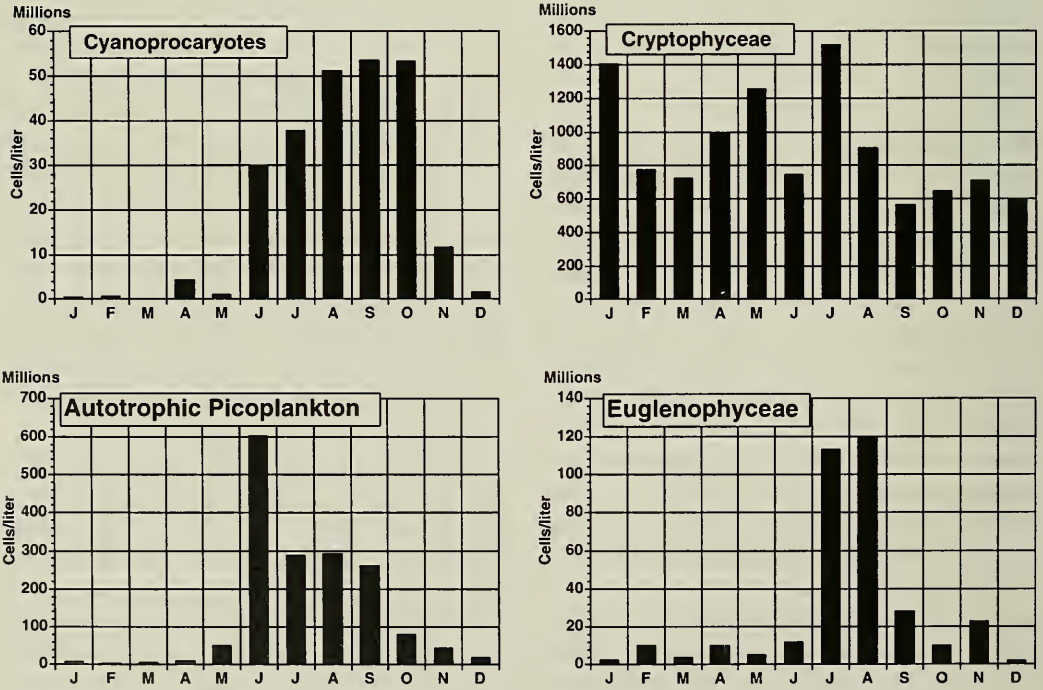

Fig. 4. Mean monthly abundance at the tidal freshwater station (TF5.5) for cyanobacteria, cryptophytes, and euglenoids from July 1986–December 1996, and for the autotrophic picoplankton July 1989–December 1996.

during a time of reduced river flow, which was then followed by a less developed fall pulse (20–25 × 10^6 cells l^{-1}) in October. The species most responsible for the spring and fall maxima were freshwater centric diatoms: *Actinocyclus normanii, Aulacoseira granulata, A. granulata* v. *angustissima, Cyclotella striata, C. meneghiniana, Cyclostephanos* spp., *Melosira varians, Skeletonema potamos, Stephanodiscus hantzschii,* and *Thalassiosira lacustris.* Of these, *Skeletonema potamos* was most abundant during seasonal maxima and present throughout the year. In addition, the abundant pennate diatoms included *Cymbella affinis, Nitzschia acicularis,* several other *Nitzschia* spp., *Staurosirella leptostauron,* and *Surirella elegans.* Many of these centric and pennate species have also been recorded downstream in the James River, but decreasing in their abundance with increased salinity (Marshall 1994). The majority of the estuarine diatoms recorded for this site were noted in <2% of the samples. More frequently recorded (13–19% of the collections) were *Skeletonema costatum, Leptocylindrus danicus,* and *L. minimus.*

Chlorophyceae.—The chlorophytes had the largest number of taxa (94) among the algae, with their greatest abundance in summer and fall (Fig. 3). Development coincided with the decrease of the spring diatom bloom, reduced river flow, and accompanied the increase of cyanobacteria. Highest numbers were recorded during this period (4–5 × 10^6 cells l^{-1}), with reduced concentrations during winter and spring. The most widely represented genera included: *Ankistrodesmus, Crucigenia, Kirchneriella, Monoraphidium, Scenedesmus, Staurastrum, Tetraedron,* and *Tetrastrum.* None of the chlorophytes dominated the phytoplankton in abundance; however, they were common constituents of the algal community throughout the year.

Cyanobacteria.—This category was represented by a variety of filamentous and colonial species that were most abundant (Fig. 4) from early summer (June) to mid-fall (October). Their peak development was at 50 × 10^6 cells l^{-1} (August–October). Cell abundance then declined rapidly into winter and remained low through spring. The most common species throughout the year were *Chroococcus minor, Dactylococcopsis acicularis, D. raphidioides, Merismopedia punctata, Oscillatoria agardhii,* and *O. limnetica.* These taxa were major contributors to the summer–fall maximum. Other species in abundance included *Anabaena solitaria, A. affinis, Gomphosphaeria lacustris, Merismopedia tenuissima,* and *M. glauca.* This group was associated with a more stratified water column, increased water temperatures, and reduced river discharge.

Cryptophyceae.—The cryptomonads represented a ubiquitous and abundant component of the phytoplankton assemblages throughout the year, and are also common in the downstream tidal sectors of the James River (Marshall & Alden 1990). Their mean monthly concentrations for the year ranged from 5–15 × 10^5 cells l^{-1} (Fig. 4). They were most abundant in winter (Dec.), late spring (May), and mid-summer (July). *Cryptomonas marssoni* was present during each season. Other widely distributed species were *Cryptomonas ovata* and *Rhodomonas minuta.* The peak abundance of cryptomonads was associated with reduced river discharge and summer.

Autotrophic picoplankton.—The autotrophic picoplankton consisted of mainly single cell cyanobacteria 0.5–1.5 μm in size (e.g. *Synechococcus* sp.) and represent a ubiquitous component of the James River and Chesapeake Bay (Marshall & Nesius 1993, Marshall 1995). Their peak abundance was during the summer months at 26–60 × 10^7 cells l^{-1} (Fig. 4). Their lowest concentrations occurred in February and March (3–5 × 10^6 cells l^{-1}). Some chlorophytes were also present in this group, but they represented only a small fraction of the composition. A major importance of the autotrophic picoplankton in the James River and the lower Chesapeake Bay is their contribution to the total summer productivity (Marshall & Nesius 1993).

Other categories.—The euglenophyceans were generally found in low concentrations throughout the year, with the exception of July and August, when their mean concentrations reached 11 × 10^5 cells l^{-1} (Fig. 4). Common taxa included *Euglena viridis* and *E. oxyuris,* with other *Euglena, Phacus, Trachelomonas,* and *Strombomonas* species less abundant. The xanthophytes were recorded throughout the year. However, they were generally noted in low concentrations, with low monthly species diversity. *Tribonema monochloris* was the most common species. Several species were associated with increased summer and fall development. These included *Dichoromococcus curvatus* and *Pseudotetraedron neglectum,* whereas *Botrydiopsis eriensis* and *B. arhiza* were noted in spring and summer. Other species within this category were less common.

The chrysophytes were represented by 5 *Dinobryon* species, *Synura uvella, Lagynion cystodini,* and *Dictyota fibula. Dinobryon sociale* was most frequently noted in late winter and early spring. *Dictyota fibula* was rare (1% of the samples), coming from an infrequent intrusion of downstream water into this region. The dinoflagellate populations were also low, with their counts enhanced by occasional sporadic growth periods. The maximum development of dinoflagellates occurred in winter (January) and between late spring (June) and fall (August), with mean concentrations of 2–6 × 10^4 cells l^{-1} during summer months. There was low species diversity of dinoflagellates throughout the year, with a limited number of dominant taxa. The genera most frequently identified were *Gymnodinium, Gyrodinium, Peridinium,* and *Prorocentrum.* Downstream species that occurred within these collections included *Heterocapsa triquetra, Prorocentrum micans,* and *P. minimum.* The more common freshwater species were *Ceratium hirundinella* and *Peridinium willei.*

Summary

The tidal fresh region of the James River contained a diverse and abundant phytoplankton flora. A total of 271 taxa were identified, with the most abundant species chlorophytes (94), diatoms (78), and cyanobacteria (36). The region was dominated by freshwater algae, but there were also some estuarine diatoms and phytoflagellates recorded for the site. The recording of estuarine taxa was probably enhanced by the extensive sampling base, which provided more opportunities for these species to be recorded for this region, e.g., during storm events and periods of low river discharge, etc., over 10.5 years. However, the majority of these species occurred in <2% of the collections. A high degree of representation by estuarine species in this region would not be expected to occur during each monthly collection.

There was monthly and annual variability in river discharge at this station. Although the use of mean discharge rates and mean phytoplankton concentrations presented here do not identify close annual relationships, a pattern is present. Peak development of diatoms (the spring pulse) occurred during periods of increased river discharge, while the high populations of chlorophytes, cyanobacteria, autotrophic picoplankton, and euglenophytes were closely associated to periods of reduced flow and more stable water conditions. These findings support results presented by Farrell (1994), Schmidt (1994), and others.

Peak periods of phytoplankton abundance extended from spring through fall, with different algal categories showing a successional pattern of development. Winter was the period of least abundance, biomass, and productivity, with low concentrations of diatoms, chlorophytes, and cryptomonads as the common constituents. The spring bloom of freshwater diatoms, mainly by *Skeletonema potamos,* was followed by increased concentrations of chlorophytes into early summer. The summer flora contained high concentrations of chlorophytes, cyanobacteria, autotrophic picoplankton, euglenoids, and diatoms. This was the period for maximum values in phytoplankton and picoplankton abundance, biomass, and productivity. Into fall, the dominance of the summer constituents declined, except for the diatoms, which produced another pulse. This was followed by reduced concentrations of total phytoplankton and the autotrophic picoplankton into winter. Common background taxa to these major components included cryptophytes, euglenophytes, xanthophytes, and chrysophytes.

Acknowledgements

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Appendix 1

Phytoplankton within the tidal fresh region of the James River.

BACILLARIOPHYCEAE

Achnanthes sp.
Actinocyclus normanii (Gregory) Hustedt
Asterionella formosa Hassall
Asterionella glacialis Castracane
Asterionella gracillima (Hantzsch) Heiberg
Aulacoseira distans (Ehrenberg) Simonsen
Aulacoseira distans v. *humilis* (A. Cleve) R. Ross
Aulacoseira granulata (Ehrenberg) Simonsen
Aulacoseira granulata v. *angustissima* (O. Müller) Simonsen
Aulacoseira herzogii (Lemmermann) Simonsen
Aulacoseira islandica (O. Müller) Simonsen
Bacillaria paxillifer (Müller) Hendy
Chaetoceros sp.
Cocconeis sp.
Coscinodiscus marginatus Ehrenberg
Coscinodiscus sp.
Cyclostephanos sp.
Cyclostephanos dubius (Fricke in A. Schmidt) F. E. Round
Cyclotella bodanica Grunow
Cyclotella caspia Grunow
Cyclotella chaetoceros Lemmermann
Cyclotella choctawhatcheeana Prasad
Cyclotella comta (Ehrenberg) Kützing
Cyclotella meneghiniana Kützing
Cyclotella sp.
Cyclotella striata (Kützing) Grunow
Cylindrotheca closterium (Ehrenberg) Reiman & Lewin
Cymbella affinis Kützing
Cymbella sp.
Diatoma sp.
Diploneis sp.
Ditylum brightwellii (T. West) Grunow
Fragilaria capucina Desmazières
Fragilaria construens (Ehrenberg) Grunow
Fragilaria crotonensis Kitton
Fragilaria sp.
Gyrosigma fasciola (Ehrenberg) Griffith & Henfrey
Gyrosigma littorale (W. Smith) Griffith & Henfrey
Gyrosigma sp.
Hantzchia sp.
Leptocylindrus danicus Cleve
Leptocylindrus minimus Gran
Licmorphora sp.
Melosira moniliformis (O. F. Müller) C. Agardh
Melosira varians C. Agardh
Meridion circulare (Greville) C. Agardh
Navicula radiosa Kützing
Navicula sp.
Nitzschia acicularis (Kützing) W. Smith
Nitzschia obtusa W. Smith
Nitzschia sigma (Kützing) W. Smith
Nitzschia sp.
Pinnularia sp.
Pleurosigma angulatum (Quekett) W. Smith
Pleurosigma elongatum W. Smith
Pleurosigma sp.
Pseudonitzschia pungens Grunow
Rhaphoneis amphiceros (Ehrenberg) Ehrenberg
Rhaphoneis surierella (Ehrenberg) Grunow
Rhizosolenia delicatula Cleve
Skeletonema costatum (Greville) Cleve
Skeletonema potamos (Weber) Hasle
Stauroneis sp.
Staurosirella leptostauron (Ehrenberg) Williams & Round
Stephanodiscus hantzschii Grunow
Stephanodiscus sp.
Surirella elegans Kützing
Surirella ovata Kützing
Surirella robusta Ehrenberg
Surirella sp.
Surirella tenera Gregory
Synedra acus Kützing
Synedra sp.
Synedra ulna (Nitzsch) Ehrenberg
Tabellaria sp.
Thalassionema nitzschioides (Grunow) Grunow
Thalassiosira lacustris (Grunow) Hasle & Fryxell
Tryblionella punctata W. Smith

CHLOROPHYCEAE

Acenedesmus acuminatus (Lagerheim) Chodat
Actinastrum hantzschii Lagerheim
Actinastrum hantzschii v. *fluviatile* Schröder
Ankistrodesmus gracilis (Reinsch) Korschikov
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus falcatus v. *acicularis* (A. Braun) G. S. Smith
Ankistrodesmus longissimus (Lemmermann) Wille
Carteria fornicata Nygaard
Carteria sp.
Chlamydomonas sp.
Chlamydomonas pertyi Goroshankin
Chlorella vulgaris Beyer
Closteriopsis acicularis (G. M. Smith) Belcher & Swale

Closteriopsis longissima (Lemmermann) Lemmermann
Closterium acutum Lyngbye ex Ralfs
Closterium sp.
Coelastrum microporum Nägeli
Cosmarium rectangulare Grunow
Cosmarium sp.
Crucigenia apiculata (Lemmermann) Schmidle
Crucigenia crucifera (Wolle) Collins
Crucigenia fenestrata (Schmidle) Schmidle
Crucigenia tetrapedia (Kirchner) W. ex G.S. West
Crucigenia quadrata Morren
Crucigenia rectangularis (A. Braun) Gay
Crucigenia sp.
Dictyosphaerium ehrenbergianum Nägeli
Dictyosphaerium tetrachotomium Printz
Didymocystis planctonica Korschikov
Diplocloris hoefleri (Bour) Hindák
Endorina cylindrica Korschikov
Euastrum gayanum DeToni
Franceia elongata Korschikov
Hyaloraphidium arcuatum Korschikov
Hyaloraphidium contortum Pascher & Korschikov
Kirchneriella contorta (Schmidle) Bohlin
Kirchneriella lunaris (Kirchner) Moebius
Kirchneriella irregularis v. *spiralis* (Smith) Korschikov
Kirchneriella obesa (W. West) Schmidle
Kirchneriella sp.
Koliella longiseta (Vischer) Hindák
Micractinium pusillum Fresenius
Monoraphidium arcuatum (Korschikov) Hindák
Monoraphidium contortum (Thuret) Komárková-Legnerová
Monoraphidium grifithii (Berkel) Komárková-Legnerová
Monoraphidium minutum (Nägeli) Komárková-Legnerová
Monoraphidium obtusum (Korschikov) Komárková-Legnerová
Monoraphidium pusillum (Printz) Komárková-Legnerová
Oocystis coronata Lemmermann
Oocystis solitaria Wittrock
Pediastrum biradiatum Meyen
Pediastrum boryanum v. *longicornum* Reinsch
Pediastrum duplex Meyen
Pediastrum duplex v. *inflata* Wolosz
Pediastrum simplex (Meyen) Lemmermann
Pediastrum tetras (Ehrenberg) Ralfs
Phacotus sp.
Phacotus lenticularis Ehrenberg
Quadrigula lacustris (Chodat) G. M. Smith
Quadrigula phitzeri (Schröder) G. M. Smith
Scenedesmus acuminatus (Lagerheim) Chodat
Scenedesmus armatus Chodat
Scenedesmus bicaudatus (Hansgirg) Chodat
Scenedesmus bijuga (Turpin) Lagerheim
Scenedesmus bijuga v. *alternans* (Reinsch) Hansgirg
Scenedesmus denticulatus Lagerheim
Scenedesmus dimorphus (Turpin) Kützing
Scenedesmus disciformis (Chodat) Fott & Komárková
Scenedesmus ecornis (Ralfs) Chodat
Scenedesmus magnus Meyen
Scenedesmus obliquus (Turpin) Kützing
Scenedesmus opoliensis Richter
Scenedesmus quadricauda (Turpin) Brébisson
Scenedesmus smithii Lemmermann
Scenedesmus sp.
Schroederia setigera (Schröder) Lemmermann
Staurastrum americanum (West) G. M. Smith
Staurastrum chaetoceras (Schröder) G. S. Smith
Staurastrum paradoxum Meyen
Staurastrum sp.
Staurastrum tetracerum Ralfs
Tetraëdron arthrodesmiforme (W. West) Woloszynska
Tetraëdron gracile (Reinsch) Hansgirg
Tetraëdron minimum (A. Braun) Hansgirg
Tetraëdron regulare Kützing
Tetraëdron sp.
Tetraëdron triacanthum Korschikov
Tetraëdron trigonium (Nägel) Hansgirg
Tetrastrum elegans Playfair
Tetrastrum heteracanthum (Nordstedt) Chodat
Tetrastrum staurogeniaeforme (Schröder) Lemmermann
Treubaria setigera (Archer) D. M. Smith
Westella botryoides (W. West) de Wildermann
Xanthidium antilopeum Ehrenberg ex Kützing

CYANOBACTERIA

Anabaena affinis Lemmermann
Anabaena flos-aquae Brébisson
Anabaena reniformis Lemmermann emend. Aptekay
Anabaena sp.
Anabaena spiroides Klebahn
Anabaena solitaria Klebs
Aphanizomenon flos-aquae (L.) Ralfs
Aphanizomenon issatschenkoi (Ussac.) Proschkina-Lavenko
Chroococcus limneticus Lemmermann
Chroococcus minor (Kützing) Nägeli
Dactylococcopsis acicularis Lemmermann
Dactylococcopsis raphidioides Hansgirg
Gomphosphaeria aponina Kützing
Gomphosphaeria fusca Skuja
Gomphosphaeria lacustris Chodat
Gomphosphaeria naegeliana (Unger) Lemmermann
Lyngbya contorta Lemmermann
Merismopedia elegans A. Braun
Merismopedia glauca (Ehrenberg) Nägeli
Merismopedia punctata Meyen
Merismopedia tenuissima Lemmermann
Microcystis aeruginosa Kützing
Microcystis firma (Brébisson & Lemmermann) Schmidle
Microcystis incerta Lemmermann

Microcystis viridis (A. Braun) Lemmermann
Microcystis wesenbergii Komárková
Nostoc commune Vaucher
Nostoc sp.
Oscillatoria agardhii Gomont
Oscillatoria limnetica Lemmermann
Oscillatoria sp.
Phormidium sp.
Spirulina major Kützing
Spirulina sp.
Spirulina subsalsa Oersted
Synechococcus sp.

XANTHOPHYCEAE

Botrydiopsis arhiza Borzi
Botrydiopsis eriensis Snow
Centritractus brunneus Fott
Centritractus capilifer Pascher
Centritractus globulosus Pascher
Characiopsis subulata (A. Braun) Borzi
Dichotomococcus curvatus Korschikov
Gleobotrys limneticus (G. M. Smith) Pascher
Goniochloris pulcherrima Pascher
Isthmochloron lobulatum (Nägeli.) Skuja
Pseudotetraedron neglectum Pascher
Tetraedriella spinigera Skuja
Tribonema aequale Pascher
Tribonema affine G. S. West
Tribonema ambiguum Skuja
Tribonema monochloron Pascher & Geitler
Tribonema pyrenigerum Pascher
Tribonema subtilissimum Pascher
Tribonema vulgare Pascher

EUGLENOPHYCEAE

Euglena acus Ehrenberg
Euglena ehrenbergii Klebs
Euglena gracilis Klebs
Euglena oblonga Schmitz
Euglena oxyuris Schmarda
Euglena tripteris (Dujardin) Klebs
Euglena viridis Ehrenberg
Phacus lemmermannii (Swirenko) Skvortzow
Phacus longicauda (Ehrenberg) Dujardin
Phacus suecicus Lemmermann
Phacus sp.
Strombomonas borysteniensis (Roll) Popova
Strombomonas sp.
Trachelomonas hispida (Perty) Stein
Trachelomonas sp.

CRYPTOPHYCEAE

Cryptomonas erosa Ehrerberg
Cryptomonas curvata Ehrenberg emend. Penard
Cryptomonas marssoni Skuja
Cryptomonas ovata Ehrenberg
Cryptomonas ovata v. *curvata* (Ehrenberg) Lemmermann
Rhodomonas minuta Skuja
Rhodomonas ovata Ehrenberg

CHRYSOPHYCEAE

Dictyota fibula Ehrenberg
Dinobryon bavaricum Imhof
Dinobryon cylindricum Imhof
Dinobryon petiolatum Willen
Dinobryon sertularia Ehrenberg
Dinobryon sociale Ehrenberg
Lagynion cystodini Pascher
Synura sp.
Synura uvella Ehrenberg

DINOPHYCEAE

Ceratium hirundinella (O. F. Müller) Dujardin
Ceratium sp.
Cochlodinium sp.
Gymnodinium sp.
Gyrodinium fusiforme Kofoid & Swezy
Gyrodinium sp.
Heterocapsa triquetra (Ehrenberg) Stein
Katodinium rotundatum (Lohmann) Loeblich III
Peridinium sp.
Peridinium willei Huitfelds-Kaas
Prorocentran micans Ehrenberg
Prorocentrum minimum (Pavillard) Schiller
Protoperidinium sp.

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the Bulletin of Zoological Nomenclature

The following Applications were published on 31 March 1998 in Vol. 55, Part 1 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

3011 *Strombidium gyrans* Stokes, 1887 (currently *Strobilidium gyrans*) and *Strobilidium caudatum* Kahl, 1932 (Ciliophora, Oligotrichida): proposed conservation of the specific names.

3055 *Osilinus* Philippi, 1847 and *Austrocochlea* Fischer, 1885 (Mollusca, Gastropoda): proposed conservation by the designation of *Trochus turbinatus* Born, 1778 as the type species of *Osilinus.*

3026 *Androctonus caucasicus* Nordmann, 1840 (currently *Mesobuthus caucasicus*; Arachnida, Scorpiones): proposed conservation of the specific name.

3031 *Paruroctonus* Werner, 1934 (Arachnida, Scorpiones): proposed conservation.

2958 *Corisa propinqua* Fieber, 1860 (currently *Glaenocorisa propinqua*; Insecta, Heteroptera): proposed conservation of the specific name.

2957 *Phytobius* Dejean, 1835 (Insecta, Coleoptera): proposed conservation.

3023 DASYPODIDAE Börner, 1919 (Insecta, Hymenoptera): proposed emendation of spelling to DASYPODAIDAE, so removing the homonymy with DASYPODIDAE Gray, 1821 (Mammalia, Xenarthra).

The following Applications were published on 30 June 1998 in Vol. 55, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

2956 *Campeloma* Rafinesque, 1819 (Mollusca, Gastropoda): proposed conservation

3008 *Euchilus* Sandberger, 1870 and *Stalioa* Brusina, 1870 (Mollusca, Gastropoda): proposed designation of *Bithinia deschiensiana* Deshayes, 1862 and *Paludina demarestii* Prévost, 1821 as the respective type species, with the conservation of *Bania* Brusina, 1896

3047 *Holospira* Martens, 1860 (Mollusca, Gastropoda): proposed designation of *Cylindrella goldfussi* Menke, 1847 as the type species

3039 *Thamnotettix nigropictus* Stål, 1870 (currently *Nephotettix nigropictus*; Insecta, Homoptera): proposed conservation of the specific name

3040 *Cicada clavicornis* Fabricius, 1794 (currently *Asiraca clavicornis*; Insecta, Homoptera): proposed conservation of the specific name

3068 *Musca rosae* Fabricius, 1794 (currently *Psila* or *Chamaepsila rosae*; Insecta, Diptera): proposed conservation of the specific name

3037 *Iguanodon* Mantell, 1825 (Reptilia, Ornithischia): proposed designation of *Iguanodon bernissartensis* Boulenger in Beneden, 1881 as the type species, and proposed designation of a lectotype

Opinions published in the Bulletin of Zoological Nomenclature

The following Opinions were published on 31 March 1998 in Vol. 55, Part 1 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

1886. *Plumularia* Lamarck, 1816 (Cnidaria, Hydrozoa): conserved by the designation of *Sertularia setacea* Linnaeus, 1758 as the type species.
1887. *Arca pectunculoides* Scacchi, 1834 and *A. philippiana* Nyst, 1848 (currently *Bathyarca pectunculoides* and *B. philippiana,* Mollusca, Bivalvia): specific names conserved.
1888. *Lirobarleeia* Ponder, 1983 (Mollusca, Gastropoda): *Alvania nigrescens* Bartsch & Rehder, 1939 designated as the type species.
1889. *Parapronoe crustulum* Claus, 1879 (Crustacea, Amphipoda): specific name conserved.
1890. *Scarabaeus rufus* Moll, 1782 (currently *Aphodius rufus*), *Scarabaeus rufus* Fabricius, 1792 (currently *Aegialia rufa*) and *Scarabaeus foetidus* Herbst, 1783 (currently *Aphodius foetidus*) (Insecta, Coleoptera): specific names conserved.
1891. *Crenitis* Bedel, 1881, *Georissus* Latreille, 1809 and *Oosternum* Sharp, 1882 (Insecta, Coleoptera): conserved.
1892. *Alcyonidium mytili* Dalyell, 1848 (Bryozoa): neotype replaced.
1893. *Bombycilla cedrorum* Vieillot, [1808] and *Troglodytes aedon* Vieillot, [1809] (Aves, Passeriformes): specific names conserved.
1894. *Regnum Animale . . .*, Ed. 2 (M.J. Brisson 1762): rejected for nomenclatural purposes, with the conservation of the mammalian generic names *Philander* (Marsupialia), *Pteropus* (Chiroptera), *Glis, Cuniculus* and *Hydrochoerus* (Rodentia), *Meles, Lutra* and *Hyaena* (Carnivora), *Tapirus* (Perissodactyla), *Tragulus* and *Giraffa* (Artiodactyla).

The following Opinions were published on 30 June 1998 in Vol. 55, Part 2 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

1895. *Riisea* and *riisei* Duchassaing & Michelotti, 1860 (Cnidaria, Anthozoa): conserved as the correct original spellings of generic and specific names based on the surname Riise
1896. *Galba* Schrank, 1803 (Mollusca, Gastropoda): *Buccinum truncatulum* Müller, 1774 designated as the type species
1897. *Glomeris* Latreille, 1802 (Diplopoda), *Armadillo* Latreille, 1802, *Armadillidium* Brandt in Brandt & Ratzeburg, [1831] and *Armadillo vulgaris* Latreille, 1804 (currently *Armadillidium vulgare*)(Crustacea, Isopoda): generic and specific names conserved
1898. *Metaphycus* Mercet, 1917 (Insecta, Hymenoptera): given precedence over *Aenasiodea* Girault, 1911
1899. *Meristella* Hall, 1859 (Brachiopoda): *Atrypa laevis* Vanuxem, 1842 designated as the type species
1900. *Trematospira* Hall, 1859 (Brachiopoda): *Spirifer multistriatus* Hall, 1857 designated as the type species
1901. *Gladiolites geinitzianus* Barrande, 1850 (currently *Retiolites geinitzianus*; Graptolithina): lectotype replaced by a neotype

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
111(3):735–736. 1998.

BIOLOGICAL SOCIETY OF WASHINGTON

125th Annual Meeting, 7 May 1998

President Stephen D. Cairns called the meeting to order at 11:00 a.m. in the Waldo Schmitt Room, National Museum of Natural History. Other council members present: Richard P. Vari (President-elect), Carole C. Baldwin (Secretary), T. Chad Walter (Treasurer), Alfred L. Gardner, Susan L. Jewett, and Rafael Lemaitre (Elected Council), C. Brian Robbins (Editor), Storrs L. Olson (Custodian of Publications), Richard C. Banks and Austin B. Williams (Finance Committee), and Bruce B. Collette and Charles Handley (past BSW presidents). Elected Council not in attendance: John A. Fornshell, Diana Lipscomb, and James N. Norris.

Following approval of the minutes of the 124th Annual Meeting of the Society, President Cairns announced that Jon L. Norenburg resigned as Associate Editor for Invertebrates and was replaced by Stephen L. Gardiner from Bryn Mawr College. On behalf of the Society, President cairns thanked Norenburg for his 4½ years of service. He further noted that the appointment of Gardiner represents the first time a scientist from outside the Smithsonian community has served as an associate editor for the *Proceedings*; the new arrangement appears to be successful and may set a new precedent for future editorial appointments.

Treasurer Chad Walter summarized Society finances for the period between 1 January and 31 December 1997 (Table 1). Total income was $75,333.27 ($40,248.25 from publication charges, $22,041.00 from dues and subscriptions, and $13,044.02 from sales of back issues and interest on Society accounts). Expenditures totaled $75,887.08 ($66,771.14 for publication costs, $8732.43 for management costs, and $383.51 for bank charges). Net change for the period was −$553.81; this is not a real loss but a relative value based on the specific range of time considered. The treasurer noted that interest income increased significantly in 1997 because of new investment strategies planned and implemented by the Finance Committee and a favorable stock market. A discussion about the purpose and ideal maximum value of the Society's Endowment Fund was initiated by NMNH Curator Brian Kensley, and President Cairns asked the Finance Committee to establish an approximate monetary figure that could serve as the Society's goal for the Fund.

Richard Banks then gave the Finance Committee Report. He noted that the Finance Committee will begin meeting quarterly rather than annually with the Treasurer in efforts to refine procedures related to establishing a meaningful annual budget for the Society. As an example of budgetary problems, Banks pointed out that the society paid ca. $10,000 in unbudgeted publication costs for Bulletin 9. Although those costs were recovered in 1998, actual expenses in 1997 greatly exceeded the amount approved in the proposed 1997 budget.

President Cairns thanked Banks, Austin Williams and Chad Walter for their help and hard work in maintaining Society finances. He then called upon Brian Robbins for the Editor's Report. Four issues of Volume 110 of the *Proceedings* were published comprising 70 papers and 692 pages. Additionally, a 149-page Bulletin (No. 9) was published in August. Submissions to the *Proceedings* increased significantly in 1997 (100 vs. 80 in 1996, 87 in 1995), but as of 1 May 1998 there were 30 submissions, down from 41 in 1997. Robbins noted that there is no backlog for accepted papers.

The President then asked Richard Banks

Table 1.—Summary financial statement for 1997.

	General fund	Endowment fund	Total assets
ASSETS: JANUARY 1, 1997	27,484.69	79,349.34	106,834.03
TOTAL RECEIPTS FOR 1997	63,125.28	12,207.99	75,333.27
TOTAL DISBURSEMENTS FOR 1997	75,887.08	—.—	75,887.08
ASSETS: DECEMBER 31, 1997	14,722.89	91,557.33*	106,280.22
NET CHANGES IN FUNDS	(−12,761.80)	12,207.99	(−553.81)

* The income from publication inventory ($4244) and remainder after opening Merrill Lynch Account ($2330.56) are part of the Endowment Fund, but were left in the General Fund (Riggs account) for cash flow maintenance.

to read the proposed changes to Article 8 of the Bylaws, which the Council had agreed in 1997 to amend. By unanimous vote, Article 8 of the Bylaws will read as follows: A Endowment Fund. There shall be an Endowment Fund which shall consist of contributions from members, miscellaneous gifts, and surplus funds from operations. At the discretion of the Council, the principal of this fund may be used (invaded for use) in publishing the Society's journal or for the general operations of the Society. At the discretion of the Council, the principal of this Fund may also be used in the publication of symposia, monographic studies, or other special publications; however, such a decision must be reached only during a regularly scheduled meeting of the Council.

Storrs Olson, Custodian of Publications, then announced that the Society had sold two complete sets of back issues of the *Proceedings* and that profits from those sales exceeded labor, shipping, and advertising costs. Olson noted that four complete sets of back issues remain but that no additional sets will be compiled because reserves of many issues are depleted. Instead, Olson proposed that the remaining back issues that were published as separates (rather than as quarterly issues) be compiled into subject sets, e.g., on fishes, birds, crustaceans, etc., and be advertised and sold this way. There was general agreement that subject sets would be marketable, and Olson agreed to initiate and oversee the sorting.

The President thanked Janet W. Reid and Michael D. Carleton for serving on the Nominating Committee for the 1998 election of officers. Election results, announced by the Secretary, are as follows: President-elect—Brian F. Kensley; Secretary—Carole C. Baldwin; Treasurer—T. Chad Walter; Elected Council—Michael D. Carleton, W. Duane Hope, Susan L. Jewett, Rafael Lemaitre, Roy W. McDiarmid, James N. Norris. President Cairns then turned the meeting over to incoming President Richard P. Vari who thanked Cairns for his service. Vari adjourned the meeting at 11:34 a.m.

Respectfully submitted,
Carole C. Baldwin
Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON," a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Appendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $65.00, figures @ $10.00, tabular material @ $3.00 per printed inch per column. One ms. page = approximately 0.4 printed page.

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Sponges, genus *Mycale* (Poecilosclerida: Demospongiae: Porifera), from a Caribbean mangrove and comments on subgeneric classification

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Abstract.—Eight species of *Mycale* Gray (Mycalidae, Poecilosclerida, Demospongiae) are described from marine mangroves on the barrier reef of Belize, Central American Caribbean. Two are new: *Mycale* (*Aegogropila?*) *carmigropila* and *M.* (*Ae.*) *citrina.* Other species found are *M.* (*Ae.*) *arndti*, *M.* (*Arenochalina*) *laxissima*, *M.* (*Carmia*) *magnirhaphidifera*, *M.* (*C.*) *microsigmatosa*, *M.* (*Mycale*) *laevis* and *M.* (*Paresperella*) sp. A key to the 17 recognized Caribbean species of *Mycale* is provided. Ectosomal skeletal patterns currently used as diagnostic characters for subgenera of *Mycale* may be inadequate for phylogenetic analysis, but reliable alternative congruent traits have not yet been identified to replace these.

More than 150 species of *Mycale* Gray have been described worldwide (Doumenc & Lévi 1987), with representatives in most marine habitats. They are common in both polar and tropical seas, and have been reported from intertidal pools abyssal depths (Hartman 1982). Contemporary monographs have added great numbers of new species (Lévi 1963, van Soest 1984, Bergquist & Fromont 1988, Hajdu & Desqueyroux-Faúndez 1994), indicating that many more undescribed taxa are yet to be found. Our study of the rich marine mangrove ecosystem of Belize (Rützler & Feller 1988, 1996; de Weerdt et al. 1991) is no exception and has revealed two new species of *Mycale.* Recent findings of metabolites with pharmacological potential from species of *Mycale* (e.g., Capon & Macleod 1987; Perry et al. 1988, 1990; Fusetani et al. 1989; Corriero et al. 1989; Butler et al. 1991; Northcote et al. 1991; Hori et al. 1993) have strengthened the need for a better assessment of the genus' biodiversity, for a stable system of classification, and for better descriptions to differentiate between allopatric sibling species.

It has been convincingly argued that descriptions of *Mycale* are often unreliable in respect to noting size categories of microscleres (Hentschel 1913, Doumenc & Lévi 1987). Accordingly, special attention was here paid to this important characteristic. Details of microsclere shape too were long considered to be useful characters because of their low adaptive value (Ridley & Dendy 1887, Dendy 1921, Hajdu et al. 1994a, Hajdu & Desqueyroux-Faúndez 1994). This view is adopted here and supported by our scanning electron micrography.

Materials and Methods

Sponges were collected by the authors and Kathleen P. Smith during several sur-

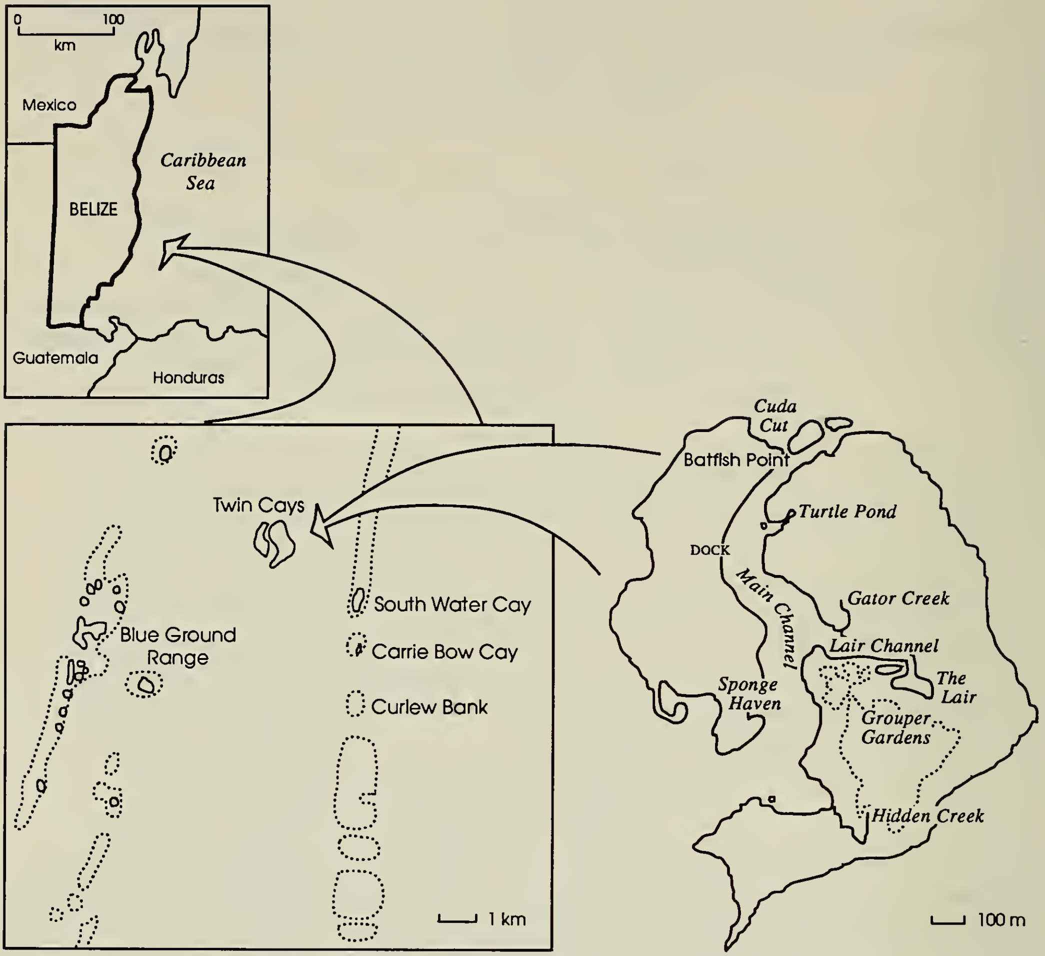

Fig. 1. Map of collecting area on the barrier-reef platform of Belize. Geographical coordinates for principal localities are 16°48.18′N, 88°04.93′W, Carrie Bow Cay; 16°49.95′N, 88°06.34′W, Twin Cays; and 16°48.55′N, 88°08.89′W, Blueground Range.

veys of mangroves in the vicinity of Carrie Bow Cay, Belize (16°48′N, 88°05′W) (Fig. 1). Specimens are deposited in the sponge collection of the National Museum of Natural History, Washington, subsamples were donated to the Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil. Schizotypes of the two new species were also deposited in The Natural History Museum, London, Queensland Museum, Brisbane, and Zoölogisch Museum Amsterdam.

Most anatomical preparations were made according to Rützler (1978) and Hajdu (1994). Additionally, skeletons for study by scanning electron microscopy (SEM) were prepared in one of the two following ways: Samples in ethanol were washed of debris with several jets of ethanol, air dried in an oven, and mounted on SEM stubs by applying a thin layer of Entellan (Merck); samples from ethanol were washed in warm water (ca. 1 min), immersed in a saturated solution of soda, and heated to 50–70°C (30 min). Then they were again washed in warm water (1 min) and etched in 20% HNO_3 at room temperature. After a few minutes under observation, samples were rinsed with warm-water jets (1 min) and a few drops of hydrogen peroxide (H_2O_2) solution added to the last change of water. After 30 min at 50–70°C the samples were rinsed in warm water (1 min), transferred to ethanol (96%, 30 min), air-dried in an oven, and mounted on SEM stubs.

Abbreviations used are: BMNH (The Natural History Museum, London), INV-POR (Invemar-Porifera Collection, Universidad Nacional de Colombia, Santa Marta), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge), MNHN (Muséum National d'Histoire Naturelle, Paris), MNRJ (Museu Nacional, Universidade Federal do Rio de Janeiro), MSNG (Museo Civico di Storia Naturale di Genova), MUT (Museo della Universitá di Torino), NNM (National Natuurhistorisch Museum, Leiden), QM (Queensland Museum, Brisbane), UFRJPOR (Universidade Federal do Rio de Janeiro, Porifera collection), USNM (National Museum of Natural History, Washington), and ZMA POR (Zoölogisch Museum Amsterdam, Porifera collection).

Systematic Descriptions

Order Poecilosclerida Topsent, 1928
Suborder Mycalina Hajdu et al., 1994
Family Mycalidae Lundbeck, 1905
Genus *Mycale* Gray, 1867; sensu Hajdu & Desqueyroux-Faúndez 1994

Diagnosis.—Mycalidae with skeleton of subtylostyles and palmate anisochelas; additional microscleres may include sigmas, toxas, micracanthoxeas, raphides, unguiferate anisochelas, and palmate isochelas.

Subgenus *Aegogropila* Gray, 1867

Diagnosis.—*Mycale* with tangential ectosomal skeleton of reticulate spicule tracts (often easily peeled off), without serrated sigmas. Type species: *Aegogropila varians* Gray, 1867 (=*M.* [*Ae.*] *contarenii* [von Martens, 1824, as *Spongia contarenii.*]).

Remarks.—Bergquist & Fromont (1988) in quoting *Halichondria aegagropila* Johnston, 1842 (misspelled as *H. aegogropila*) as a type-species of *Aegogropila* (Thiele 1903) overlooked Gray's (1867) name, *Aegogropila varians*. Because *Ae. varians* was probably a replacement name in order to avoid tautology, although not clearly stated so by Gray (1867), we choose the figured specimen of *H. aegagropila* in Johnston (1842, BMNH 1847.9.7.39) as lectotype of *Ae. varians*. In this way, both species become objective synonyms. This point was made clear by L. B. Holthuis (in lit.).

The plasticity reported here for the presence of ectosomal reticulation in *Mycale* (*Ae.?*) *carmigropila* new species is taken as indication that some representatives of *Carmia* (see below) are more closely related to *Aegogropila* than to other species of *Carmia*, suggesting paraphyly of the former subgenus and polyphyly of the latter. Additionally, some *M.* (*Mycale*) species may have their confused tangential ectosomal skeleton developed so thinly as to make spicules strewn at random appear reticulated to the casual observer (cf. *M.* [*M.*] *thielei* Hajdu & Desqueyroux-Faúndez 1994). Species like this have been assigned to *Aegogropila* in the past, for instance *M.* (*M.*) *flagelliformis* (Bergquist & Fromont, 1988) which has pore-grooves and a confused ectosomal skeleton. It becomes apparent that the monophyletic status of *Aegogropila* may not hold up in a thorough revision of all species. Such a revision is not yet possible, given that collections are dispersed, many new taxa are still being discovered, and, more importantly, no other congruent characters are yet apparent to replace the existing system.

Mycale (*Aegogropila*) *arndti* van Soest, 1984

Figs. 2, 3, 17a; Table 1

Esperia macilenta.—Carter 1871:276, pl. 17, fig. 8; not *Hymeniacidon macilenta* Bowerbank, 1866 (=*Mycale* (*Carmia*) *macilenta*).

Mycale macilenta.—Arndt 1927:143, in

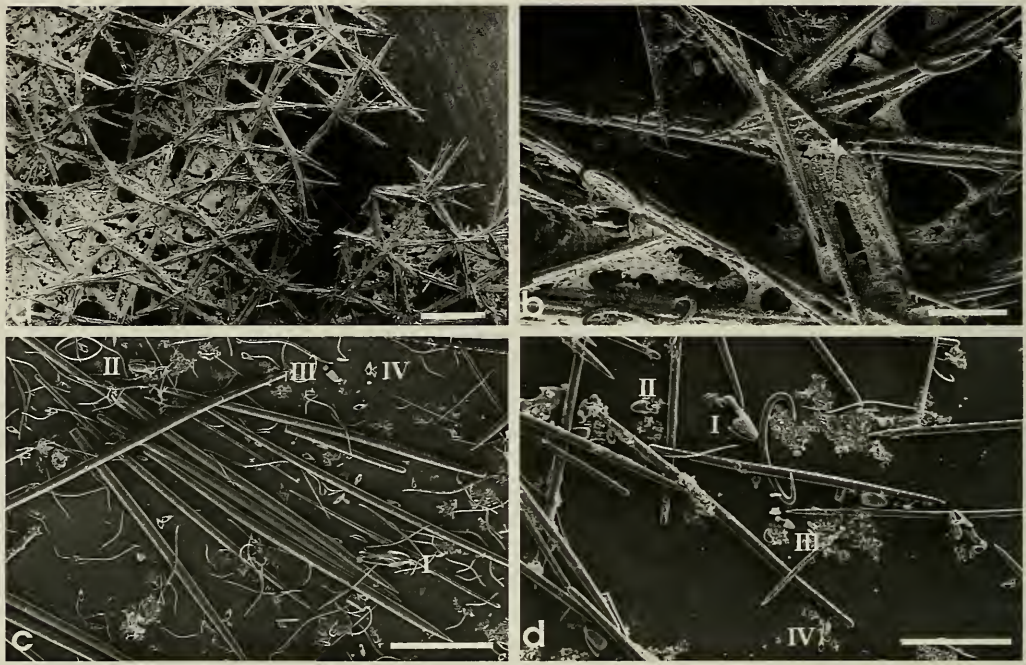

Fig. 2. *Mycale arndti*, skeleton: a, Peeled-off surface showing ectosomal reticulation; scale equals 500 μm; b, Detail of surface reticulation showing sigmas-I disposed around the bundles of megascleres, and disposition of rosettes (R) in the corners of the meshes; scale equals 100 μm; c, d, Fusiform subtylostyles and all four categories of anisochelas (I–IV); scale equals 100 μm. (a–c, USNM 39329; d, holotype ZMA POR 3675.)

part (not the figured specimen); not *Hymeniacidon macilenta* Bowerbank, 1866 (=*Mycale* (*Carmia*) *macilenta*).

M. (*Aegogropila*) *arndti* van Soest, 1984: 19, pl. II, fig. 1. Zea 1987:140.

Material studied.—ZMA POR 3675, holotype, Curaçao; ZMA POR 3842, paratype, Florida. USNM 43032, Belize, Twin Cays, Batfish Point, <1 m, coll. K. Rützler, 27 Apr 1989; USNM 39329 (MNRJ 630), Belize, Blue Ground Range, 1 m, coll. E. Hajdu & K. Smith, 12 Aug 1993; USNM 47871, Blueground Range, on red-mangrove stilt root, <1 m, coll. K. Smith, Nov 1996.

Diagnosis.—Bluish, crustose *Aegogropila* with sigmas (three categories) and toxas; four categories of anisochelas, with categories II and IV having exceptionally long frontal alae (alae of head and foot nearly fused), covering the entire shaft in frontal view.

Description.—Macroscopic appearance: Grayish blue to gray crust or cushion with oscules often raised like small chimmneys; non-slimy when rubbed. Preserved material is composed of seven main fragments, the largest is 55 mm long, 30 mm wide, and up to 4 mm thick. The color in alcohol is drab or pink, varying from light pink to almost violet. The fragments have firm consistency and microhispid surface texture. The ectosome has sand grains embedded in the surface and is easily peeled off. No oscules are apparent.

Skeleton: The ectosomal skeleton is a tangential reticulation of 120 μm thick subtylostyle bundles (Fig. 2a), with no apparent cementing spongin. Meshes are mostly triangular and up to 400 × 200 μm in diameter. Microscleres occur in abundance and may be playing the structural role of holding the reticulation intact. Sigmas I (as many as 10 per linear mm) and rosettes

(135 μm, 6 per mm) of anisochelas I can be seen surrounding the megasclere bundles (Fig. 2b). These and other microscleres, occur in great numbers inside the meshes.

The choanosome area appears light brown in transmitted light, with dark-brown blotches of fibrous spongin. The spiculation here is not very dense and no clear pattern is apparent which may be due to the slightly macerated condition of the specimen. Microscleres are scattered throughout this area.

Spicules (Figs. 2c, d, 3; Table 1): Subtylostyles fusiform, gradually tapering to a point, generally slightly bent in upper third and thickest at mid length, with long neck and eliptical head. Anisochelas I stout, with head length 50% of total length, foot in side view at about 110° angle to shaft; frontal alae of foot may bear denticulation on top (Fig. 3e). Anisochelas II similar to anisochelas I but even stouter, with head length 70% of total length, shaft not visible in frontal view, lateral alae of head arcuate. Anisochelas III slender, with head length 70% of total length, shaft slightly bent at the end of the lateral alae of the head. Anisochelas IV very slender, with both frontal alae prolonged into thin, digitiform processes that sometimes cross each other. Sigmas I stout, abruptly bent into very sharp hooks, with almost straight inner faces. Sigmas II slender, with gradual curve and sharp hooks. Sigmas III similar to sigmas II but smaller. Toxas very gently bent (more pronounced in short forms).

Ecology.—Associated with mangrove and shallow seagrass bottoms in bays and lagoons.

Distribution.—Florida, St. Vincent (Virgin Islands), Curaçao, Colombia, Belize.

Remarks.—Only one of this species specimen was found, suggesting that it may be uncommon in the survey area. Details of spicule morphology and presence of four types of anisochelas agree well with the holotype (Figs. 2d, 3b–d).

It should be emphasized that proper assessment of microsclere categories is essential if a morphological-phylogenetic classification of *Mycale* is to be achieved. In many taxonomic descriptions, one or the other microsclere category is often overlooked or lost to lumping decisions, as in the present species where anisochelas-category III was not recognized by previous authors (van Soest 1984, Zea 1987). Consequently, anisochelas II of *M. arndti* should be described as arcuate because the lateral alae of the head are partly separated from the shaft (Hajdu et al. 1994).

The stout sigmas I are comparable to those of *Esperella simonis* as figured by Ridley & Dendy (1887) and of *M. quadripartita* Boury-Esnault (Hajdu & Desqueyroux-Faúndez 1994), and may be homologous to the diancistras of *Hamacantha* Gray (Hajdu 1994). This similarity is based on the straight inner face and the abrupt tapering of the hooks in this type of sigma and is enhanced by a faintly marked notch at mid-length of some of these spicules (Fig. 3h). Toxas show a remarkable range of size but size-frequency analysis of 100 toxas in the Belizean specimen failed to reveal distinct categories.

Mycale (*Aegogropila?*) *carmigropila*, new species

Figs. 4, 17b; Table 2

Type material.—Holotype, USNM 34560, Twin Cays, Sponge Haven, on roots of *Rhizophora*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993. Paratypes: USNM 42997, Belize, Twin Cays, Batfish Point, on red-mangrove stilt root and peat bank, <1 m, coll. K. Rützler and K. Smith, 5 May 1986; USNM 43048, Belize, Twin Cays, Hidden Creek, on red-mangrove stilt root, <1 m, coll. K. Rützler, 8 May 1987; USNM 43047, Belize, Twin Cays, Hidden Creek, encrusting a cluster of algae, genus *Halimeda*, <1 m, coll. K. Smith, 8 May 1987; USNM 47870, Belize, Twin Cays, Sponge Haven, peat bank with algae, genus *Halimeda*, 1 m, coll. K. Smith, 5 Jul 1990; USNM 34561, Twin Cays, Sponge Haven,

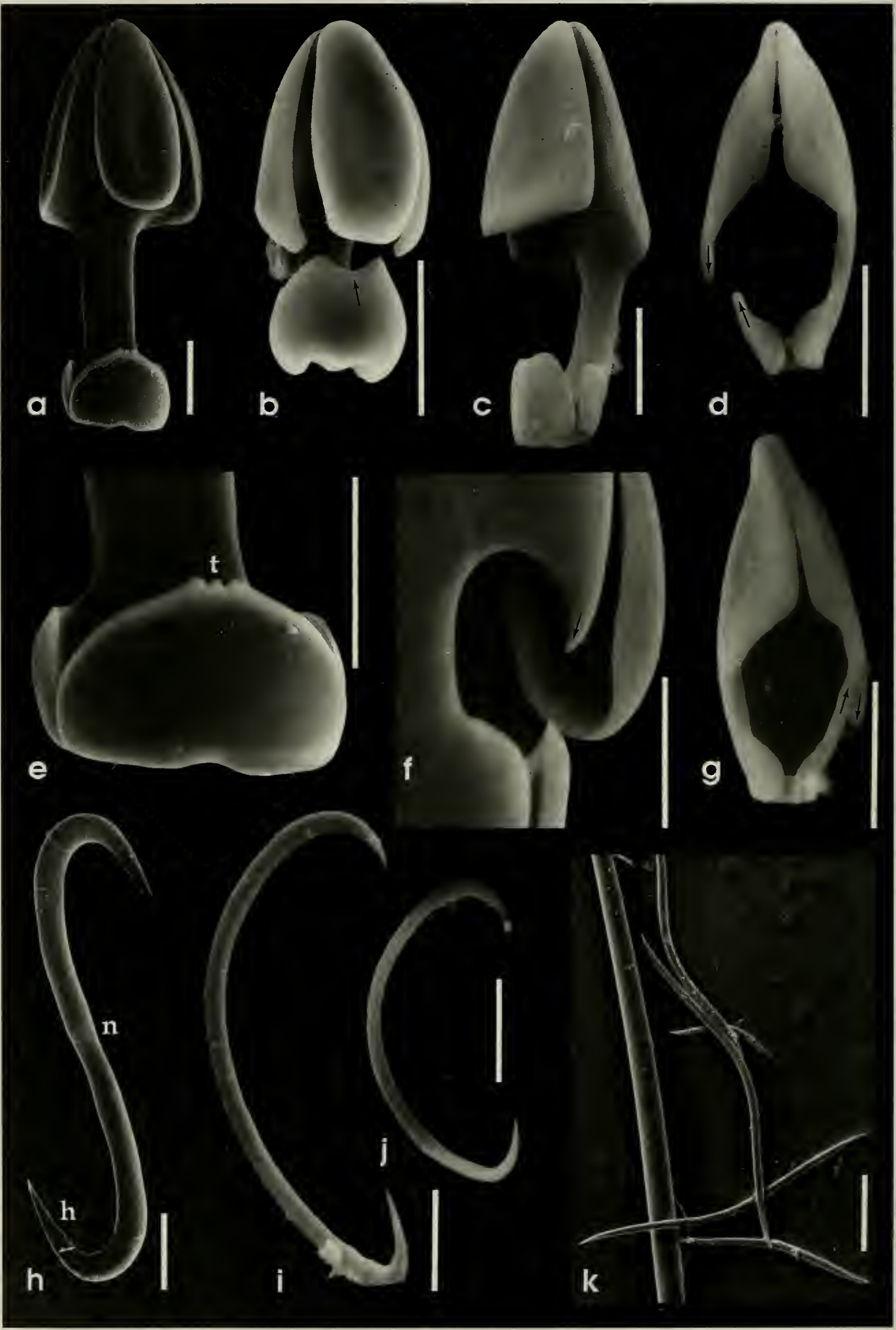

Fig. 3. *Mycale arndti*, spicules: a, Face view of anisochela-I; scale equals 10 μm; b, Face view of anisochela-II showing robustness and extremely long frontal ala of head, almost fusing with foot; note deeply concave top portion of frontal ala of the foot (arrow); scale equals 10 μm; c, Oblique frontal view of anisochela-III; scale equals 5 μm; d, Profile view of anisochela-IV showing thin digitiform prolongations from both frontal alae (arrows) almost fusing; scale equals 5 μm. e, Detail of foot of anisochela-I in Fig. 3a showing tridentate (t) top

on roots of *Rhizophora*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993; USNM 34587, Twin Cays, Sponge Haven, on roots of *Rhizophora*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993; USNM 38768, Twin Cays, Sponge Haven, on *Halimeda*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993. Schizotypes from holotype, BMNH 1994.3.1.1, QM G313152, MNRJ 631, ZMA POR 10708; fragments of paratypes, MNRJ 632, 633, 634.

Diagnosis.—Intensely blue to greenish, encrusting *Mycale* (*Aegogropila*?) with three categories of anisochelas and one type of small (<70 μm) sigmas.

Description.—Macroscopic appearance: Specimens were encrusting (≤20 cm^2) on roots of *Rhizophora*, or occurred intermingled with *Halimeda.* In the first case they were cobalt-blue, while in the second they appeared very light green. Other specimens observed alive were blue to violet, turning tan when dying. Subectosomal canals converging on oscules in a star-like pattern are visible in live specimens. The consistency is very soft, slimy, and fragile, the texture rather smooth.

Skeleton: The ectosomal skeleton is a polymorphic feature in this species. Two specimens (USNM 34560, 34587) have a tangential reticulation of subtylostyles, single or in 50 μm thick bundles, with large amounts of cementing spongin. Meshes are mostly triangular (250 × 150 μm). Up to 12 pores (40 × 20 to 80 × 50 μm in diameter) of the aquiferous system can be seen within a single mesh. A few rosettes of anisochelas I (≤110 μm in diameter), and sigmas I occur scattered among the meshes, frequently around the bundles. The other two specimens USNM 34561, 38768 lack the specialized tangential ectosomal skeleton, having just a few scattered megascleres, rosettes, and abundant sigmas near the surface.

The choanosomal skeleton is relatively low in spicule density, which accounts for the extreme softness and fragility. Subtylostyles occur scattered in great numbers and also form longitudinal bundles (≤30 μm wide), frequently meandriform, that end in fan-like brushes (≤500 μm wide) in the subectosome. These brushes support the tangential ectosomal reticulation, when present, or the rosettes alone; generally, fibers protrude slightly from the surface of the sponge.

Spicules (Fig. 3, Table 2): Subtylostyles slender, slightly fusiform, straight or slightly bent in central part, with eliptical head well marked, shaft gradually tapering to a sharp point. Anisochelas I with straight shaft, head 40% of total length; frontal alae forming narrow angle (30°) with shaft (profile view), frontal alae of feet lower than lateral alae, general aspect narrow in both frontal and profile views. Anisochelas II shaft markedly bent at head 50% of total length, lateral alae of head longer than frontal alae. Anisochelas III very slender, with shaft gradually curved in profile view, head 40–50% of total length, frontal alae of foot distally extended by angled spurs. Sigmas with markedly bent hooks, gradually sharpening ends.

Etymology.—The name *carmigropila* is derived from the juxtaposition of *Carmia* and *Aegogropila.* These are the two subgenera with which specimens of this spe-

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portion of frontal ala; scale equals 10 μm; f, Oblique view from the back of an anisochela-II showing arcuate-like pattern exhibited by the lateral alae of its head, which are elongated (arrow), rather than cut-off from the shaft; scale equals 5 μm; g, Profile view of cleistochela-like anisochela-IV showing thin digitiform prolongations from both frontal alae intercrossing each other (arrows); scale equals 5 μm; h, S-shaped, diancistra-like sigma-I showing almost straight inner-face of hooks (h), and rare, notch-like constriction (n) at tortion point; scale equals 20 μm; i, Sigma-II; scale equals 5 μm; j, Sigma-III; scale equals 5 μm; k, Toxas of stable geometry, but variable length; scale equals 20 μm. (a, e–k, USNM 39329; b–d, holotype ZMA POR 3675.)

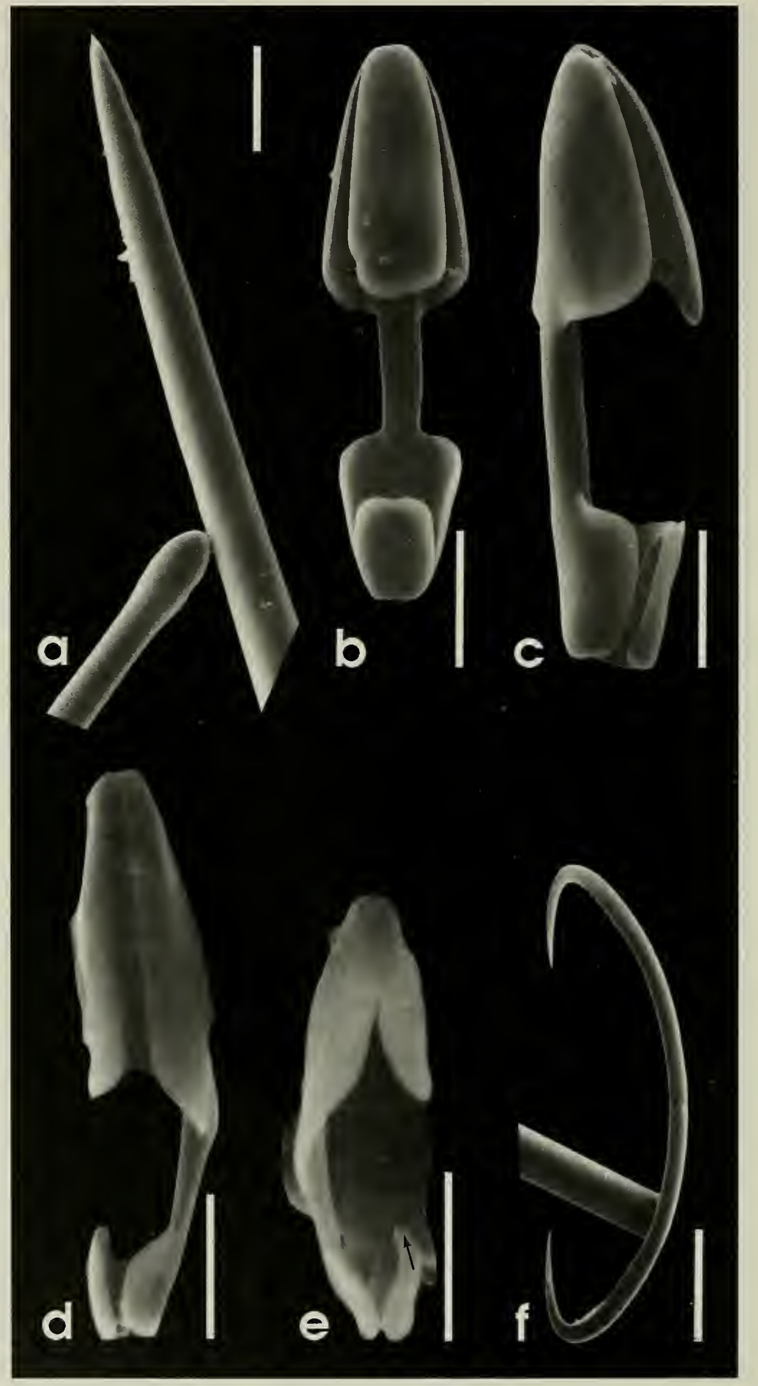

Fig. 4. *Mycale carmigropila*, spicules: a, Terminations of subtylostyles; scale equals 10 μm; b, Face view of anisochela-I showing narrow aspect; scale equals 10 μm; c, Profile view of anisochela-I; scale equals 10 μm. d, Profile view of anisochela-II showing narrow aspect, and shaft markedly bent at middle portion; scale equals 5 μm; e, Profile-view of anisochela-III, note short, and thin digitiform spur on top of frontal ala of foot (arrow); scale equals 5 μm; f, Sigma; scale equals 20 μm. (a, d–f, *Aegogropila*-like holotype, USNM 34560; b, c, *Carmia*-like paratype, USNM 34561.)

Table 1.—Spicule measurements (in µm) for *Mycale arndti* (ranges of length, or length × width, with means in italics; *n* = 20, unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Anisochelas III	Anisochelas IV	Sigmas I	Sigmas II	Sigmas III	Toxas
Curaçao (holotype ZMA POR 3675 remeasured)	249–*278.8*–313 × 8–*9.3*–10	42–*46.7*–53	21–*24.2*–29	19–*20.2*–23	10–*12.0*–14	89–*99.9*–109 × 6–8	21–*29.7*–41	13–*15.5*–17	18–*66.3*–78
Florida (paratype ZMA POR 3842 remeasured)	297–*323.3*–355 × 3–*6.2*–8	35–*45.4*–50	22? (*n* = 1)	19–*21.3*–24	11–*12.1*–13	91–*103.2*–116 × 2–*5.1*–8	31–*42.6*–62	29–*33.7*–39	15–17 (*n* = 2)
Colombia Zea 1987	297–*306.9*–332 × 4–*7.1*–10	46–*49.6*–53	not reported	18–*20.5*–23	18–*12.8*–15	97–*102.9*–109 × 6–*7.0*–8	14–*22.7*–38	not reported	14–*35.0*–85
Belize MNRJ 630	281–*309.0*–323 × 8–*9.4*–12	44–*49.1*–51	22–*26.7*–30	19–*20.2*–22	11–*12.0*–13	94–*99.1*–108 × 6–7	20–*27.7*–34	13–15 (*n* = 4)	13–*36.3*–83

cies show affinities in ectosomal skeletal patterns.

Ecology.—On *Rhizophora* mangrove stilt roots and *Halimeda* algae bordering a large mangrove channel with strong water flow.

Distribution.—Belize.

Remarks.—Of the four specimens studied, two have *Aegogropila*-like ectosomal skeletons and two lack it, thus resembling *Carmia* (*Arenochalina* species are also without ectosomal skeleton but instead have a stout choanosomal reticulation). Both forms are indistinguishable in the field and have identical spiculation. The assignment to *Aegogropila* is tentative but justified by the view that the ectosomal reticulation is more likely to be lost in a species of *Aegogropila* than acquired spontaneously in one of *Carmia.*

Mycale (*Aegogropila?*) *carmigropila* is close to *Mycale* (*Carmia*) *magnirhaphidifera* (see below) except for the possession of one more category of anisochelas, slight differences in the shape of anisochelas and lack of raphides and of a second category of sigmas. Both species may have blue or bluish color in life.

Mycale (*Aegogropila*) *citrina*, new species

Figs. 5, 6, 17c; Table 3

Mycale americana van Soest, 1984:22 (in part).—Zea 1987:138.

Type material.—Holotype, USNM 38942, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith, 13 Aug 1993. Paratypes, USNM 43031, Belize, Twin Cays, Cuda Cut near Batfish Point, encrusting a cluster of algae, genus *Halimeda*, <1 m, coll. K. Rützler, 27 Apr 1989; USNM 38956, 38958, 38963, 38967, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith, 11 Aug 1993; USNM 47872, Belize, Twin Cays, Cuda Cut, peat bank, <1 m, coll. K. Rützler, 10 May 1997; USNM 41443 Belize, Twin Cays, Cuda Cut, peat bank, <1 m, coll. K. Rützler, 10 May 1997. Schizotypes from holotype, BMNH 1994.3.1.2, QM G313153, MNRJ 635, and ZMA POR

10709; fragments of paratypes, MNRJ 636–639.

Diagnosis.—Lemon-yellow crustose *Aegogropila* with three categories of anisochelas, one type of large sigmas (>60 μm), and copious mucus production when handled.

Description.—Macroscopic appearance: Thick incrustations (5 mm; 30 cm^2) with protruding oscules encircled by a thin membrane. Extremely soft and fragile, and releasing copious amounts of mucus upon handling. Live-color is lemon yellow to light orange, turning pale yellow in alcohol. Numerous, pronounced subectosomal channels may cover most of the sponge surface and converge toward the oscules. Most specimens contained embryos during August.

Skeleton (Fig. 5): The ectosomal skeleton peels off easily and is made of a remarkably pure (no scattered megascleres) tangential reticulation of bundled (≤85 μm thick) subtylostyles (Fig. 5a), mostly forming triangular meshes (660 × 400 μm), with no apparent cementing spongin. Rosettes of anisochelas-I (130 μm in diameter) occur in places (Fig. 5b, c). Sigmas are very abundant, scattered among the meshes (up to 35 per mesh), and along the strands (30 per mm; Fig. 5d); they seem to play an important structural role in the skeleton.

The choanosome is crowded with dark-brown granules (about 40 μm in diameter), presumably of mangrove peat, which hamper observation of the skeletal architecture. The underlying pattern seems to be densely spicular, with crisscrossing megasclere bundles (150 μm thick) and abundant microscleres.

Spicules (Fig. 6, Table 3): Subtylostyles straight, slender and slightly fusiform, with poorly marked eliptic head. Anisochelas I with straight shaft, head 50% of total length. Anisochelas-II with shaft bent at head, head 50–60% of total length; frontal alae of foot with short, digitiform processes on top (Fig. 6c). Anisochelas-III very slender, with shaft gradually curved (profile

Table 2.—Spicule measurements (in μm) for *Mycale carmigropila* (ranges of length, or length × width, with means in italics; n = 20).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Anisochelas III	Sigmas
Holotype					
USNM 34560 (MNRJ 631)	276–*311.1*–345 × 5–*6.8*–9	36–*38.6*–44	19–*19.9*–21	13–*13.1*–14	58–*59.7*–64
Paratypes					
USNM 34561 (MNRJ 632)	302–*322.2*–360 × 4–*4.9*–7	33–*35.5*–37	18–*19.4*–21	10–*11.7*–13	52–*56.8*–63
USNM 34587 (MNRJ 633)	281–*297.9*–323 × 6–*7.2*–9	41–*42.8*–45	19–*20.0*–23	12–*12.7*–14	52–*58.0*–67
USNM 38768 (MNRJ 634)	254–*281.4*–302 × 4–*5.3*–6	35–*37.0*–40	19–*20.1*–21	13–*13.3*–14	51–*54.7*–58

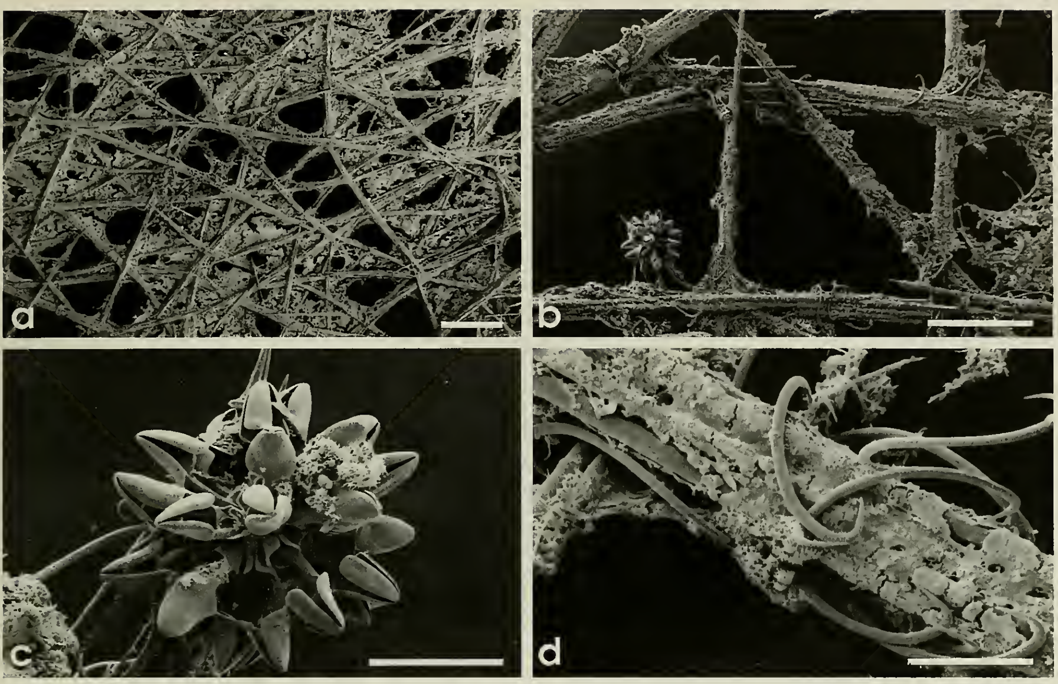

Fig. 5. *Mycale citrina*, skeleton: a, Peeled-off surface showing ectosomal reticulation; scale equals 500 μm; b, Detail of surface reticulation showing sigmas disposed abundantly around the bundles of megascleres, and rosette of anisochelas-I; scale equals 200 μm; c, Detail of rosette of anisochelas-I shown on below left corner of Fig. 5b; scale equals 50 μm; d, Detail of bundle of megascleres showing abundance of sigmas around it; scale equals 50 μm. (a–d, paratype USNM 38963.)

view) head 40% of total length, foot with very small alae, the frontal one ending on top in a thin digitiform process (Fig. 6d). Sigmas slender, markedly bent on hooks.

Etymology.—The name *citrina* is derived from citrus, for the lemon-yellow color of the live sponge.

Ecology.—Specimens were found under the roofs of mangrove overhangs, or, less commonly, on peat banks where they were protected from direct sunlight by neighboring bushy algae (e.g., species of *Halimeda*, *Caulerpa*, *Jania*).

Distribution.—Belize.

Remarks.—This species is close to *Mycale americana* van Soest (Fig. 7), but differs by the possession of a third category of anisochelas, larger megascleres and sigmas, and lemon-yellow color. *M. americana* was originally described as red (van Soest 1984), but orange-yellow and olive-yellow specimens have also been reported (Zea 1987). Reexamination of Zea's material revealed the occurrence of an intermediate-size category of anisochelas, overlooked by the author. This feature and the larger dimensions of spicules in the Colombian material make us confident in assigning the Colombian specimens to *M. citrina.*

Only one specimen quoted by van Soest (1984) in the type-series of *Mycale americana* was not collected in a mangrove (ZMA POR 3889, on *Halimeda*). Unfortunately the live color of the specimen was not registered but comparison with the holotype (Table 3) revealed three categories of anisochelas, instead of two as originally quoted, thicker megascleres, and slightly larger sigmas. We suggest to assign this specimen to *M. citrina.*

Subgenus *Arenochalina* Lendenfeld, 1887

Diagnosis.—*Mycale* without ectosomal skeleton, with choanosomal skeleton of

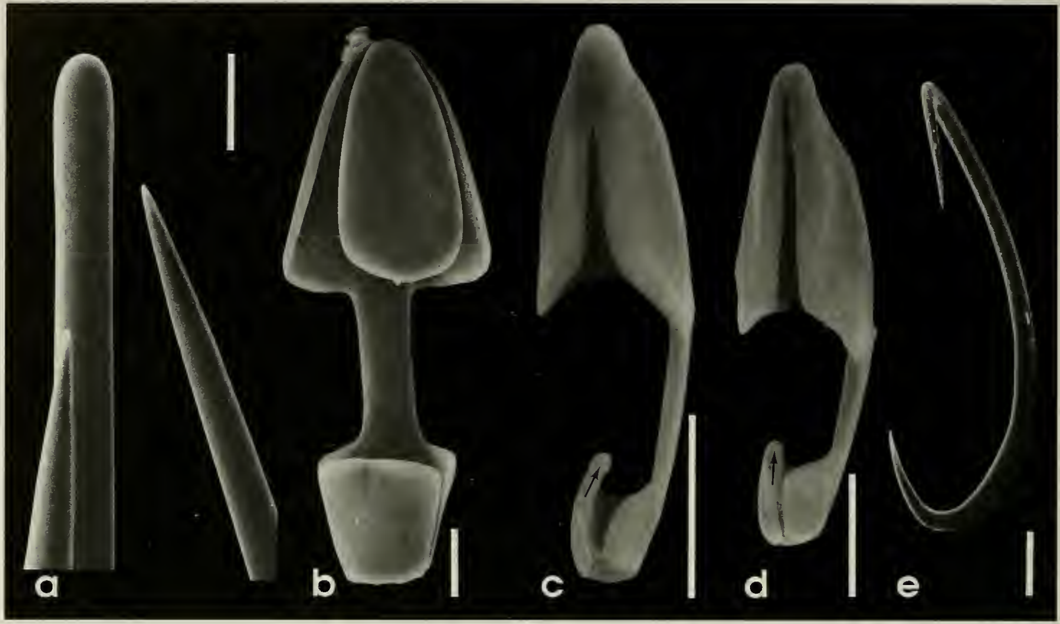

Fig. 6. *Mycale citrina*, spicules: a, Terminations of subtylostyles; scale equals 10 µm; b, Face view of anisochela-I; scale equals 5 µm; c, Profile view of anisochela-II, note short and thin digitiform spur on top of frontal ala of foot (arrow); scale equals 5 µm; d, Profile view of anisochela-III, note thin digitiform prolongation on top of poorly developed frontal ala of foot (arrow); scale equals 5 µm; e, Slender sigma; scale equals 10 µm. (a–e, holotype USNM 38942.)

stout fibers forming a coarse rectangular reticulation, and with simple spicule complement. Species of this subgenus are known to exude large amounts of mucus upon handling. Type species: *Arenochalina mirabilis* von Lendenfeld, 1887 (=*M. mirabilis*, sensu Wiedenmayer 1989).

Remarks.—The status of *Arenochalina* is uncertain. The diagnosis is in essence that provided by van Soest (1984) for *Acamasina* de Laubenfels, 1936a. Wiedenmayer's (1989) addition with respect to the frequent coring of fibers by foreign debris is not upheld here as this seems to be noteworthy for Australian species only. Shared traits among populations from both sides of the Atlantic, the Indo-west Pacific and southern Australia, seem to be the choanosomal, coarse, rectangular reticulation of spiculofibers, the low diversity of categories in the spicule complement, and the production of abundant mucus. Nonetheless, the derived condition of these characters is far from being established, as suggested by similar occurrences here and there in *Mycale* assigned to other subgenera.

Mycale (*Arenochalina*) *laxissima*
(Duchassaing & Michelotti, 1864)
Figs. 8, 9, 17d; Tables 4, 5

Acamas laxissima Duchassaing & Michelotti, 1864:95, pl. XXII, fig. 3.

Esperella nuda Ridley & Dendy, 1886:339; 1887:70, pl. XV, figs. 5, 11, 14; pl. XVI, fig. 1.

Hircinia cartilaginea.—Hyatt 1877:549 (not *Spongia cartilaginea* Esper, 1798).

Hircinia cartilaginea (Esper) var. *horrida* Hyatt, 1877:549; pl. 17, fig. 29.

Hircinia purpurea Whitfield, 1901:49, pl. 4 (not *H. purpurea* Hyatt, 1877:550).

Mycale angulosa.—De Laubenfels 1936a: 116, fig. 2, pl. 15, 1.—? Lévi 1959:129; fig. 19; pl. 6 fig. 5; López & Green 1984:

Table 3.—Spicule measurements (in µm) for *Mycale citrina* and *Mycale americana* (ranges of length, or length × width, with means in italics; *n* = 20, unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Anisochelas III	Sigmas
Mycale citrina					
Holotype					
USNM 38942 (MNRJ 635)	339–*382.4*–456 × 8–*8.6*–9	32–*45.5*–48	19–*21.6*–24	13–*13.1*–14	70–*74.9*–79
Paratypes					
USNM 38963 (MNRJ 636)	376–*418.4*–461 × 8–*9.1*–10	41–*45.5*–54	20–*21.4*–24	12–*12.6*–14	69–*77.7*–88
USNM 38956 (MNRJ 637)	350–*427.4*–477 × 7–*8.6*–11	44–*49.4*–52	19–*23.2*–26	12–*12.9*–14	75–*80.4*–88
USNM 38958 (MNRJ 638)	408–*422.9*–456 × 8–*9.2*–11	43–*49.7*–54	21–*23.0*–25	12–*13.2*–15	72–*78.3*–86
USNM 38967 (MNRJ 639)	366–*399.1*–424 × 7–*8.1*–10	45–*49.2*–54	18–*21.0*–23	12–*12.7*–14	76–*78.7*–85
M. americana (Zea 1987)	309–*341.1*–371 × 3–*7.1*–9.5	35–*40.4*–47	not reported	10–*11.6*–13	60–*66.9*–70
INV-POR 0241 (remeasured)	318–*328.9*–366 × 5–*6.9*–9	33–*38.4*–41	21 (*n* = 1)	10–13	63–*68.4*–74 × 3–4
INV-POR 0276 (remeasured)	276–*311.1*–350 × 2–*4.5*–7	33–*36.0*–40	16–19 (n = 5)	11–13	58–*64.9*–72 × 2–4
M. americana (van Soest 1984)	190–*265.6*–338 × 5–*7.2*–10	30–*36.9*–40	10–*13.9*–22	not reported	23–*47.6*–63
Holotype					
(ZMA POR 4074, remeasured)	196–*242.9*–260 × 5–*6.8*–8	34–*36.9*–40	not found	12–*13.3*–14	32–*47.0*–52
Paratype					
(ZMA POR 3889, remeasured)	276–*309.5*–329 × 7–*9.0*–11	34–*37.6*–42	18–*20.6*–22	11–*12.4*–14	54–*61.4*–67

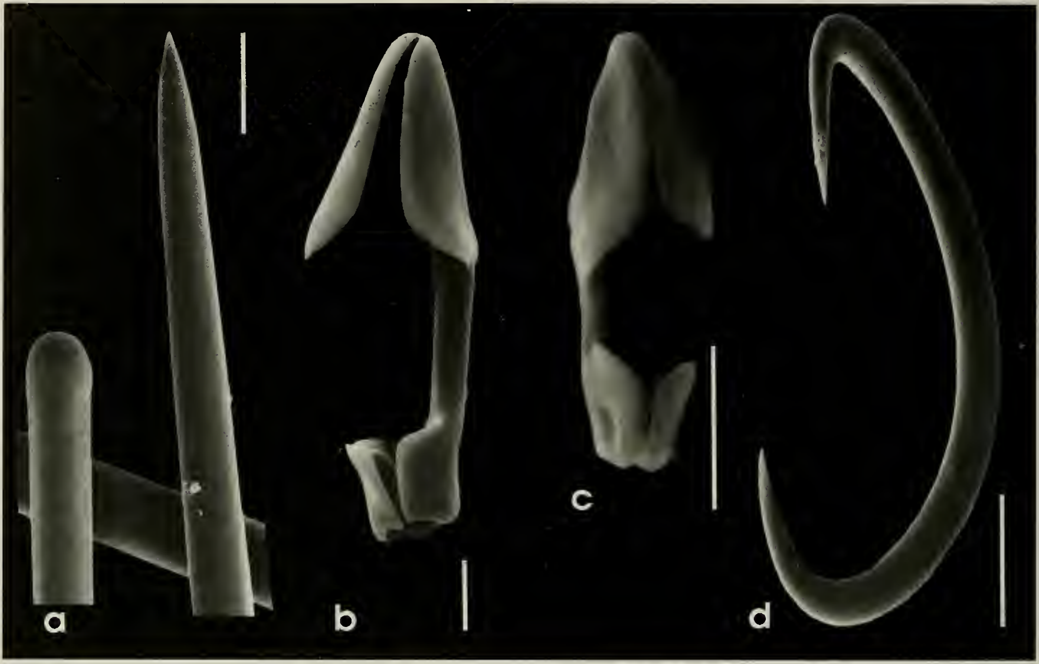

Fig. 7. Spicules of *Mycale americana*, for comparison with *Mycale citrina* (Fig. 6): a, Terminations of subtylostyles: scale equals 10 μm; b, Profile view of anisochela-I; scale equals 5 μm; c, Profile view of anisochela-III, note absence of digitiform process on top of well developed frontal ala of foot (compare with Fig. 6c); scale equals 5 μm; d, Stout sigma; scale equals 10 μm. (a–d, holotype ZMA POR 4074.)

79 (not *Pandaros angulosa* Duchassaing & Michelotti, 1864:89; pl. IX fig. 4).
Mycale sp.—Reiswig 1973.
Thorecta horridus.—Wiedenmayer 1977: 70, pl. 8, figs. 2–4; pl. 9, fig. 1.
Acamasina laxissima.—Wiedenmayer 1977:146–147, 255.
Mycale laxissima.—van Soest 1981:12.—van Soest et al. 1983:200.—Pulitzer-Finali 1986:119.—Rützler 1990:455.—Vacelet 1990:25.
?*Mycale imperfecta.*—Winterman-Kilian & Kilian 1984:133.
Mycale (*Acamasina*) *laxissima.*—Van Soest 1984:29; pl. III, 1; fig. 9.—Zea 1987:143, 255.
Mycale mucifluens Pulitzer-Finali, 1986: 121.
Mycale nuda.—Mello-Leitão et al. 1961: 12.—Hechtel 1976:254.—van Soest 1984:31.—Hajdu & Boury-Esnault 1991: 504.
Mycale jamaicensis Pulitzer-Finali, 1986: 125.
Mycale whitfieldi Pulitzer-Finali, 1986:127.
Mycale hyatti Pulitzer-Finali, 1986:129.

Material studied.—MUT POR 34, holotype, St. Thomas, Virgin Islands. MSNG, no register number; Jamaica, Port Royal, on submerged ruins, 5–10 m, 27 Mar 1964 (*M. laxissima* sensu Pulitzer-Finali, 1986; number PR. 40); MSNG 47695, Jamaica, Port Royal cays, 10–25 m, 22 Mar 1964 (*M. mucifluens* Pulitzer-Finali, 1986; holotype); MSNG 47697, Jamaica, Duncans, fore-reef slope, 35 m, 30 Mar 1964 (*M. jamaicensis* Pulitzer-Finali, 1986; holotype); ZMA POR 5192, Jamaica, Runaway Bay, 33.5 m, 14 Aug 1969, coll. and det. H.M. Reiswig (*Mycale* sp.). MCZ 7008/cat. 440, Florida, Key West; *Hircinia cartilaginea* sensu Hyatt, 1877 (*M. hyatti* Pulitzer-Finali, 1986; holotype); MCZ 7071/cat. 441, Florida,

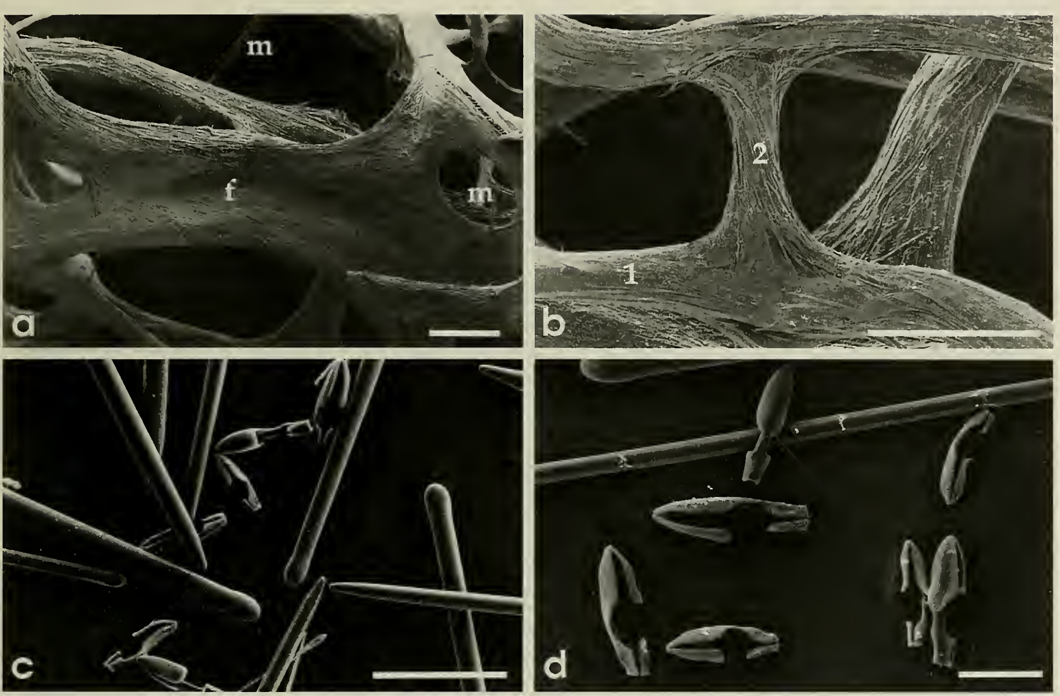

Fig. 8. *Mycale laxissima*, skeleton: a, Detail of skeleton showing fused fibers (f), and meshes of widely variable dimensions (m); scale equals 500 μm; b, Detail of skeleton showing primary (1) and secondary (2) interconnecting fibers; scale equals 500 μm; c, Stout megascleres with blunt apex, and anisochelas, young megasclere is seen below center; scale equals 50 μm; d, Anisochelas of variable geometry; scale equals 20 μm.

Key West; *H. cartilaginea* sensu Hyatt, 1877 (*M. hyatti* Pulitzer-Finali, 1986; paratype); MCZ 7073/cat. 222, Florida, Cape Florida; *H. cartilaginea* var. *horrida* Hyatt, 1877; *M. hyatti* Pulitzer-Finali, 1986; paratype. UFRJPOR 3578, Brazil, Angra dos Reis, Rio de Janairo State. USNM 41273, Belize, Twin Cays, Cuda Cut near Batfish Point, <1 m, coll. K. Rützler, 4 Jun 1983; USNM 39281 (several lots), Belize, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu and K. Smith, 11 Aug 1993.

Diagnosis.—Dark red, spiny, tubular *Arenochalina* with stout spiculo-fibers enveloped by great amounts of spongin and forming large rectangular meshes. Choanosome cavernous, without noticeable fleshy parts, with only one category of anisochelas and large (>50 μm) sigmas.

Description.—Macroscopic appearance: Specimens are tube shaped, some in clusters up to six, up to 50 cm tall, 15 cm in diameter, and thin-walled (0.5–2 cm). The color is dark wine red. A large pseudoscule (6 cm diameter) on top of the tubes is encircled by a transparent membrane. The smaller specimens (about 6 × 6 × 6 cm) are globular and already bear an apical pseudoscule. The sponge is tough but elastic, compressible, spiny to the touch, and releases copious amounts of sticky mucus when squeezed. The surface is coarsely conulose from projecting spiculo-fibers.

Skeleton (Fig. 8a, b): The surface membrane can be peeled off in places and contains a few scattered spicules and paucispicular strands of subtylostyles. The choanosomal skeleton is made up of a stout, rectangular reticulation of spiculofibers. Meshes formed are generally within the range of 100–150 μm up to 3–4 mm (Fig. 6a). One can distinguish between primary and secondary fibers (50–300 μm thick; Fig. 8b), the latter showing clearer spongin

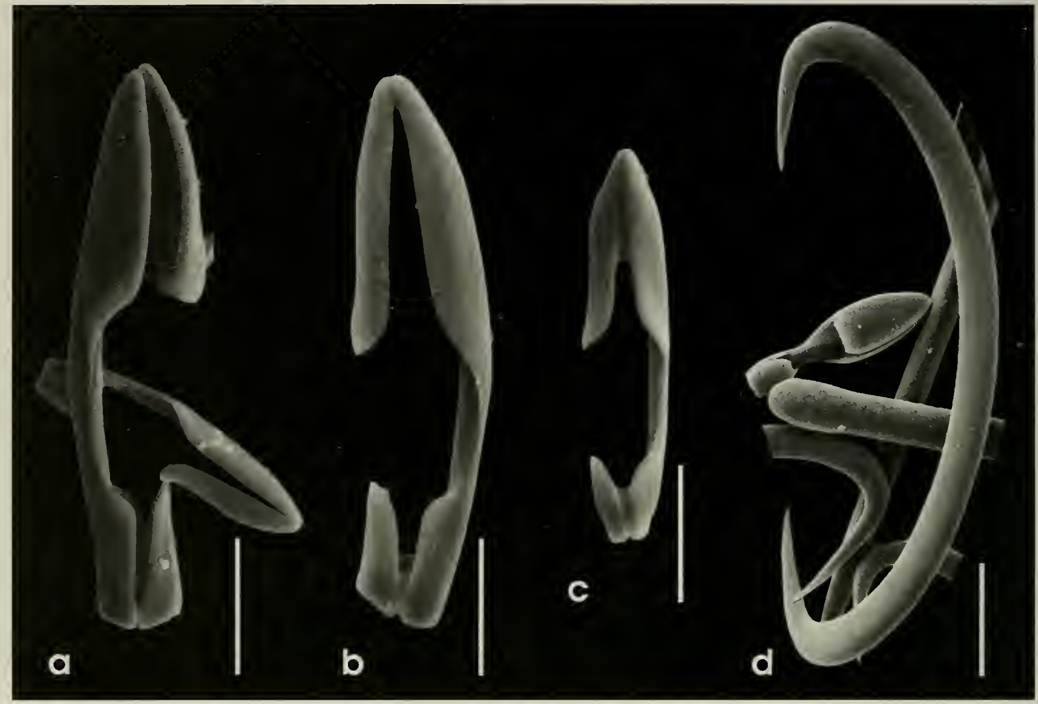

Fig. 9. *Mycale laxissima*, spicules: a, Rare larger, and common smaller anisochelas; scale equals 10 μm; b, Common anisochela of intermediary size; scale equals 10 μm; c, Common anisochela of smaller size; scale equals 10 μm; d, Stout sigmas, and anisochelas of intermediary size; scale equals 20 μm.

in transmitted light. The fibers end as subectosomal, paucispicular tufts. Anisochelas are particularly abundant in a subectosomal layer of spongin where they are spread out without order. Rosettes of anisochelas are seen on the basal plate of spongin in a specimen from Angra dos Reis, Rio de Janeiro State, Brazil; UFRJPOR 3578. Sigmas are very common along the spiculofibers of the choanosome. Isolated megascleres and sigmas occur in abundance, strewn at random inside the skeleton meshes.

Spicules (Figs. 8c, d, 9; Table 4): Subtylostyles are straight, variably thick, abruptly tapering to a blunt apex, with ovoid head. Anisochelas are variable in dimensions and geometry, generally appear narrow in profile and face views, have a curved shaft and a head 40–50% of total length. Sigmas are generally stout and

Table 4.—Spicule measurements (in μm) for *Mycale laxissima* (fragments of different specimens) from Belize (ranges of lengths, or length × width, with means in italics; *n* = 10).

Material	Subtylostyles	Anisochelas	Sigmas
USNM 39281 (MNRJ 640)	270–*283.6*–302 × 5–*6.5*–8	20–*23.9*–31	83–*94.5*–106 × 4–6
MNRJ 641	249–*272.4*–292 × 5–*6.1*–10	22–*23.6*–29	83–*93.3*–112 × 2–*3.2*–6
MNRJ 642	249–*277.2*–297 × 6–*6.5*–9	18–*24.5*–30	79–*96.1*–108 × 3–5
MNRJ 643	260–*279.8*–297 × 3–*7.5*–9	21–*27.2*–32	80–*96.7*–112 × 4–6
MNRJ 644	249–*281.7*–307 × 5–*6.9*–9	22–*27.6*–33	87–*96.3*–105 × 4–*4.8*–7
MNRJ 645	244–*262.9*–286 × 4–*6.6*–8	18–*24.8*–32	90–*100.9*–114 × 6
MNRJ 646	265–*285.7*–302 × 5–*6.3*–8	21–*25.8*–32	83–*94.3*–110 × 4–6
USNM 41273	265–*285.1*–302 × 5–*5.9*–7	19–*25.6*–34	87–*97.0*–112 × 4–6

Table 5.—Spicule measurements (in μm) for *Mycale laxissima* from Belize compared to other Caribbean locations (ranges of length, or length × width, with means in italics; *n* = 20, unless stated).

Material	Subtylostyles	Anisochelas	Sigmas	Raphides
Belize (population, *n* = 80)	244–*278.6*–307 × 3–*6.5*–10	18–*25.4*–34	79–*96.1*–114 × 3–7	not found
Holotype (MUT 34/USNM 31001, remeasured)	224–*248.5*—272 × 3–4	14–*18.6*–21	not found	not found
Holotype (cf. Pulitzer-Finali 1986)	230–260 × 2.5–3.5	16–20	50–71 (rare)	not reported
van Soest 1984	209–*223.2*–240 × 2–3.5	16–*20.0*–23	70–*75.0*–81	not reported
Pulitzer-Finali 1986	220–250 × 3.5–4.5	20–23	69–80 × 3.5	not reported
remeasured	227–*249.9*–269 × 4–*4.5*–6	21–*22.4*–23	73–*79.5*–84 × 3–4	not found
Zea 1987 (Providencia)	219–*276.0*–304 × 4–*5.7*–6	16–*20.1*–23	75–*83.7*–93 × 2–*2.8*–4	not reported
Zea 1987 (Santa Marta)	223–*254.1*–271 × 2–*4.3*–6	16–*19.7*–21	72–*78.3*–85 × 2–*2.8*–4	not reported
Zea 1987 (Cartagena)	242–*294.5*–323 × 3–*8.1*–11	26–*30.2*–33	109–*118.3*–128 × 5–*6.2*–9	not reported
Zea 1987 (San Bernardo)	213–*279.3*–313 × 3–*9.0*–11	25–*29.9*–36	109–*118.7*–133 × 6–*6.7*–8	not reported
Ridley & Dendy 1887 (as *Esperella nuda*)	245 × 16	25	120	not reported
remeasured	235–*259.8*–283 × 5–*9.0*–13	22–*26.1*–30	76–*100.9*–112 × 4–6	not found
Pulitzer-Finali 1986 (as *M. mucifluens*)	250–290 × 3.5–4.5	19–29	77–93 × 2–3.5	not reported
remeasured	258–*278.2*–294 × 3–*4.5*–6	21–*25.1*–29	84–*88.8*–95 × 2–*3.4*–4	not found
Pulitzer-Finali 1986 (as *M. jamaicensis*)	250–280 × 3–3.5	16–23	65–90 × 2–2.5	100 (rare)
remeasured	249–*266.4*–283 × 3–*4.4*–6	15–*19.5*–25	76–*80.0*–87 × 2–*2.8*–3	not found
Pulitzer-Finali 1986 well, I (as *M. whitfieldi*)	214–270 × 2.5	18.5–22.5	71–76	not reported
Pulitzer-Finali 1986 (as *M. hyatti*)	230–300 × 3–11.5	23–26	75–105 × 7.5	not reported
remeasured	224–*276.8*–322 × 4–*6.8*–11	23–*24.8*–29	78–*88.8*–106 × 4–*4.4*–6	not found

abruptly bent into hooks with sharp endings.

Ecology.—Moderately common in shaded marine mangrove environments with strong tidal water flow, on protected patch reefs below 5 m, and in fore-reef habitats below 12 m (compare also the detailed analysis of reef populations by Reiswig (1973) in Jamaica (as *Mycale* sp.). The heavy spongin fibers are known to be bored and occupied by filamentous algae (Rützler 1990) and experimental work by one of us (KR) has shown that the coring of siliceous spicules contribute photosynthetically useful light levels inside the dark sponges, comparable to glass-fiber light guides in optical applications (similar observations for other siliceous sponges were reported by Gaino & Sarà 1994, and Cattaneo-Vietti et al. 1996).

Distribution.—Florida, Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Netherlands Antilles, Colombia, Belize, Mexico, Brazil, West Africa.

Remarks.—This species was subject of several misinterpretations in the literature. *Esperella nuda* Ridley & Dendy, 1886 from Brazil (holotype BMNH 1887.5.2.171) turns out to be a junior synonym and the originally reported (Ridley & Dendy 1887) exceptional thickness of its megascleres (16 μm) was found to be only in the range of 5–13 μm. Specimens described by Pulitzer-Finali (1986; as *M. hyatti*) and Zea (1987) possess comparable megascleres (4–11 μm and 2–11 μm thick; Table 5), an isolated characteristic that does not justify separating a species. The species was also confused with *Mycale angulosa* (de Laubenfels 1936a, Lévi 1959), as discussed by van Soest (1984). Another erroneous identification may have been the report of *M. imperfecta* Baer from Colombia (Winterman-Kilian & Kilian 1984). The suggestion of possible amphi-Atlantic distribution of *M. laxissima* (van Soest 1984) raises the question of apomorphies of other distant species, such as *M. setosa* (Keller 1889) and *M. euplectellioides* (Row 1911) from the Red Sea and Indian Ocean, respectively, because our examinations suggest that there is greater intra-than interspecific variation in this taxonomic complex, for instance, of anisochelas in a single specimen. Clarification of this problem will ultimately depend on study of populations from many localities worldwide and we caution from new descriptions based on poorly preserved or unrepresentative material (e.g., related new taxa in Pulitzer-Finali 1986).

The growth form of *Mycale laxissima* is generally tube or funnel shaped. In Belize, even in shallow water, neither encrusting nor cushion-shaped specimens were seen and early globular stages develop directly into long, thin-walled tubes. This is in contrast to observations in Brazil (between latidudes 8°–24°S; EH) where encrusting forms prevail among shallow-water populations of this species. The consistency of specimens varies, suggesting polymorphism in patterns of skeleton reticulation. Likewise, abundance of microscleres varies among specimens but no attempt was made to quantify differences within and between individuals because these sponges were often large and only fragments have been collected to allow cut specimens to regrow to protect their apparently small population size.

Subgenus *Carmia* Gray, 1867

Diagnosis.—*Mycale* without ectosomal skeleton, with loose choanosomal skeleton composed mainly of plumose, isolated spiculofibers which are often paucispicular. Type species: *Hymeniacidon macilenta* Bowerbank, 1866 (=*M.* [*C.*] *macilenta* sensu Topsent 1924).

Remarks.—The absence of an ectosomal skeleton is likely to be a homoplastic occurrence in *Mycale* because it is found in all species of *Carmia* and *Arenochalina*, and possibly also in the subgenus *Mycale*, (for instance, *M.* (*M.*?) *lapidiformis* (Ridley & Dendy), Hajdu & Desqueyroux-Faúndez 1994). As such, it is a weak character on

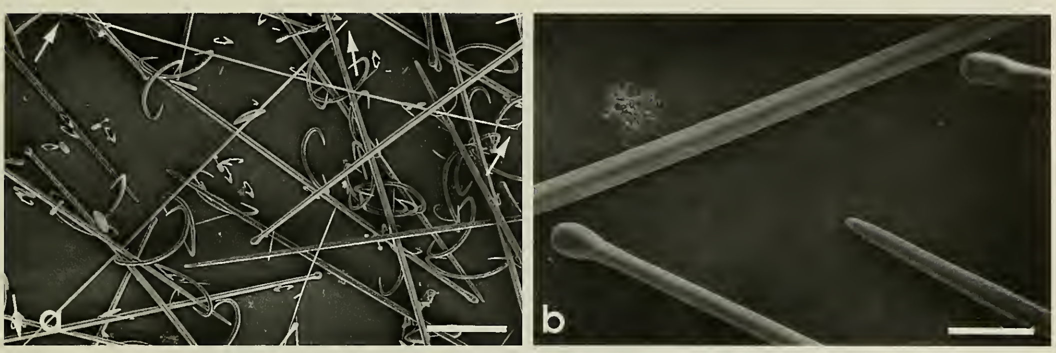

Fig. 10. *Mycale magnirhaphidifera*, spicules: a, Set of spicules showing raphides-I (arrows mark the extremities); scale equals 50 μm. b, Terminations of tylostyles, note blunt apex, and well-marked oval head; scale equals 10 μm. (a, b, USNM 39278.)

which by itself to base a subgeneric diagnosis.

Mycale (*Carmia*) *magnirhaphidifera* van Soest, 1984

Figs. 10, 11, 17e; Table 6

M. (*C.*) *magnirhaphidifera* van Soest, 1984: 27; pl II, 7.

M. cecilia.—Wells & Wells, in Wells et al. 1960:212 (not *M. cecilia* de Laubenfels, 1936b:447).

Material studied.—ZMA POR 4885, holotype, Curaçao. USNM 23633, North Carolina, Hatteras Harbor, coll. and det. H. W. & M. J. Wells (as *M. cecilia*), 21 Nov 1959. USNM 42878, Belize, Twin Cays, Lair Channel, on red-mangrove stilt root, <1 m, coll. K. Rützler, 10 May 1985 (dark royal-blue, sigmas rare); USNM 42979, Belize, Twin Cays, Main Channel, on red-mangrove stilt root, <1 m, coll. K. Rützler and K. Smith, 26 Apr 1986 (purplish, with sabellid worm tubes; many sigmas); USNM 42949, Belize, Twin Cays, Main Channel, on red-mangrove stilt root, <1 m, coll. K. Rützler and K. Smith, 26 Apr 1986 (dark wine red, tan below surface; no sigmas); USNM 47874, Belize, Twin Cays, Grouper Gardens entrance, on a strand of rope tied to a plastic pipe protruding from the channel bottom, 1 m, coll. K. Rützler, 1 Feb 1986 (ochre, sigmas rare); USNM 43029, Belize, Twin Cays, Sponge Haven, 1 m, coll. K. Rützler, 26 Apr 1989 (purplish wine red; sigmas moderately common and clearly in 2 size classes); USNM 43040, Belize, Twin Cays, Hidden Creek, <1 m, coll. K. Rützler, 1 May 1989 (gray, dirty yellow inside and where dying, enveloping sabellid tubes; without sigmas); USNM 43033, Belize, Twin Cays, Hidden Creek, <1 m, coll. K. Rützler, 1 May 1989 (gray; sigmas abundant); USNM 43036, Belize, Twin Cays, Gator Creek, <1 m, coll. K. Rützler, 3 May 1989 (grayish ochre; sigmas very abundant); USNM 43037, Belize, Twin Cays, Gator Creek, <1 m, coll. K. Rützler, 3 May 1989 (grayish ochre, massive; sigmas very abundant; with embryos); USNM 39278, Belize, Twin Cays, Hidden Creek, 1 m, coll. E. Hajdu & K. Smith, 9 Aug 1993 (bluish purple, sigmas common); USNM 39279, Belize, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith, 11 Aug 1993 (bluish purple, sigmas common; with larvae); USNM 39280, Belize, Twin Cays, Turtle Pond, 1 m, coll. E. Hajdu, 17 Aug 1993 (bluish purple, sigmas common); USNM 41442, Belize, Twin Cays, Cuda Cut, on red-mangrove stilt root, <1 m, coll. K. Rützler, 2 May 1994 (grayish blue, very thin crust; sigmas very rare); USNM 47865, Belize, Twin Cays, Hidden Creek, <1 m, coll. K. Rützler, 29 Mar 1997 (blue, sigmas abundant).

Diagnosis.—Bluish-purple to brown-gray, crustose *Carmia* with two types of an-

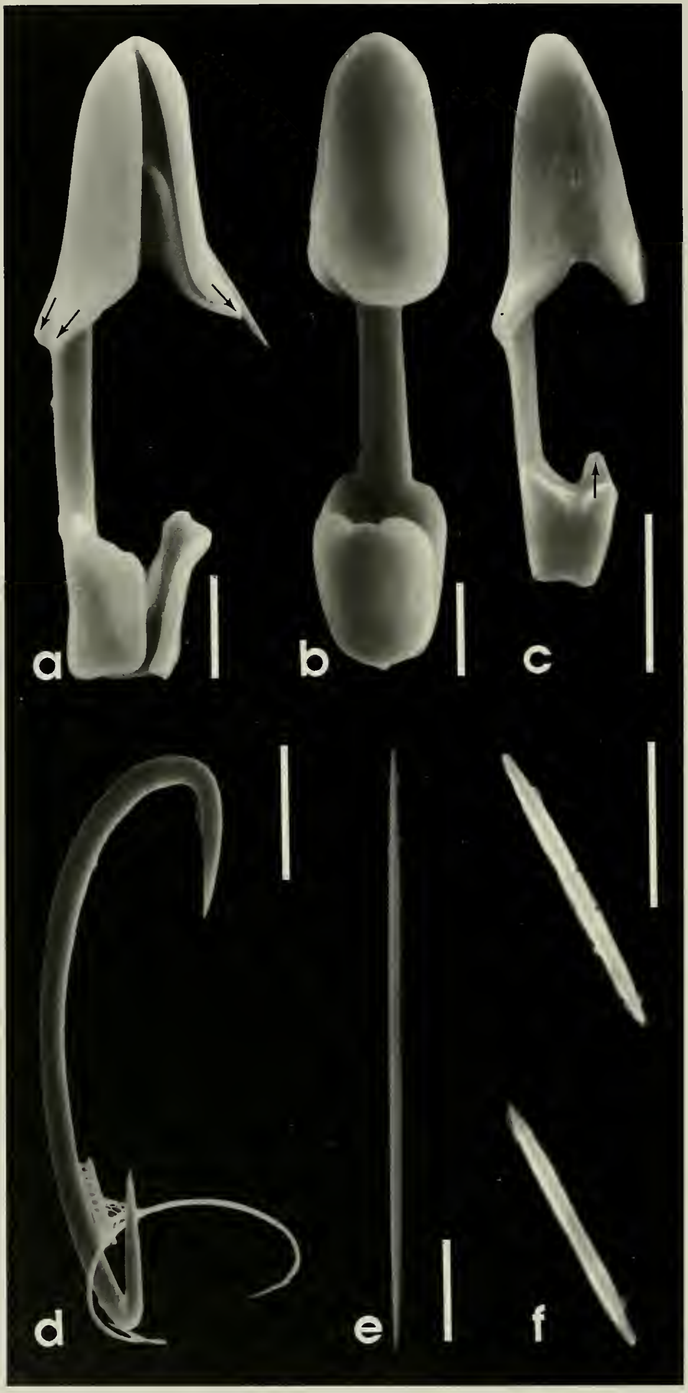

Fig. 11. *Mycale magnirhaphidifera*, spicules: a, Profile view of anisochela-I, note basal portion of lateral and frontal alae of the head diverging from each other (arrows), the lateral ones projecting behind the shaft; scale equals 5 μm; b, Face view of narrow anisochela-I, and part of anisochela-II on top; scale equals 5 μm; c, Profile view of anisochela-II showing short, thin digitiform spur on top of frontal ala of its foot (arrow); scale equals 5 μm; d, Sigmas-I and -II; scale equals 10 μm. e, Raphides-I; scale equals 5 μm; f, Raphides-II; scale equals 5 μm. (a, b, d, e, USNM 39278; c, f, holotype ZMA POR 4885.)

Table 6.—Spicule measurements (in µm) for *Mycale magnirhaphidifera* (ranges of length, or length × width, with means in italics; *n* = 20, unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Sigmas I	Sigmas II	Raphides I	Raphides II
Curaçao							
Holotype (ZMA POR 4885)	236–*254.2*–270 × 1.5–*2.2*–3	19–*27.6*–33	10–*12.4*–17	not found	not found	260–*291.3*–310	8–*9.4*–11
North Carolina							
Wells & Wells 1960 (USNM 23633, as *M. cecilia*)	250–270 × 4–6	30–36	14–16	50–58	not reported	not reported	not reported
remeasured	196–*231.0*–258 × 4–6	30–*30.9*–35	13–*15.6*–18	46–*49.1*–55	not found	168–204 (*n* = 7)	11–20 (*n* = 4)
Belize							
USNM 39278 (MNRJ 647)	196–*258.2*–286 × 4.4	31–35 (*n* = 4)	11–13	32–*43.6*–50	13–21 (*n* = 3)	90–*143.4*–241	13–*17.5*–22
MNRJ 648	232–*266.6*–294 × 4.4–6.0	21–*24.4*–35	12–*13.4*–15	26–31 (*n* = 2)	not found	280–*304.9*–322	15–*17.0*–19
MNRJ 649	232–*278.0*–308 × 3.9–5.0	29–36 (*n* = 5)	9–*11.3*–13	45–*47.1*–52	not found	112–*189.8*–249	13–*20.9*–28
MNRJ 650	258–*283.1*–308 × 3.9–5.5	29–*31.6*–34	10–*11.2*–13	37–*43.7*–47	19–*23.0*–26	120–*153.7*–260	14–*19.3*–37
MNRJ 651	232–*269.4*–283 × 4.4–5.3	31–*32.7*–36	11–*14.1*–16	40–*43.1*–48	19 (*n* = 1)	95–*154.3*–252	11–*14.1*–16
MNRJ 652	274–*303.0*–322 × 4.4–6.6	33–37 (*n* = 5)	11–*11.9*–18	42–*45.0*–47	20 (*n* = 1)	109–*192.6*–255	15–*18.5*–21
USNM 39280 (MNRJ 653)	255–*279.2*–300 × 4.2–5.4	31–*32.8*–36	11–*12.0*–13	40–*43.2*–46	not found	129–*214.8*–286	13–*16.4*–19
MNRJ 654	238–*275.0*–294 × 4.2–6.1	31–*31.8*–34	12–*12.7*–13	37–*44.9*–48	22 (*n* = 1)	101–*213.1*–280	14–*19.3*–23

isochelas, with or without sigmas, and with two size classes of raphides, the larger ones reaching more than 200 µm in length.

Description.—Macroscopic appearance: Encrusting, up to (5 mm thick) very soft and fragile. Subectosomal channels of the aquiferous system converging to oscula (≤3 mm diameter) which are raised and surrounded by transparent collars. Color in life is highly variable (see material section above), burgundy to bluish-purple and grayish blue in light-exposed areas, cream to yellowish in shaded zones; drab in dying tissue parts. Most specimens collected (May to August) contained larvae (150–300 µm in diameter) in the choanosome; many were associated with clusters of serpulid polychaete tubes.

Skeleton: The ectosome, lacking a special skeleton, consists of a superficial membrane bearing pores (30–50 µm diameter) and is supported by terminal brushes of choanosomal spiculofibers. A few sigmas and single anisochelas are seen between the pores, rosettes of anisochelas I (ca. 70 µm diameter) occur in the subectosomal zone.

The choanosome has a low spicule density, with subtylostyles organized in paucispicular (3 to 10) ascending tracts of 15–30 µm in diameter. The fibers branch seldomly and generally run parallel to each other without anastomosing. Close to the surface they diverge to form brushes. Sigmas are very common throughout the sponge. Raphides too are dispersed, not organized into trichodragmas.

Spicules (Figs. 10, 11; Table 6): Subtylostyles straight, slender, blunt, with characteristic irregularly-oval head. Anisochelas I, narrow in face and side views, head about 50% of total length, base of frontal ala of the head curved forward, base of lateral alae of the head curved backward and slightly protruding over the shaft (in side view). Anisochelas II slender, head about 50% of total length, frontal ala of foot extended on top in a short digitiform process. Sigmas I with almost straight inner face, abruptly bent into very sharp hooks. Sigmas II delicate with sharp points. Raphides I slender, straight, sharply pointed. Raphides II stout, straight, sharply pointed.

Ecology.—A common species in the survey area where it prefers shaded substrates. Many specimens were found on the bare tips of new *Rhizophora mangle* prop roots suggesting capacity to quickly colonize newly available substrate (R-strategist). The common association with polychaete worms was also observed by Wells et al. (1960, as *M. cecilia*) and van Soest (1984).

Distribution.—North Carolina, Curaçao, Belize.

Remarks.—In contrast to the holotype from Curaçao, most Belizean specimens contain abundant sigmas (see material section above). On the other hand, color, shape, and morphology of all spicules other than sigmas agree well, including the second smaller category of raphides that was found in the holotype (Fig. 11f) but was not originally reported (van Soest 1984). Nevertheless, the abundance of sigmas in some specimens is striking (see material section above) and may justify separating the sigma-bearing population as a different species if more supporting data become available.

The material from North Carolina identified by Wells & Wells, *in* Wells et al. (1960) as *Mycale cecilia* has previously been referred to both *M. microsigmatosa* (Hechtel 1965) and *M. americana* (van Soest 1984). We have analyzed the specimen (USNM 23633) and found it conspecific with *M. (C.) magnirhaphidifera*, also bearing sigmas (Table 6). Wells & Wells, *in* Wells et al. (1960) described their material as pale yellowish-green or yellowish-tan, similar to the color of *M. (C.) magnirhaphidifera* from shaded habitats.

Mycale (*Carmia*) *microsigmatosa* Arndt, 1927

Figs. 12, 13, 17f; Table 7

Mycale fistulata var. *microsigmatosa* Arndt, 1927:144, pl. I, 9.

Mycale microsigmatosa.—Burton 1956:

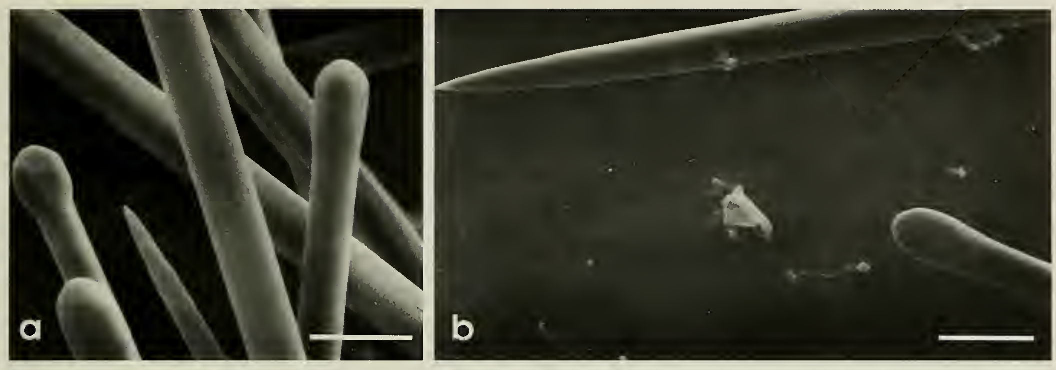

Fig. 12. *Mycale microsigmatosa*, spicules: a, Terminations of subtylostyles showing heads, and gradually sharpening apex; scale equals 10 μm; b, Terminations of subtylostyles showing head and gradually sharpening apex; scale equals 10 μm. (a, USNM 33580; b, holotype ZMA POR 1593.)

129.—Hechtel 1965:47.—van Soest 1981:12.—Winterman-Kilian & Kilian 1984:132.—Pulitzer-Finali 1986:124.—Rützler 1986:120.

Mycale (*Carmia*) *microsigmatosa.*—van Soest 1984:24; pl.II, fig. 6.—Zea 1987: 142. Not sensu Green & Gomez 1986: 284 (=*M. cecilia* de Laubenfels).

Carmia microsigmatosa.—Hajdu & Boury-Esnault 1991:510.

Material studied.—ZMA POR 1593, holotype, Curaçao. USNM 22207, holotype of *M. cecilia*, Panama City, Panama. USNM 33580, Belize, Twin Cays, Turtle Pond entrance, on root of *Rhizophora*, coll. I. Goodbody, 24 Feb 1985; USNM 34625, Belize, Twin Cays, coll. I. Goodbody, Feb 1986; USNM 41258, Belize, Twin Cays, Main Channel south of dock, on mangrove roots, coll. K. Rützler, 12 Jun 1983; USNM 39302 (several lots), Belize, Twin Cays, Cuda Cut, coll. E. Hajdu & K. Smith, 13 Aug 1993; USNM 39326 (several lots), Belize, Twin Cays, Sponge Haven, coll. E. Hajdu & K. Smith, 9 Aug 1993; USNM 47873, Belize, Blueground Range, <1 m, coll. K. Rützler, 6 May 1994. USNM 42951, Belize, Twin Cays, Batfish Point, <1 m, coll. K. Rützler, 19 Apr 1996.

Diagnosis.—Orange-dotted to reddish, crustose *Mycale* (*Carmia*), with two categories of small (<30 μm) anisochelas and small (<50 μm) sigmas.

Description.—Macroscopic appearance: Specimens are encrusting or cushion-shaped (5 cm thick), very soft and fragile. Subectosomal channels of the aquiferous system converge to scattered oscula (<5 mm) with transparent, membranous collar. Live color is highly variable but predominantly reddish orange. Even grayish-greenish specimens have recognizable bright orange specks which aid in field recognition of the species. Specimens with larvae were found during August.

Skeleton: A thin surface membrane with scattered megascleres and a few paucispicular (3 to 6 spicules wide) bundles can be peeled off and terminal spicule brushes of the ascending choanosomal fibers reach and penetrate the ectosome.

The choanosome is supported by meandering tracts of subtylostyles (50 μm thick) which may be more or less replaced by foreign structures, such as algae and sabellid polychaete tubes. These tracts split up and anastomose near the surface where they fan out in brushes. Scattered megascleres are common throughout and sigmas are seen here and there in large concentrations.

Spicules (Figs. 12, 13; Table 7). Subtylostyles slender, mostly straight, with faintly marked oval head, apex sharpening gradually or abruptly. Anisochelas I, head about 60% of total length, shaft gradually curved, basal portion of frontal and lateral alae

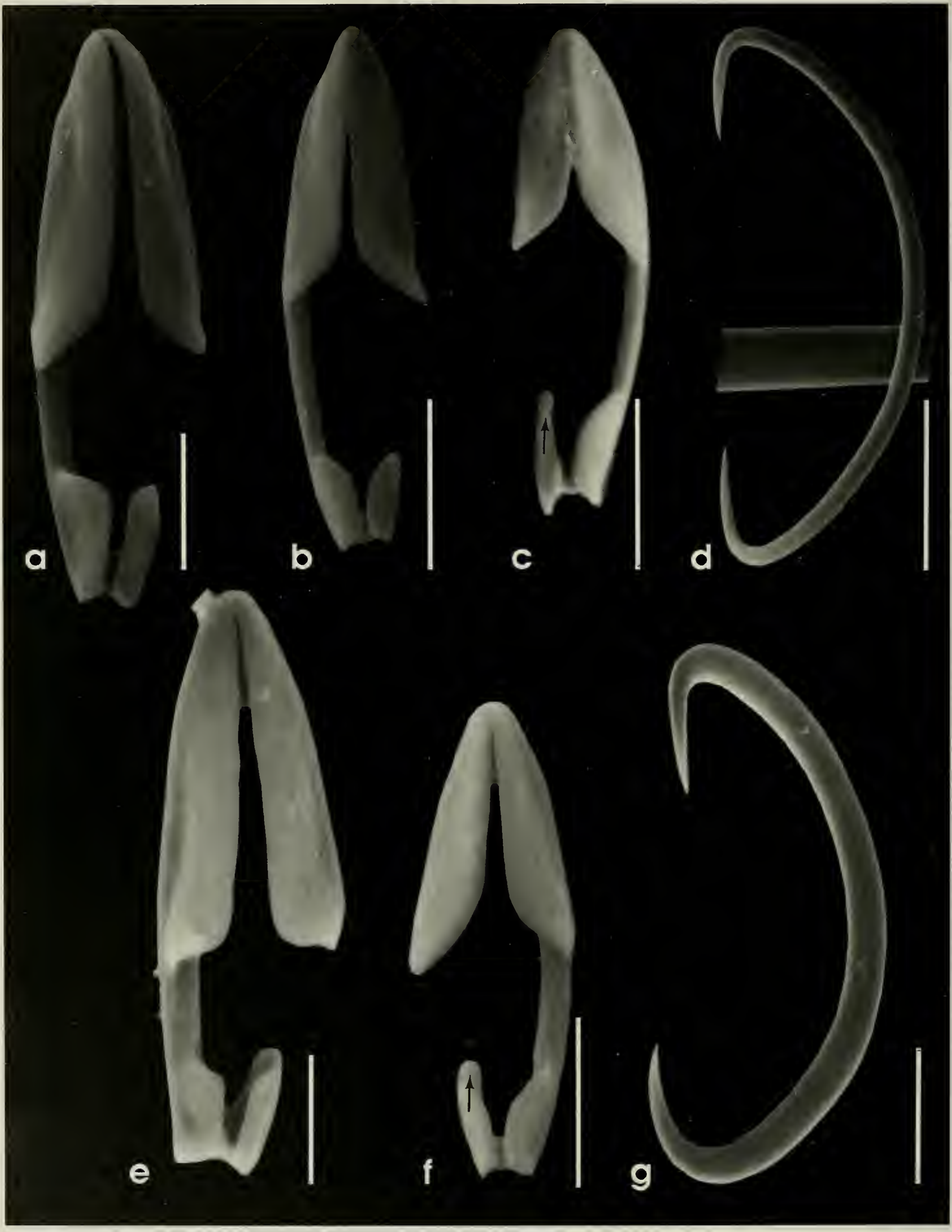

Fig. 13. *Mycale microsigmatosa*, spicules: a, Profile view of anisochela-I; scale equals 5 μm; b, Profile view of anisochela-II; scale equals 5 μm; c, Profile view of anisochela-II showing thin digitiform process on top of frontal ala of foot (arrow); scale equals 5 μm; d, Slender sigma; scale equals 10 μm; e, Profile view of anisochela-I; scale equals 5 μm; f, Profile view of anisochela-II showing thin digitiform process on top of frontal ala of foot (arrow); scale equals 5 μm; g, Stout sigma; scale equals 10 μm. (a, b, d, USNM 33580; c, holotype ZMA POR 1593; e–g, holotype of *M. cecilia*, USNM 22207.)

Table 7.—Spicule measurements (in µm) for *Mycale microsigmatosa* (ranges of length, or length × width, with means in italics; $n = 20$, unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Sigmas
Holotype (ZMA POR 1593, Arndt 1927)	250–294 × 4.8	8–19	not given	32–38
remeasured	232–*260.8*–283 × 4–6	16–*18.0*–20	13–*13.3*–14	30–*32.4*–37
USNM 33580	224–*241.9*–263 × 4–6	18–*19.3*–21	13–*14.1*–15	30–*35.0*–42
USNM 34625	213–*237.4*–252 × 6–7	18–*19.0*–20	12–*14.0*–15	25–*33.8*–36
USNM 41258	216–*241.6*–260 × 3–4	18–*18.6*–20	13 ($n = 3$)	30–*38.3*–45
USNM 39302 (MNRJ 655)	235–*253.8*–274 × 3–5	18–*19.5*–20	13–14 ($n = 3$)	29–*33.8*–37
MNRJ 656	224–*236.9*–249 × 2–*4.1*–5	17–*18.9*–21	12–*13.5*–15	34–*35.0*–37
MNRJ 657	216–*239.7*–277 × 3–*4.1*–6	17–*19.6*–21	14–*14.3*–16	30–*33.2*–35
MNRJ 658	244–*269.6*–288 × 4–*4.7*–7	19–*20.3*–24	12–*13.8*–15	33–*36.9*–41
MNRJ 659	235–*247.0*–263 × 4–6	18–*18.7*–20	13–*13.8*–15	32–*34.8*–39
MNRJ 660	246–*267.7*–288 × 4–6	18–*20.6*–23	14–*14.8*–15	31–*36.6*–42
MNRJ 661	238–*252.0*–273 × 3–5	18–*18.8*–20	12–*13.4*–15	32–*35.7*–39
MNRJ 662	227–*240.5*–258 × 3–*4.2*–6	17–*18.2*–20	13–*13.4*–15	36–*37.8*–39
MNRJ 663	232–*251.7*–267 × 3–*4.2*–6	17–*18.6*–20	11–13 ($n = 2$)	31–*34.4*–39
USNM 39326 (MNRJ 664)	243–*266.1*–288 × 4–6	18–*19.5*–21	13–*13.8*–15	32–*37.0*–43
MNRJ 665	230–*240.2*–259 × 4–*5.0*–7	18–*20.2*–21	12–14 ($n = 6$)	31–*35.9*–39
MNRJ 666	224–*255.4*–274 × 3–*4.5*–6	18–*20.0*–23	13–*14.6*–16	32–*34.7*–36
MNRJ 667	221–*249.2*–269 × 3–4	18–*19.0*–20	13–*14.1*–15	32–*35.5*–39

slightly divergent. Anisochelas II, head about 50% of total length, shaft gradually curved, with basal portion of frontal and lateral alae of head slightly divergent; in some of these spicules the top of the frontal ala of the foot tapers to a thin digitiform process (Fig. 13f). Sigmas slender, both ends markedly bent into sharp hooks.

Ecology.—Common on mangrove prop roots, including new growth tips, and all other light-exposed substrates in shallow lagoon and harbor habitats (R-strategist). The species is also reported as tolerant of oil and domestic wastes (Muricy 1989). Sabellid polychaetes are commonly associated with and overgrown by this sponge.

Distribution.—Bermuda, Florida, Bahamas (?), Cuba (?), Jamaica, Puerto Rico, Venezuela, Netherlands Antilles, Colombia, Belize; also from Brazil, West Africa (?), Açores (?), and Eastern Mediterranean (?).

Remarks.—Agreement with the holotype (Figs. 12b, 13c) is excellent, including the presence of two categories of anisochelas which has not before been reported for the species. Because anisochelas are rare in this species (van Soest 1984, Hajdu & Boury-Esnault 1991), it is not surprising that occurrence of a second category was previously overlooked.

Mycale microsigmatosa is very common in Belizean mangroves, displaying mainly reddish-orange color but also red and translucent gray. Similar color variability was reported by Hechtel (1965, Jamaica), van Soest (1984; Curaçao, Bonaire, Margarita, and Florida), and Zea (1987, Colombia). Hajdu & Boury-Esnault (1991) found Brazilian specimens (collected between latitudes 13° and 24°S) to be exclusively red but subsequent observations (EH) found pale-yellow specimens from Angra dos Reis (Rio de Janeiro state).

Bergquist (1965) and Hechtel (1965), suggested the synonymy of *Mycale microsigmatosa* with *M. cecilia* de Laubenfels. Another opinion by van Soest (1984) favored a close relationship between *M. cecilia* and *M. americana.* The present finding of two categories of anisochelas in *M. microsigmatosa* rather supports the former view, agreement with *M. cecilia* (holotype, Fig. 13e–g). Furthermore, de Laubenfels (1936b) describes *M. cecilia* as "basically green, abundantly provided with bright red specks", similar to our own observations on *M. microsigmatosa.* However, we prefer to keep *M. cecilia* as a valid name for eastern Pacific records of the sponge, basing this decision on geographic separation and small differences in spicule dimensions. Therefore we propose to assign the record of *M.* (*C.*) *microsigmatosa* from the Pacific coast of Mexico (Green & Gómez 1986) to *M. cecilia*, this sponge has relatively thick subtylostyles (5–9 μm) and anisochelas with a large range of length (12–21 μm), possibly representing two categories. Van Soest (1984) also suggested possible synonymy of *Mycale microsigmatosa* with *M. senegalensis* Lévi, 1952, *M. sanguinea* Tsurnamal, 1969, and *Desmacella meliorata* Wiedenmayer, 1977. To this list we may add *Desmacella janiae* Verril, 1873, *Biemna microstyla* de Laubenfels, 1950a, and *Prosuberites scarlatum* Alcolado, 1984, but formal decision must await re-examination of all types.

Subgenus *Mycale* Gray, 1867

Diagnosis.—*Mycale* with ectosomal skeleton of confused tangential megascleres over perpendicular, dendritic choanosomal spicule tracts that end in subectosomal brushes. Type species: *Hymeniacidon lingua* Bowerbank, 1866 (Hajdu & Desqueyroux-Faúndez 1994).

Remarks.—A subgenus *Anomomycale* was erected by Topsent (1924) for *Desmacidon titubans* Schmidt (1870). This sponge, however, has most characteristics of the subgenus *Mycale*, including the subectosomal brushes, large megascleres (one size class >700 μm), and possibly tangential subtylostyles in the ectosome (Lundbeck 1905). Only the distinctive shape of its anisochelas separates it. This single fea-

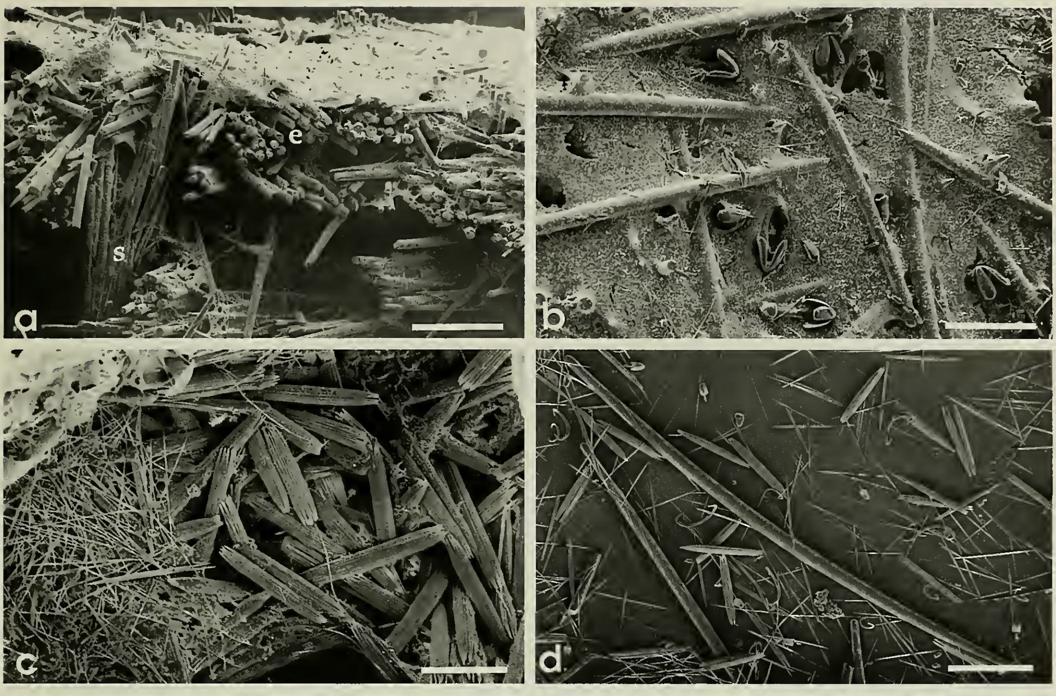

Fig. 14. *Mycale laevis*, skeleton: a, Transverse section showing terminally divergent spicule brushes (s) of ascending choanosomal tracts supporting the tangential ectosomal skeleton (e); scale equals 200 μm; b, Detail of surface showing tangentially disposed megascleres, and abundance of microscleres; scale equals 100 μm; c, Detail of subectosomal area showing typical patches of trichodragmas, and also of isolated raphides; scale equals 50 μm; d, Fusiform, bent subtylostyle, note abundance of trichodragmas; scale equals 100 μm.

ture is insufficient to justify subgeneric separation and it seems appropriate to keep *M. titubans* in the subgenus *Mycale*.

Mycale (*Mycale*) *laevis* (Carter, 1882)
Figs. 14, 15, 17g; Table 8

Synonymy, see Hajdu & Desqueyroux-Faúndez (1994); in addition:
Mycale fusca.—Mello-Leitão et al. 1961: 12; Hechtel 1976:254; Hajdu & Boury Esnault 1991:504.
Mycale (*Mycale*) *laevis*.—Lehnert 1993:54.

Material studied.—USNM 41267, Belize, Twin Cays, Sponge Haven, <1 m, on mangrove roots, coll K. Rützler, 13 June 1983; USNM 39328 (3 lots), Belize, Blue Ground Range, 1 m, coll. E. Hajdu & K. Smith, 12 Aug 1993.

Diagnosis.—Orange to yellow, encrusting or massive *Mycale* with large (>500 μm) megascleres and two size classes of anisochelas; with basal, spur-like projections on the smaller anisochelas; also present, two classes of sigmas and raphides in trichodragmas.

Description.—Macroscopic appearance: Thick cushions (up to 5 cm) or clusters of 20 or more branches (1–10 cm diameter, up to 50 cm tall) rising from a massive base and often with apical oscula (up to 4 cm diameter). Oscula have fibrous-looking collars made up of tracts of megascleres. Consistency is rough but compressible and the texture rough. Color in life is a bright orange-yellow, but also a few whitish specimens were seen. Specimens with embryos were seen in August.

Skeleton (Fig. 14a–c): The ectosome is reinforced by a thin layer of tangentially strewn subtylostyles interspersed with abundant microscleres. A very dense, con-

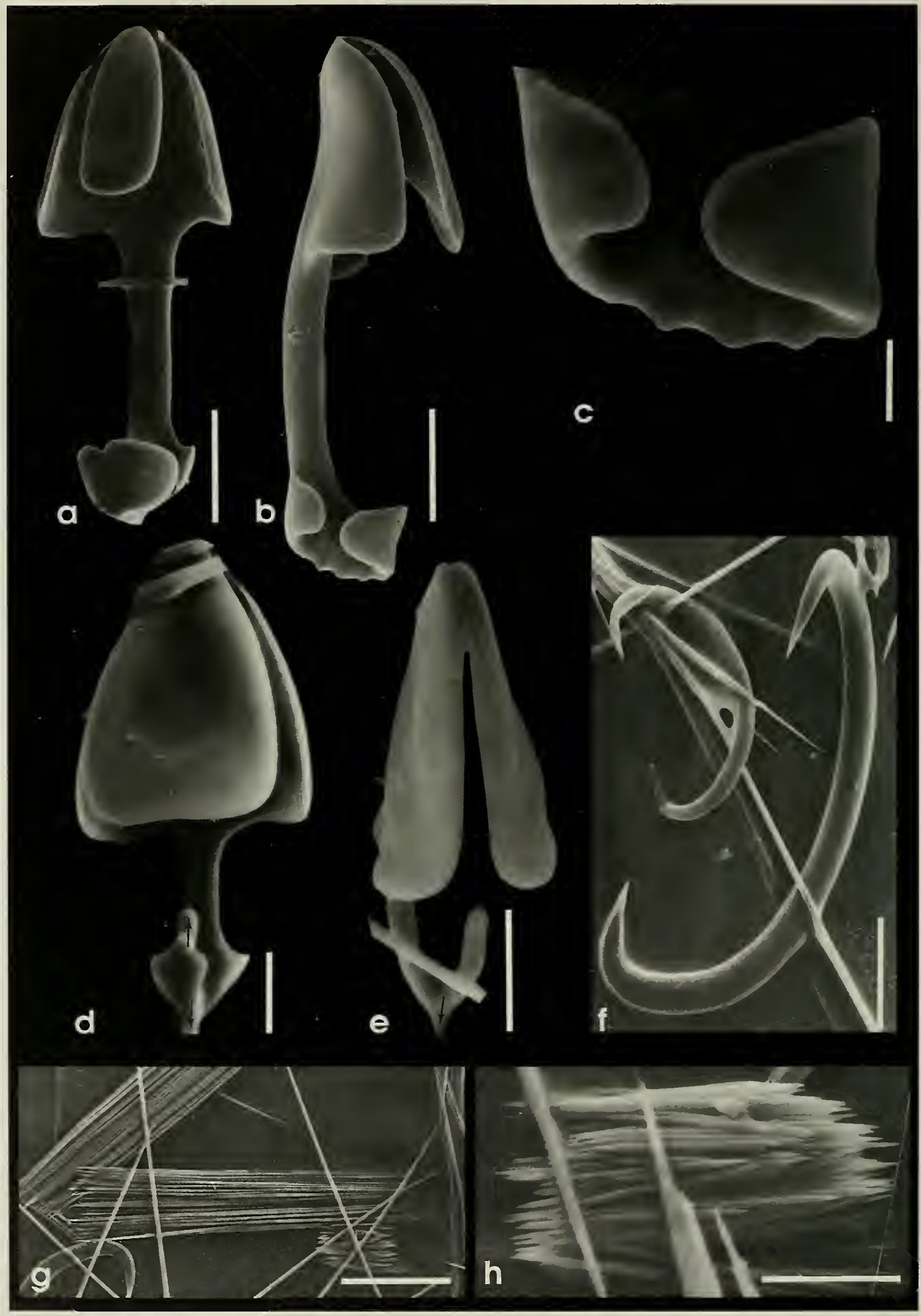

Fig. 15. *Mycale laevis*, spicules: a, Face view of anisochela-I; scale equals 20 μm; b, Profile view of anisochela-I, note slight s-shape of shaft; scale equals 20 μm; c, Detail of foot of anisochela-I shown in Fig. 15b, with an undulated basal portion of the falx; scale equals 5 μm; d, Face view of rare, robust anisochela-III showing thin digitiform prolongation on top of frontal ala of foot (arrow up), and basal spur (arrow down); scale equals 5 μm; e, Profile view of typical anisochela-III showing basal spur (arrow), note reduced foot without alae; scale equals 5 μm; f, Sigmas-I and -II; scale equals 10 μm; g, Trichodragmas-I and -II; scale equals 20 μm; h, Rare trichodragmas-II; scale equals 5 μm.

Table 8.—Spicule measurements (in µm) for *Mycale laevis* (ranges of length, or length × width, with means in italics; *n* = 20, unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Sigmas I	Sigmas II	Trichodragmas I	Trichodragmas II
USNM 39238 (MNRJ 668)	429–*504.6*–551 × 6–*15.9*–20	78–*83.5*–89	18–*18.7*–21	29–*42.0*–50 × 2–3	15–*20.2*–23	74–*77.4*–86 × 8–12	not found
MNRJ 669	509–*550.7*–610 × 9–*16.0*–23	72–*81.8*–95	19–*22.1*–33	31–*39.5*–47 × 2	18–22 (*n* = 5)	72–*80.1*–87 × 4–*8.5*–17	not found
MNRJ 670	525–*566.0*–588 × 13–*15.8*–21	72–*80.1*–89	17–*24.7*–33	32–*39*–49 × 3	14–*16.8*–21	72–*79.6*–90 × 8–10	11–*13.0*–15 × 4–*5.9*–8
USNM 41267	514–*560.7*–610 × 12–*14.2*–18	73–*83.4*–91	17–*18.8*–28	32–*43.3*–52 × 3	17–*20.1*–24	70–*78.4*–85 × 5–*9.2*–15	13–*17.6*–26 × 3–*4.8*–8

fused subectosomal reticulation of multispicular subtylostyle tracts (up to 300 µm thick) is oriented mainly parallel to the surface. Spaces between tracts are filled by large amounts of scattered subtylostyles, anisochelas I, and patches of trichodragmas I (by far the most common microscleres, Fig. 14c). Brushes of subtylostyles support the ectosomal network (Fig. 14a), and pierce the surface slightly. Anisochelas I form a few rosettes (160 µm) but more often occur scattered or surrounding the bundles of megascleres.

The choanosome shows high spicule density and includes criss-crossing subtylostyle tracts with loose subtylostyles and patches of numerous trichodragmas I in between. Digitiform processes of the larger specimens are supported by longitudinal spicule tracts and a secondary, transverse plumo-reticulate skeleton.

Spicules (Figs. 14d, 15; Table 8): Subtylostyles fusiform, mostly bent with faintly marked, oval head and abruptly sharpened, or strongyloid apex. Anisochelas type I, with shaft slightly s-shaped, head ca. 40% of total length, basal portion of falx on foot undulated (Fig. 15c). Anisochelas type III slender, head 70% of total length, foot often reduced (lacking alae) and with basal spur. Sigmas I stout, with sharply bent hooks Sigmas II similar to I but more slender. Trichodragmas I; trichodragmas II.

Ecology.—This is a well known reefal species (Goreau & Hartman 1966) and is widely distributed in the shallow parts (16–25 m) of the fore-reed of Carrie Bow Cay (see Rützler & Macintyre 1982 for the bionomy of the reef). In the mangroves, *Mycale laevis* is restricted to areas with good exposure to the open, near-reef lagoon (it is common at Blue Ground Range and Cat Cay Lagoon, but very rare at Twin Cays). There, however, the sponges attached to red mangrove roots can grow to record size. Specimens laying unattached on the bottom (presumably fallen from the roots) and intergrown with turtle grass survive well and appear healthy.

Distribution.—Cuba, Jamaica, Dominican Republic, Puerto Rico, Venezuela, Colombia, Belize, Mexico; also Brazil.

Remarks.—A few details should be added to former descriptions of the species. Notably, we recognize two categories of sigmas (smaller one can be rare) rather than a large size range of one, and two categories of trichodragmas in some of the specimens (again, the smaller being rare see Hajdu & Desqueyroux-Faúndez 1994, tab. 1, and references therein). No taxonomic importance is given to these characters here.

Esperia massa Schmidt, 1862 sensu Schmidt 1870:58 and *Mycale massa* (Schmidt, 1862) sensu Winterman-Kilian 1984:133, are likely to be synonyms of *Mycale laevis* because the latter species was originally described from the Mediterranean Sea and a West-Indian distribution is highly unlikely despite the similarities in skeleton morphology.

Subgenus *Paresperella* Dendy, 1905

Diagnosis.—*Mycale* with an ectosomal skeleton of reticulated tangential megascleres and with serrated sigmas among the microscleres. Type species: *Esperia serratohamata* Carter, 1880.

Remarks.—Van Soest (1984), based on the very peculiar characteristics of serrated sigmas, considers *Paresperella* a monophyletic group. Nevertheless, in the absence of another congruent diagnostic character, *Paresperella* may fall to *Aegogropila* (see comments on *Anomomycale*, above, under subgenus *Mycale*). However, until further study of species in *Paresperella* and other closely related subgenera (*Aegogropila, Carmia*), it is convenient to maintain this subgenus for the 20 or so species already described with serrated sigmas.

Mycale (*Paresperella*) species indet.
Fig. 16

Material studied.—Spicules found contaminating sample of *Mycale citrina*, USNM 38967, Belize, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith 13 Aug 1993.

Spicules.—Sigmas (Fig. 16), slender, o- or s-shaped, shaft subcylindrical (flattened in cross section), with ca. 10 spines each along the outer bends of the hooks; spines single or double and directed toward spicule center.

Remarks.—These distinctive spicules are the only material found, thus making species diagnosis impossible. The sigmas came in abundance from a very small specimen or fragment (used up in making the preparation) inadvertently collected as part of a specimen of *M. citrina.*

Comparison with the only *Paresperella* species described from the western Atlantic, *Mycale* (*P.*) *spinosigma* (Boury-Esnault 1973; MNHN D NBE 968), indicates that the latter is most likely contaminated with *Paresperella* spicules. The anisochelas reported by Boury-Esnault (1973) were not found in a preparation of the type specimen and sigmas were very rare. The ZMA collection has a very small macerated specimen (ZMA 5389) from inside Curaçao (Barbara Beach, 1–3 m) which, from the appearance of serrated sigmas may be conspecific with the Belizean material. The Curaçao specimen has slender subtylostyles (270–323 μm long), one category of anisochelas (24–30 μm long), and the serrated sigmas (78–98 μm long). One toxa (34 μm long) was also seen but may be foreign. We refrain from making an identification until more material is available.

Discussion

Some names associated with Caribbean *Mycale* are still in need of a reappraisal. Winterman-Kilian & Kilian (1984) listed *M. cleistochela flagellifer* Vacelet & Vasseur, 1971 (a species from Madagascar) in Colombia, with sigmas twice the size of the original report. We have not examined the Colombian material but assume that it is conspecific with *M.* (*Ae.*) *diversisigmata*

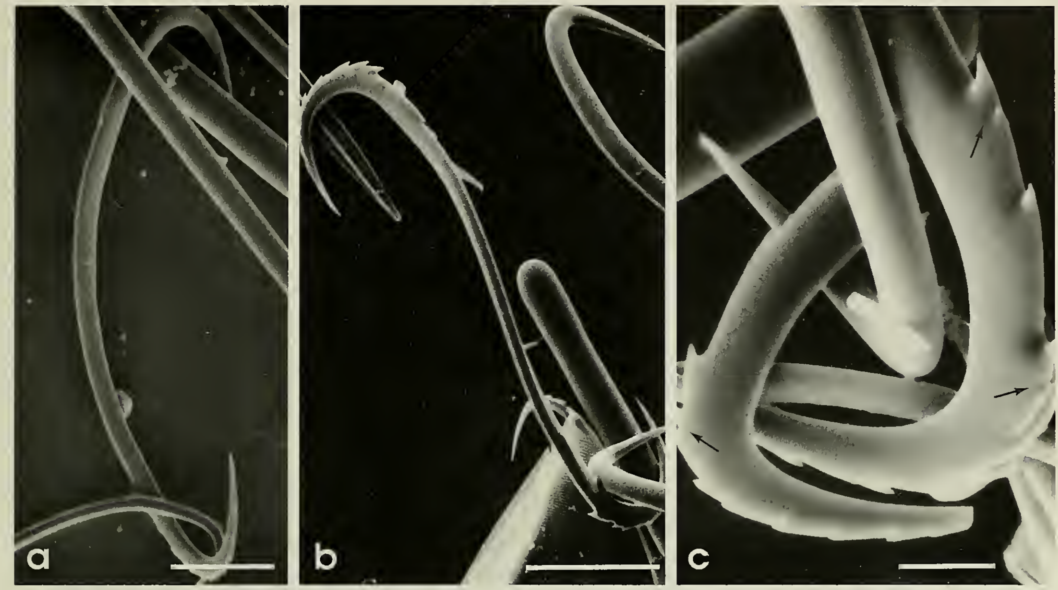

Fig. 16. *Mycale* (*Paresperella*) sp., characteristic sigmas (other spicules belong to *M. citrina*): a, Serrated sigma; scale equals 20 μm; b, Serrated sigma showing non-cylindrical shaft, note narrower middle portion when compared to wider hooks; scale equals 20 μm; c, Detail showing spines on hooks of serrated sigmas, note heterogeneous distribution with the occurrence of twins (arrows); scale equals 5 μm.

van Soest, 1984 (from Curaçao), which contains flagelliform sigmas (150–200 μm), as well as semi-closed anisochelas. Similarity of the latter species with *M. cleistochela flagellifer* was suspected by van Soest (1984) who must have been unaware of the morphology of true cleistocheles which was only recently revealed by scanning electron microscopy (Pulitzer-Finali 1996:fig. 15; for *M.* (*Ae.*) *peculiaris*).

Schmidt (1870) cited five species from Florida under genera *Esperia* Nardo, 1833 and *Desmacidon* Bowerbank, 1864, that were referred to *Mycale* by subsequent authors. The specimen originally named *Esperia renieroides* Schmidt (1870) was referred to *Oxymycale* by van Soest (1984) and to *Mycale* by Pulitzer-Finali (1986). Neither author had examined Schmidt's preparation (BMNH 1870.5.3.31) which reveals an isotropic reticulation of small oxeas, part of a haplosclerid sponge, and a single rosette of anisochelas of the type that is indicative of *M. immitis* (Schmidt 1870). The specimen identified as *Esperia massa* Schmidt, 1862 (sensu Schmidt 1870) is considered dubious by Topsent (1924), and unrecognizable by van Soest (1984). Winterman-Kilian & Kilian (1984) report *M. massa* from Colombia. However, data indicate that these specimens are conspecific with *M. laevis* which has indeed very similar spiculation.

As argued above, *Desmacidon titubans* described by Schmidt (1870) is best identified as *Mycale* (*M.*) *titubans*, although the conspecificity of populations from Florida (Schmidt 1870), the northeastern-Atlantic (Lundbeck 1905, Topsent 1924) and the Antarctic (Boury-Esnault & Van Beveren 1982) is certainly unlikely and needs to be confirmed. *Esperia diaphana* Schmidt (1870; material examined: dissociated spicules mount made by Schmidt, BMNH 1870.5.3.32) and *Esperia immitis* Schmidt (1870; material examined: dissociated spicules mount made by Schmidt, BMNH 1870.5.3.30, MCZ No. 42; label could be in Schmidt's handwriting but depth of 274 m differs from that of 230 m in the original

Fig. 17. Underwater photographs of live *Mycale* specimens representing seven of the eight species found at Twin Cays: a, *M. arndti*, grayish-colored specimen, ×1.0; b, *M. carmigropila* new species, on red-mangrove stilt root, ×0.9; c, *M. citrina* new species, on mangrove peat, ×1.3; d, *M. laxissima*, on red-mangrove stilt roots, ×0.3; e, *M. magnirhaphidifera*, overgrowing serpulid polychaete tubes on red-mangrove stilt roots, ×0.5; f, *M. microsigmatosa*, ×1.0; g, *M. laevis* on red-mangrove stilt root, ×0.3.

account) are regarded as good species of *Mycale* (*Mycale*). *Esperia diaphana* has two categories of megascleres (721–827 µm and 509–604 µm), three categories of anisochelas (148–170 µm, 31–40 µm, 19–25 µm), one category of sigmas (16–23 µm), and one category of trichodragmas (41–70 µm), and seems close to *M.* (*M.*) *grandis* Gray, 1867 (Indo-west Pacific), and *M.* (*M.*) *anisochela* Lévi, 1963 (south and southwestern Africa). Abundant material from the Gulf of Mexico, agreeing with *M.* (*M.*) *diaphana* is in the USNM collection. *M.* (*M.*) *immitis* has two categories of megascleres (996–1198 µm and 466–530 µm), three categories of anisochelas (90–105 µm, 29–33 µm, 20–25 µm), one category of sigmas (35–45 µm), and two categories of trichodragmas (90–108 µm, 18–33 µm).

Van Soest (1984) considers Little's (1963) *Mycale macilenta* from the Gulf of Mexico to be a likely new species in the subgenus *Aegogropila.* In the account below we will treat it as *Mycale* (*Ae.*) species.

The following key to 17 recognized species of *Mycale* of the Caribbean should be used in conjunction with the relevant literature (most recent reliable or available reference).

Mycale (*Aegropila*) *americana* van Soest	van Soest 1984
M. (*Ae.*) *angulosa* (Duch. & Mich.)	van Soest 1984
M. (*Ae.*) *arndti* van Soest	van Soest 1984
M. (*Ae.*) *carmigropila* new species	this paper
M. (*Ae.*) *citrina* new species	this paper
M. (*Ae.*) *diversigmata* van Soest	van Soest 1984
M. (*Ae.*) *escarlatei* Hajdu et al.	Hajdu et al. 1995
M. (*Ae.*) species indet.	Little 1963 (as *M. macilenta*)
M. (*Arenochalina*) *laxissima* (Duch. & Mich.)	this paper
M. (*Carmia*) *magnirhaphidifera* van Soest	van Soest 1984
M. (*C.*) *microsigmatosa* Arndt	this paper
M. (*Grapelia*) *unguifera* Hajdu et al.	Hajdu et al. 1995
M. (*Mycale*) *diaphana* (Schmidt)	Schmidt 1970 (as *Esperia*); this paper (discussion)
M. (*M.*) *immitis* (Schmidt)	Schmidt 1970 (as *Esperia*); this paper (discussion)
M. (*M.*) *laevis* (Carter)	this paper
M. (*M.*) *titubans* (Schmidt)	Schmidt, 1870 (as *Desmacidon*); this paper (comment, subgenus Mycale)
M. (*Paresperella*) species indet.	this paper

Key to the species of Caribbean *Mycale*

1. Megascleres near 500 µm common . . 2
   Megascleres always <500 µm 5
2. Two categories of megascleres 3
   One category of megascleres, trichodragmas often abundant . . . . *Mycale* (*M.*) *laevis*
3. Three categories of anisochelas, anisochelas I >60 µm 4
   One category of anisochelas <60 µm, twisted . . . . *M.* (*M.*) *titubans*
4. Anisochelas I ≤150 µm common . . . . *M.* (*M.*) *diaphana*
   Anisochelas I <110 µm, with shaft markedly curved in profile view . . . . *M.* (*M.*) *immitis*
5. Serrated sigmas present . . . . *M.* (*Paresperella*) species indet.
   Serrated sigmas absent 6
6. Three or more categories of anisochelas 7
   One or two categories of anisochelas . . . 12
7. Sigmas present 8
   Sigmas absent, two categories of toxas . . . . *M.* (*Aegropila*) species indet.
8. Two or more categories of sigmas . . . 9
   One category of sigmas 10
9. Two categories of sigmas, anisochelas II very narrow ("duck's-bill") . . . . *M.* (*Ae.*) *escarlatei*
   Two categories of flagelliform sigmas, three of normal ones . . . . *M.* (*Ae.*) *diversisigmata*
   Three categories of sigmas, four categories of anisochelas . . . . *M.* (*Ae.*) *arndti*
10. Anisochelas only palmate 11

Anisochelas I and II unguiferate, anisochelas III palmate with spur .... *M. (Grapelia.) unguifera*

11. Sigmas ≥70 μm common, live sponge lemon-yellow .... *M. (Ae.) citrina*
Sigmas <70 μm, live sponge blue ... . *M. (Ae.) carmigropila*

12. Raphides common 13
Raphides absent or very uncommon (possibly contaminants) 14

13. Two categories of raphides, raphides I >100 μm, isochelas absent .... *M. (Carmia) magnirhaphidifera*
One category of raphides <50 μm, isochelas present .... *M. (Ae.) angulosa*

14. With tangential ectosomal reticulation .... *M. (Ae.) americana*
Without tangential ectosomal skeleton 15

15. Sigmas common, >50 μm, coarse choanosomal spongin fibers, massive sponges .... *M. (Arenochalina) laxissima*
Sigmas <40 μm, delicate choanosomal skeleton strands, encrusting sponges .. .. *M. (C.) microsigmatosa*

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First record and new species of *Gastrophanella* (Porifera: Demospongiae: Lithistida) from the central East Pacific

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Abstract.—A new species of sponge, *Gastrophanella primore* (Lithistida, Demospongiae), is described from the continental shelf off Guerrero, Mexico, central East Pacific at a depth of 45 m. This is the first record of a species of *Gastrophanella* and the second member of the Lithistida reported from the East Pacific. Its cup shape, tight choanosomal mesh and zygoses of desmas are similar to those of *Gastrophanella implexa* from the West Indies. Its tylostrongyles and desmas are similar to those of *G. mammilliformis* from South Africa. The perpendicular arrangement of the tylostrongyles, the outwardly directed tyles, the choanosomal desma, and the tylostrongyle type all resemble those of *Siphonidium capitatum* from the Indo-Pacific. *Gastrophanella primore* and *Corallistes isabela* (Corallistidae), the only lithistid previously recorded from the central East Pacific, lack common morphological characteristics.

There have been few studies of the sponge fauna of the central East Pacific. Early studies near the present collection site do not report any lithistid and are old or incomplete descriptions (Carter 1882, Wilson 1904, Dickinson 1945, Hofknecht 1978). More recently, Green & Gómez (1986), Gómez & Bakus (1992) and Hidalgo (1994) described several species in more detail. A search for records of lithistids from the Mexican Pacific (Gulf of California 31°42′N, 114°48′W to the Isthmus of Tehuantepec 14°30′N, 92°10′W, Fig. 1), as well as published studies of areas to the north and south of Mexico, have found only one lithistid sponge, *Corallistes isabela* (Corallistidae) from the Galapagos Islands at 78 m (Desqueyroux-Faúndez & van Soest 1997). I presently describe a new species of the genus *Gastrophanella* (Demospongiae: Lithistida: Siphonidiidae) from the Mexican coast, central East Pacific.

Materials and Methods

The lithistid sponge was dredged by the R/V *El Puma* in April 1982, at Guerrero, Mexico (Fig. 1). Thirty spicules were measured (in μm) for the mean size and ranges of each type. For scanning electron microscopy (SEM) of spicules, sponge tissue was digested in boiling nitric acid containing glass pearls and was subsequently washed and centrifuged (80 g) twice. Two drops of the resulting liquid were dried on a glass slide, placed on a stub and sputter coated with gold paladium (300 Å thick). Spicules were observed with a JEOL JSM-35 scanning electron microscope. The holotype (USNM 51303) is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Class Demospongiae Sollas, 1888
Order Lithistida Schmidt, 1870

Order used for convenience as it is considered to be polyphyletic (van Soest & Stentoft 1988).

Family Siphonidiidae Sollas, 1888
Genus *Gastrophanella* Schmidt, 1879

Definition.—(Sub)tylostrongyles and (sub)tylostyles arranged perpendicularly to the surface (van Soest & Stentoft 1988).

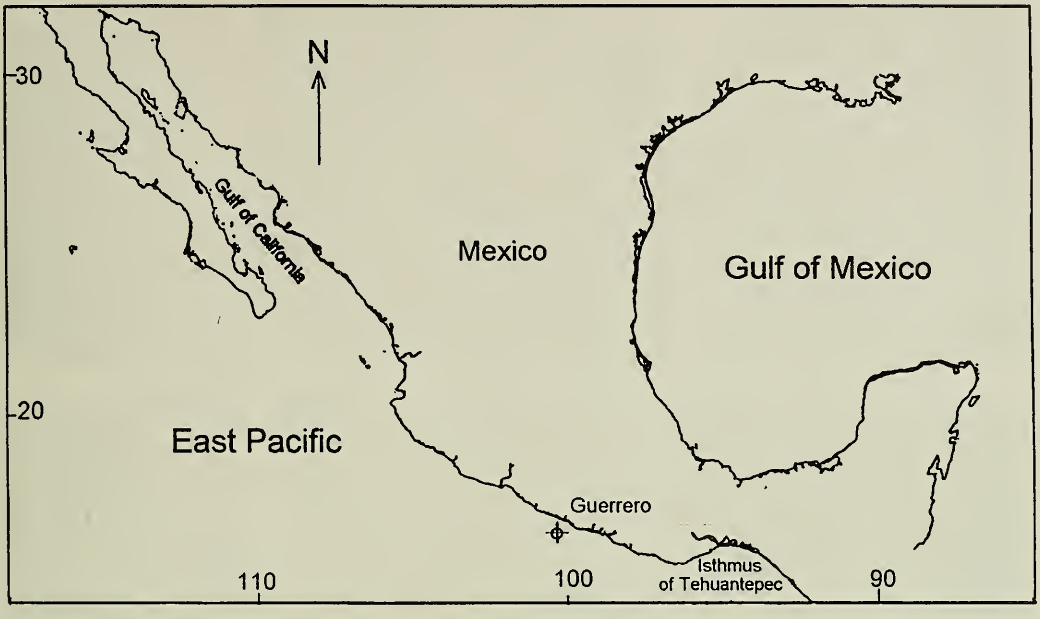

Fig. 1. Map showing collection site, Guerrero, Mexico, central East Pacific.

Gastrophanella primore, new species

Figs. 2A–I, 3

Material examined.—Holotype (USNM 51303), Guerrero, Mexico (16°15′24″N, 98°40′W).

Description.—Cup like, 3 cm high by 3.5 cm wide with an apical oval cavity that constitutes the atrium, 10 mm long by 4 mm wide by 14 mm deep, provided with a diaphragm 9 mm below the rim (Fig. 2A, B). Color: grey when alive, nearly white in spirit. Consistency hard; surface apparently smooth, rough to the touch. Oscula on the surface 500 μm in diameter and inside the atrium 90–180 μm. Barely visible ectosomal membrane with ostia 2.5 μm in diameter. Ectosomal skeleton (Fig. 2C, D) sieve-like with strong zygosed desmas, mesh sizes 62–127.5 μm in diameter, with monaxons (sub)tylostrongyles or (sub)tylostyles perpendicular to the surface, loosely interspersed among the desmas and with their tyles directed outwardly, reaching, at the base of the sponge, 11.5 μm beyond the surface. Choanosomal desma skeleton (Fig. 2E) with more tightly packed mesh than the ectosomal skeleton; monaxons continue traversing the body internally.

Spicules.—Desmas rhizoclone (Fig. 2F–H): 147-220.5-274 μm by 12-15-18 μm (minimum-mean-maximum); (sub)tylostyles to (sub)tylostrongyles (Fig. 3) with rugose tyles, occasionally rugose at both ends: 109-326-600 μm by 2.5-5.3-11 μm, tyle diameter (Fig. 2I) 5.8-8.4-11 μm.

Distribution.—So far known only from the type locality, off the coast of Guerrero, Mexico, East Pacific.

Etymology.—Named *primore* as it is the first species of the genus *Gastrophanella* found in the East Pacific [*primore* is the feminine of *primoris* (first) in Latin].

Ecology.—The type locality (Guerrero, Mexico) is characterized by considerable amounts of river runoff due to the outlets of several rivers. Three of the rivers are permanent, but the remainder are active only during the rainy season. The sponge was collected on a sandy bottom, adhering to fine grained calcareous material at a depth of 45 m. Temperature was 24°C and salinity was 34‰.

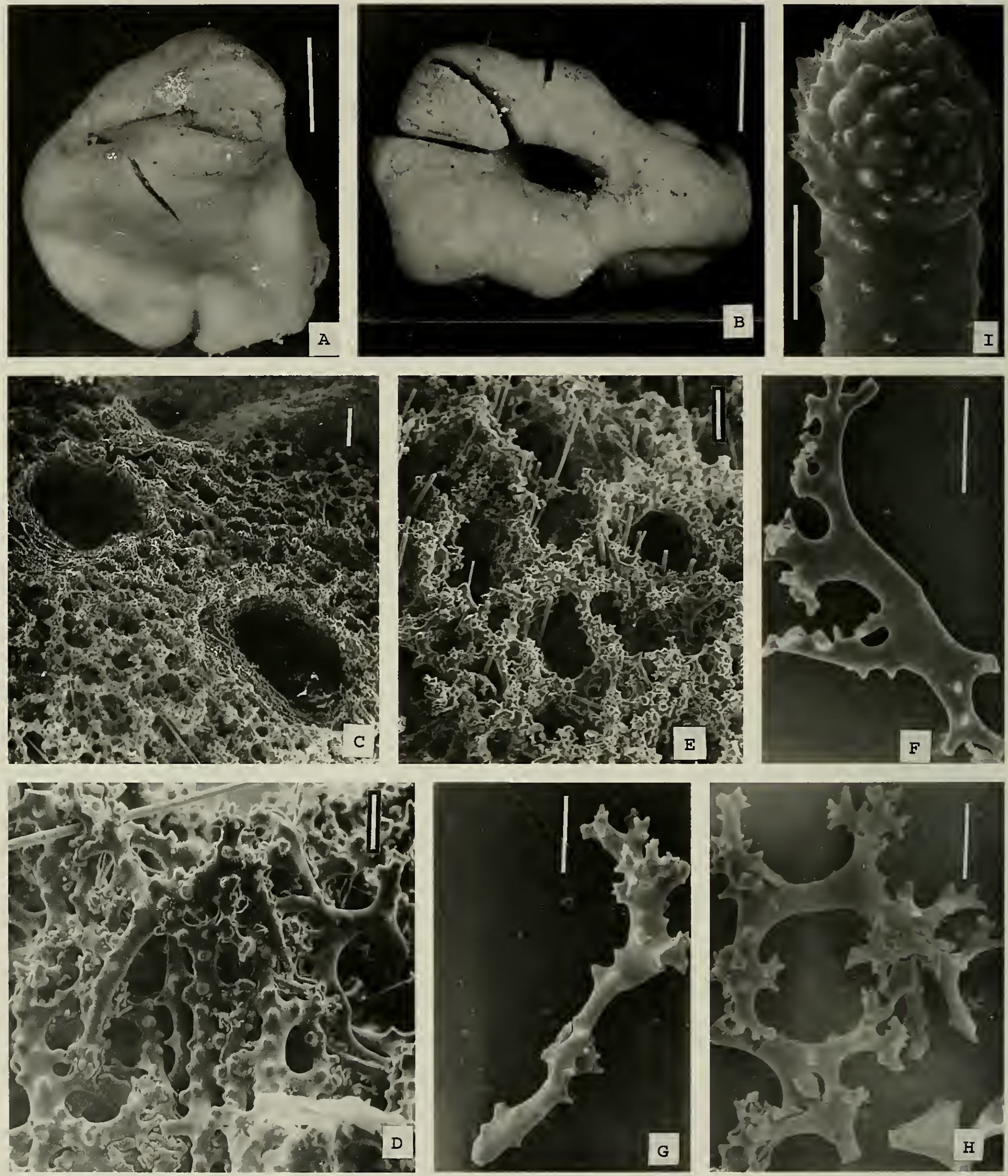

Fig. 2. *Gastrophanella primore*, new species: A, holotype habitus, lateral view; B, view from above showing atrium; C, SEM of peripheral skeleton showing ectosomal mesh and oscular morphology (40×); D, SEM of perpendicular section through peripheral skeleton (200×); E, SEM of choanosomal desma reticulum (94×), note broken perpendicular monaxons; F–H, SEM of desmas rhizoclone (400×, 320× and 300×, respectively); I, SEM of enlarged rugose tyle of tylostrongyle (4800×). Scale bars: A, B = 1 cm; C = 200 μm; D = 50 μm; E = 100 μm; F–H = 50 μm; I = 5 μm.

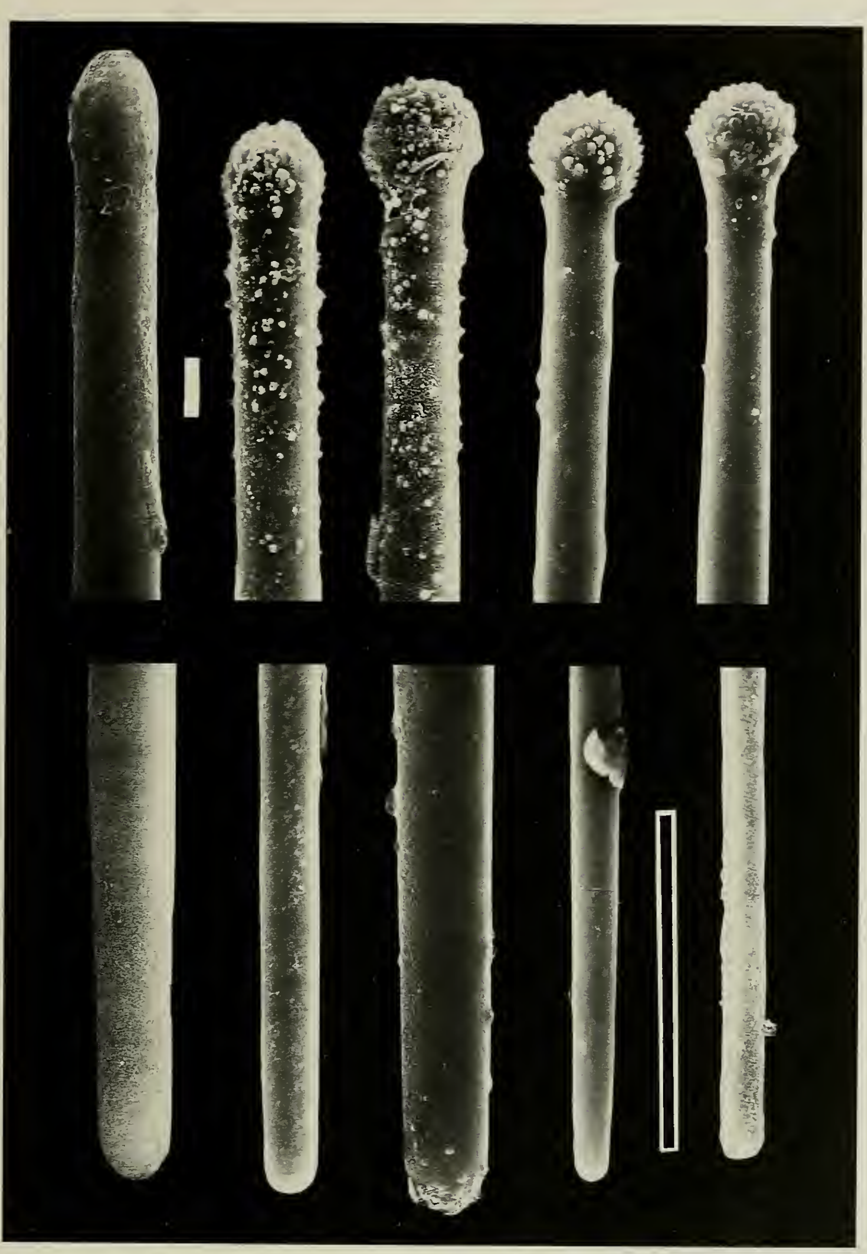

Fig. 3. *Gastrophanella primore*, new species: SEM of variations of monaxon: subtylostyles to subtylostrongyles and tylostrongyles (all same magnification, 2000×). Scale bar = 25 μm.

Discussion

The "order Lithistida" has been recognized as an artificial group, designated as *incertae sedis* by Lévi (1973) and other authors. Van Soest & Stentoft (1988) discussed the likely polyphyletic origin of different forms of this order, emphasizing the need for a revision of all lithistids. For this reason, the new species, *Gastrophanella primore*, is assigned only tentatively to the "order Lithistida."

Comparisons of *G. primore* with other species are as follows (see Table 1): *Gastrophanella implexa* Schmidt, 1879 sensu van Soest & Stentoft (1988:68), from the West Indies, is the closest species in external appearance, with its cup shape and tight-meshed choanosomal reticulum, as well as the zygoses of desmas, but differs in the desma shape, spicule bundles and overall measurements. *G. mammilliformis* Burton (1929:7), from South Africa, agrees in the shape of monaxons and desmas, but the shape of the habitus does not correspond to that of the Mexican species, nor does the size of the spicule types and presence of tylostrongyle bundles. *Siphonidium capitatum* Sollas (1888:317), from the Indo-Pacific, agrees in the perpendicular tylostrongyle arrangement and the outward direction of the tyles, its similar choanosomal desma and tylostrongyle type, but differs in its fistulose habitus and ramified ectosomal desmas, as well as in the diameter of the monaxons.

Lithistids occur in deep waters, 100 m to 250 m in average depth. From the most studied regions of the world, the southwest Pacific possesses a rich fauna of about 36 lithistids (taxonomic status unknown): 11 species from Kei Island, Fiji Islands and South Papua at depths of 250 m to 673 m (Sollas 1888), including two shallow-water species at 32 m and 60 m; two species from New Zealand at 108 m and 180 m (Bergquist 1968); and 23 lithistids from New Caledonia between 175 m and 570 m (Lévi & Lévi 1983, 1988). Similar lithistid diversity (32 species) has been reported for the West Indies: 22 species from Cuba, Lesser Antilles and Florida Keys at depths of 100 m to 1450 m (Schmidt 1879, 1880), and 17 valid species, including seven also recorded by Schmidt, from Barbados and other West Indian localities at depths of 100 m to 200 m (van Soest & Stentoft 1988). This contrasts with the single lithistid *Corallistes isabela* Desqueyroux-Faúndez & van Soest 1997, reported in the central East Pacific, even though deep-water sponges have been

Table 1.—Comparison of *Gastrophanella primore*, new species with other species of lithistids (length/diameter measurements in μm, depth in meters).

Species	Locality	Shape	Monaxons	Desmas	Depth/bottom type
G. implexa Schmidt 1879	Florida Cays	Tube	480/5	100/19–27.5	182–228/not given
G. implexa van Soest & Stentoft 1988	Barbados	Cup	200–395/3–6.5	150–220/20–25	153/carbonate, biogenic
G. mammilliformis Burton 1929	South Africa	Pear, base expanded	524/16	108/32–60	90–180/not given
S. capitatum Sollas 1888	Indo-Pacific	Fistulose	420–570/5	280/not given	252/blue mud
G. primore n. sp. Present work	Central East Pacific	Cup-like	109–600/2.5–11	147–274/12–18	45/sand-gravel

collected from the East Pacific: cold temperate waters of Southern California, U.S.A. between 0 m and 1865 m (de Laubenfels 1926, 1932; Bakus & Green 1987; Green & Bakus 1994), the warm temperate Gulf of California in 92 m to 240 m (Dickinson 1945), and the tropical waters from the Mexican Pacific coast to Central America in 95 m to 4433 m (Wilson 1904, Desqueyroux-Faúndez & van Soest 1996). Indeed, further studies of lithistids in this region are needed to determine whether lithistids are scarce along the central East Pacific.

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Asexual reproduction in *Linuche unguiculata* (Swartz, 1788) (Scyphozoa: Coronatae) by planuloid formation through strobilation and segmentation

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Abstract.—Scyphistomae of *Linuche unguiculata* from São Paulo State, Brazil, were reared for one year to study the life cycle of this warm-water species (in subtropical western South Atlantic waters). We found *L. unguiculata* reproduces more by the development of planuloids than by medusae. The scyphistoma is rejuvenated by an operculated regression-regeneration cycle. We hypothesize that reproduction of the species by production, either via segmentation or strobilation, and liberation of planuloids explains the absence of reports of ephyrae and medusae in the area.

Jarms (1997) reviewed the history of knowledge about scyphistomae of Coronatae. The only records of coronate Scyphozoa from the Brazilian coast are of the medusa stage of *Nausithoe punctata* Kölliker, 1853, from the north of Bahia State (Goy 1979) and material recorded during study of the life cycle of *Nausithoe aurea* Silveira & Morandini, 1997, from the north of São Paulo State. Silveira & Morandini (1996) redescribed the scyphistoma of a coronate, *Stephanoscyphistoma corniformis* (Komai, 1936), from the south-east Brazilian coast. The present study on the life cycle of *L. unguiculata* was undertaken over a 14 month interval. Observations were based on cultures of the scyphistomae from southeast Brazil.

We found colonial coronate scyphistomae (presumed to be *L. unguiculata*) frequently in São Sebastião Channel, and we asked: why are there no records of medusae or of any dermatitis caused by their planulae? We presumed three possible explanations to account for this: the ephyrae belong to suprabenthic communities and are transported to distant places, so that medusae of this species are not found near the coast; *L. unguiculata* typically passes intervals of many years between periods of production of large numbers of medusae (Russell & Tomchik 1993, Black et al. 1994); therefore it would not be strange that between these periods the probability of finding medusae were very small; the species was not *L. unguiculata*, although the characters of the periderm tubes of our material were similar to that reported in the species.

Our field observations were that no ephyrae/medusae occurred in plankton or suprabenthic samples during 1 yr and our laboratory observations were that few polyps strobilated producing a small number of ephyrae, but many planuloids were produced together with segmentation of other scyphistomae. Thus, few ephyrae were produced, which supports the second explanation.

Material and Methods

Colonial scyphistomae (Fig. 1) were sampled from calcareous debris, mainly fragments of the stony coral *Mussismilia hispida* (Verrill, 1902) (Scleractinia, Mussidae) at 2–6 m depth by SCUBA diving, in São Sebastião Channel (23°50′S,

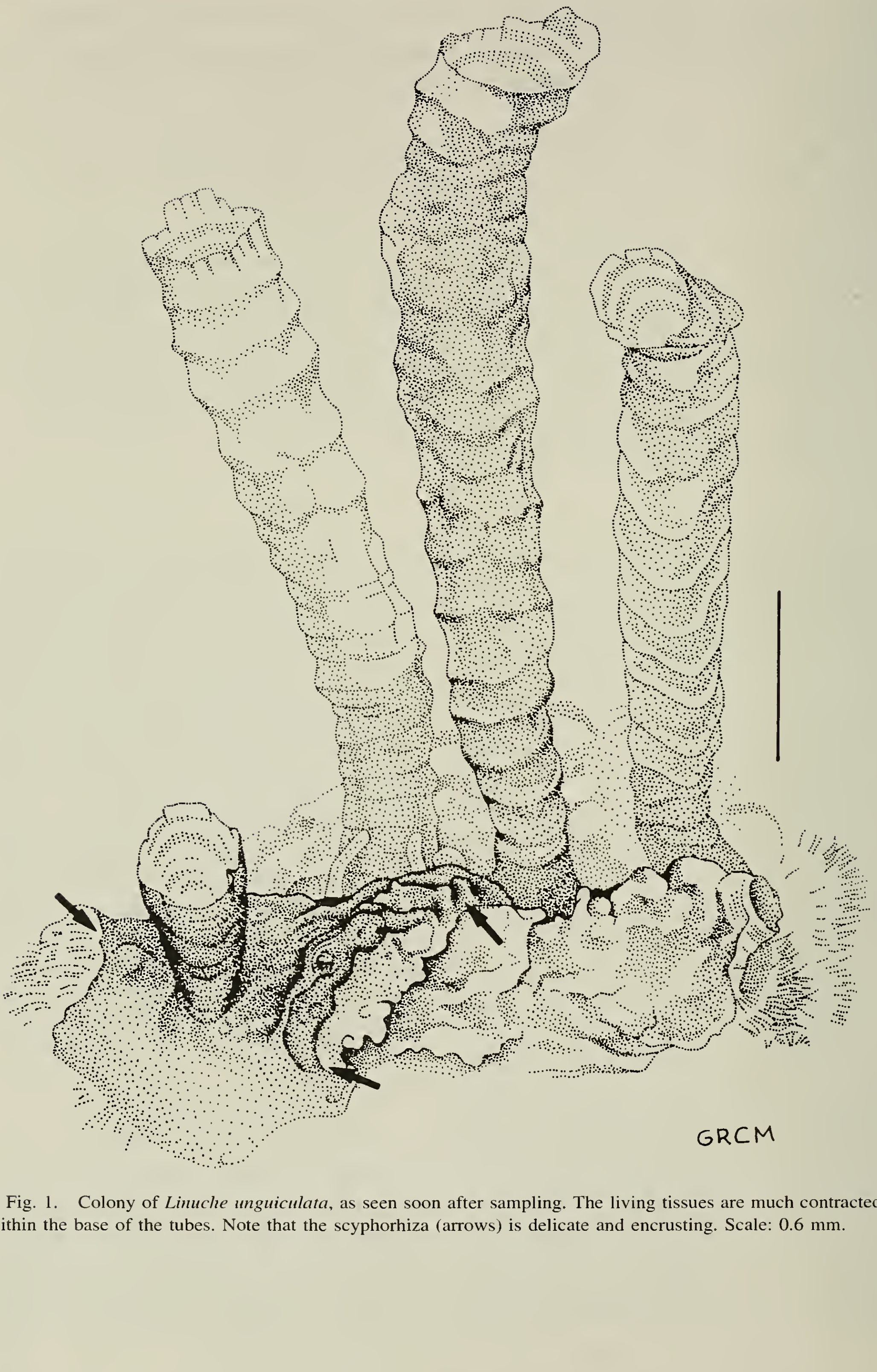

Fig. 1. Colony of *Linuche unguiculata*, as seen soon after sampling. The living tissues are much contracted within the base of the tubes. Note that the scyphorhiza (arrows) is delicate and encrusting. Scale: 0.6 mm.

Fig. 2. Colony of *Linuche unguiculata*. The oral discs of the scyphistomae are partly or fully extended. Scale: 1.25 mm.

45°25′W), of the rocky shore at Urubu Point and on Praia Grande reef, Ilhabela County, SP. Sampling was done on one or two days of every month, except August, from June 1996 until May 1997. We searched for the colonies on lumps of the calcareous substratum collected, with the aid of a stereomicroscope. Each monthly sample included a minimum of 15 colonies, each with 2 to 8 living polyps (Fig. 2). The colonies were transferred into and maintained in small Petri dishes containing about 70 ml of filtered sea-water. At least twice a month, the colonies were cleaned by gentle rubbing with a delicate brush or by removing the many filamentous algae with fine forceps.

In each search for medusae or ephyrae,

three plankton and suprabenthic faunal samples were taken on three consecutive days following the sampling of calcareous debris. Twenty-minute tows were made in the vicinity of the sampling sites of the debris with a plankton net and a dredge (the last equipment according to Wakabara et al. 1993) at a depth of 5 to 10 m, both with 0.5 mm stretch mesh, using a small outboard motor boat. Two divers followed the equipment to maintain the plankton net at 3 m below the surface and to prevent the dredge from being clogged with bottom sediments.

The scyphistomae reared in the Centro de Biologia Marinha da Universidade de São Paulo (CEBIMar USP), at São Sebastião, SP, were treated as follows. From 6 June to 25 July 1996 all colonies were kept at room temperature (18°C–28°C) and from 1 April to 7 June 1997 half were kept at room temperature (21°C–30°C, although during 24 h the temperature range never exceeded 4°C) and one-half were treated with temperature changes, 18–27–18°C (based on the monthly averages of surface water temperature for winter and summer in the area), at 7-day intervals and $^{1}/_{23}$ h light/dark regime inside an incubator (FANEM® 347-CDG). The scyphistomae reared in the Zoology Department (IB, USP), at São Paulo, SP, were treated as follows. From 26 July 1996 to 11 June 1997 the June–February samples were kept at controlled temperature (August–mid February a monthly increase of 1°C starting at 21°C; mid February–June, a monthly decrease of 1°C starting at 26°C—following the natural surface water temperature monthly averages) and $^{6}/_{18}$ h light/dark regime inside an incubator. The sea water was changed and the animals were fed every other day with a deep-frozen stock of homogenate of the clam *Perna perna* (Linnaeus, 1767) (Bivalvia, Mytilidae). Some of the specimens collected in April 1997 were used to measure the periderm tube (total length, diameter at aperture and base), and the internal cusp was examined in 42 polyps.

Free-swimming ephyrae, from strobilating scyphistomae, were transferred into single airtight pots (universal samplers for medical analysis ZESTER® 140 ml). They were fed from a deep-frozen stock of homogenized clam gonads. The ephyrae and medusa were fed every day. They were individually immersed in the homogenized food, observed under a stereomicroscope until their stomachs were full, and removed to a new pot with clean filtered sea water.

Free-swimming planuloids (samples of March, April and May 1997), produced by strobilating or from segmenting scyphistomae, were transferred into single dishes, at 24 h intervals, for further observations.

We studied the cnidome of live specimens and of specimens preserved in seawater-formaldehyde solution. In preserved tissues, only undischarged nematocysts were measured.

Voucher specimens are: National Museum of Natural History, Smithsonian Institution (USNM 99376, 99377); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP 12.355, 12.356); Museu Nacional Universidade Federal do Rio de Janeiro, Brazil (MNRJ 3126, 3127, 3128); The Royal Ontario Museum, Canada, Invertebrate Zoology (ROMIZ B3010, B3011); The Zoölogisch Museum, University of Amsterdam, The Netherlands, (ZMA Coel. 8507, 8508); Zoölogisches Museum, Universität Hamburg, Germany, (ZMH C11639, C11640, C11641); and The Natural History Museum, United Kingdom, (NHM 1998.145, 1998.146).

Results

We found no ephyrae or medusae of *Linuche unguiculata* in plankton and suprabenthic samples. During June 1996–June 1997, over 240 scyphistomae were reared in the Zoology Department, at São Paulo City, but none of them strobilated. Nevertheless, on many occasions we observed that some scyphistomae produced a periderm operculum closing the tube. The oral disc and the gastric septa of those scyphistomae regressed, but the column remained and they were able to contract and extend within the tube. We followed some closed tubes over a varied period of 1–3 d, at the end of which the operculum opened and the polyp regenerated septa and the oral disc.

During the period late March–June 1997, among 559 scyphistomae (some 130 colonies) reared at room temperature in CEBIMar, only 6 strobilated (two in the same colony) and 3 segmented irregularly.

At the start of strobilation, the polyp resorbed the oral disc, the strobilating region occurred over most of the column, disc number varied from 8 to 17, and no operculum, of either periderm or tissue was present. Initially, the discs were set well apart and the remaining column tissues between them were bulged. From a few hours to 3 d, the discs changed into irregular tissue fragments and most of the remaining and interconnecting column tissues constricted. Only the distal disc enlarged and metamorphosed into an ephyra (Fig. 3), while the other discs directly transformed into planuloids. Among the six strobilae, five released one ephyra each and in another the ephyra transformed into a planuloid within the tube. Release of the ephyra (Fig. 4) varied from 1 to 3 d after onset of strobilation (Table 1). The earliest stage at which the ephyra acquired noticeably medusa-like characters was at about 5 mm in diameter (specimen 8, Table 1). The gonad primordia were four pairs of radiating tissue cords on each side of the perradii. At about 47 d, each gonad pair had fused giving rise to four cleft crescents (Fig. 5). This medusa had an anomalous number of lappets due to an injury at early ephyra stage (fourteen lappets, two perradial pairs being fused, Fig. 5). Most of the zooxanthellae were irregularly distributed within the gastrodermis, in side view mostly below the coronal groove (Fig. 5) and in the corners of the lips of the manubrium. The lappets were round, and slightly overlapping in an orderly fashion, which made the medusa rotate clockwise upon its oral-aboral axis while swimming. The short, translucent tentacles were situated within the clefts between the lappets. The eight conspicuous rhopalia were directed outward while the medusa was at rest or downward during contraction of the bell. The ephyrae of the remaining material were preserved before reaching the medusa stage (Table 1).

At the start of segmentation, the polyp resorbed the oral disc and produced a periderm operculum, it acquired a transverse segmenting region over most of the column, and the segments tended to become spherical in shape. In one colony we observed that in one operculate scyphistoma many planuloids appeared by irregular segmentation. These fused together to restore the column of the polyp, but without differentiation of septa and oral disc (see sequence in Figs. 6, 7). Thus, the process lasted until the end of April. In some colonies, we noted that after a few weeks, near the operculum margin, a fissure developed through which a few planuloids could emerge (Fig. 8). The crack was apparently caused by the egress of the planuloids.

The measurements, length of the tubes and diameter at the base and at the aperture, are: 1.8–12.7 mm, 0.12–0.49 and 0.25–0.68 mm. Most tubes had one cusp; none, two or three were less frequent. The cusps were cup-shaped, with longitudinal ridges, mainly at the broad round margin (Fig. 9). The axis of the cusp base outline was long, narrow, and parallel with the long axis of the tube, whereas the proximal end was bulging and circular (Fig. 9).

Liberated planuloids were elliptical, swam actively by cilia, and had transparent epidermis and a gastrodermis with many zooxanthellae. Two planuloids (from specimen 8, Table 1) settled on the bottom of a small Petri dish on 27 May and 01 June respectively and were reared for 58 and 54 d. Each zooxanthellate polyp had five tentacles within 3 d. Each produced a delicate cylindrical tube, without branching and without cusps.

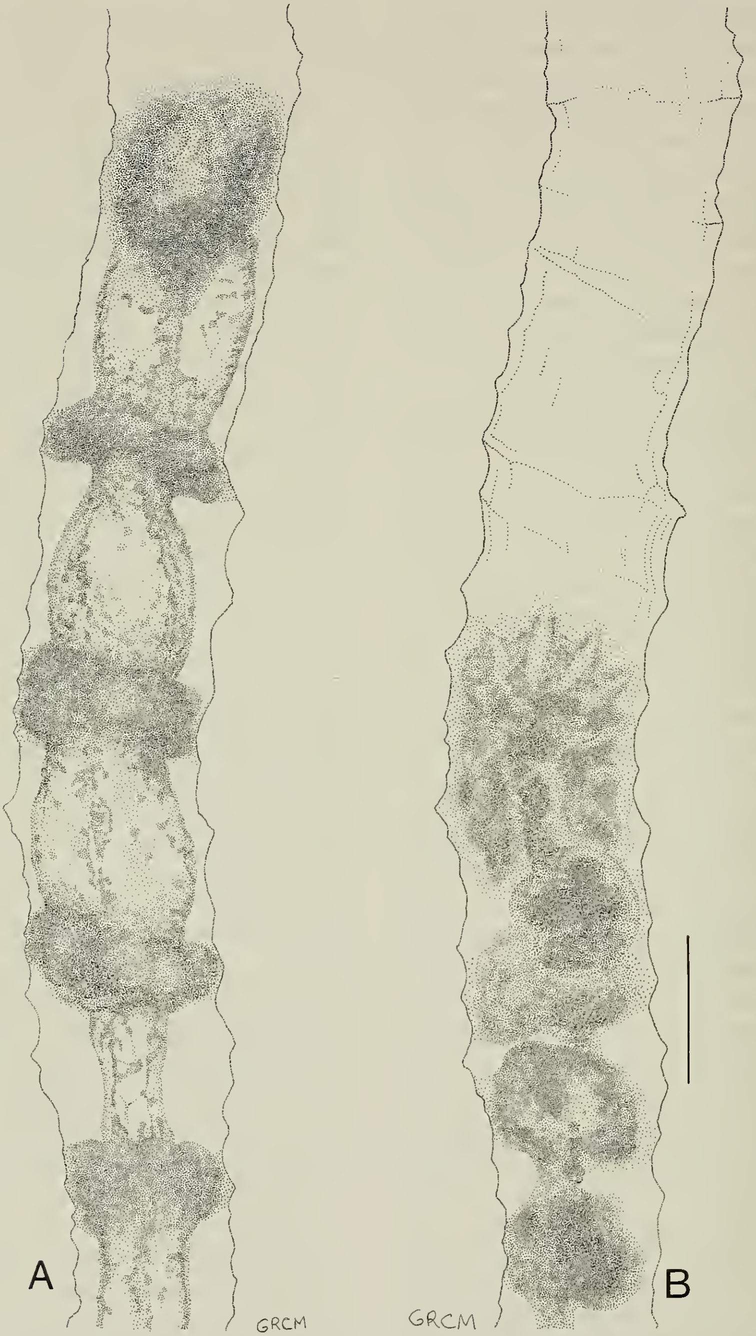

Fig. 3. Strobila of *Linuche unguiculata* (April 1997). A, early strobilation phase, at 24 h, in which the connections between the discs narrow and the distal disc is bigger; B, late strobilation phase, at 72 h, in which the distal disc has differentiated into an ephyra and the remaining ones into planuloids. Scale: 0.6 mm.

Fig. 4. Ephyra (oral view) of *Linuche unguiculata*, two days after release from the strobila. Note the many zooxanthellae. (From photomicrograph). Abbreviations: cg = coronal groove, gf = gastric filament, r = rhopalium, z = zooxanthellae. Scale: 0.6 mm.

Scyphistomae, planuloids and ephyrae (Table 2) all had holotrichous isorhizas and heterotrichous microbasic euryteles nematocysts.

Discussion

Our original assumption was that the colonial coronates in São Sebastião Channel were *Linuche unguiculata*, considering the morphology and number of the internal cusps within the tube. The cup-shaped cusp is diagnostic of polyps of *L. unguiculata* (Leloup 1937, Ortiz-Corp's et al. 1987, Jarms 1991). Moreover, the size and proportions of the periderm tubes were within the ranges of *L. unguiculata* studied by Leloup (1937), Allwein (1968) and Ortiz-Corp's et al. (1987). The original description of the species was based on the medusa stage (Swartz 1788) and it is wise to study both stages in the life-cycle to make a precise identification (Jarms 1990, 1991). Werner (1979) was first to link the polyp stage of *Stephanoscyphus komaii* with the medusa *L. unguiculata*.

The lack of either ephyrae or medusae in plankton and suprabenthic faunal samples had been difficult to explain. Their absence was evidently due to the asexual reproductive modes employed locally—direct transformation of strobilating discs and segmentation originating planuloids, newly reported reproductive strategies for *L. unguiculata* and novelties for coronates. Arai (1997:166) defined strobilation as the process by which scyphistoma produces

Table 1.—Observations on 8 colonial scyphistomae of *Linuche unguiculata.* Abbreviations: St-e—length of period of strobilation (ds) originating ephyrae, St-p—length of period of strobilation (ds) originating planuloids, Se—length of period of segmentation (ds), E—ephyra development (ds), E/M—observations (ds) of ephyrae and medusa.

Scyphistoma (sample month)	1 (Jun 96)	2 (Mar 97)	3 (Mar 97)	4 (Mar 97)	5 (Mar 97)	6 (Mar 97)	7 (Mar 97)	8 (Apr 97)
St-e	3	2 and 1	—	—	—	—	1	2
St-p	7	8 and 1	—	—	7	—	5	7
Se	—	—	8	7	—	10	—	—
E	—	—	—	—	—	—	—	30
E/M	36	2[a] and 38	—	—	—	—	27	54

[a] The ephyra was preserved to study the cnidome.

ephyrae: "This requires disc formation ('segmentation') leading to fission, and also metamorphosis in which structures of the polyp are lost and replaced in each disc with those of the developing ephyrae." Therefore, the word segmentation in this work applies to the transverse fission of the scyphistoma, within an operculate tube, comparable with the strobilation in which all discs metamorphose into ephyrae. Wer-

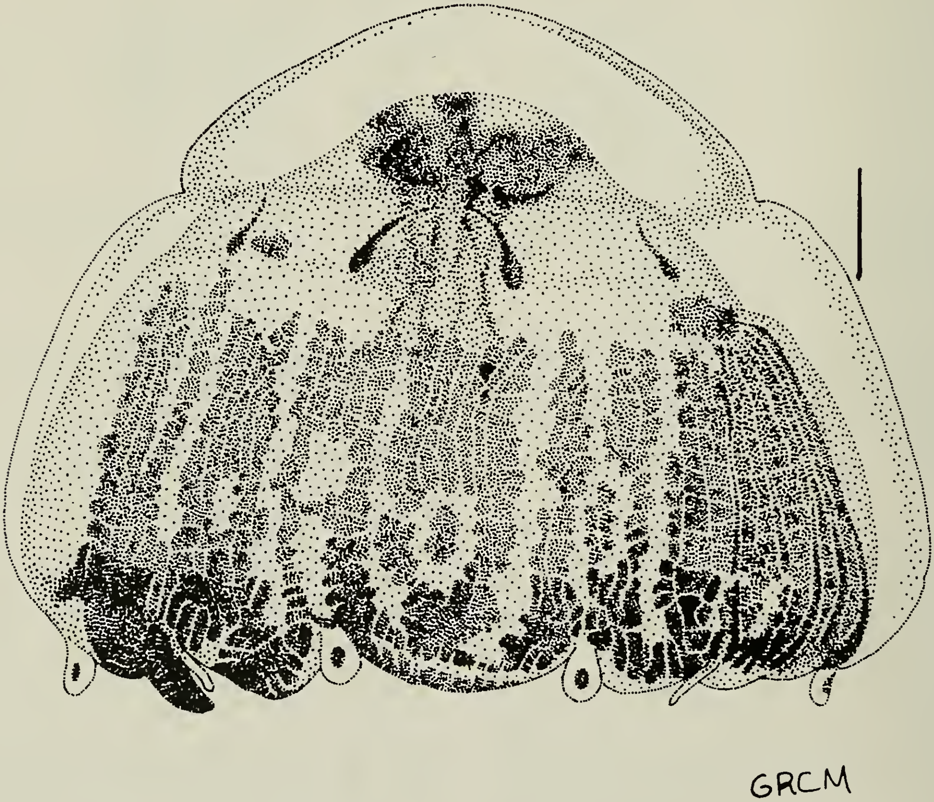

Fig. 5. Young medusa of *Linuche unguiculata.* The animal is shown in side view, to show the dark pattern due to the zooxanthellae in the gastrodermis and the arrangement of the paired gonads in cleft crescents. Note that the nearest lappet is enlarged as result of injury and later fusion of two original lappets. (From life and close-up VHS). Scale: 1 mm.

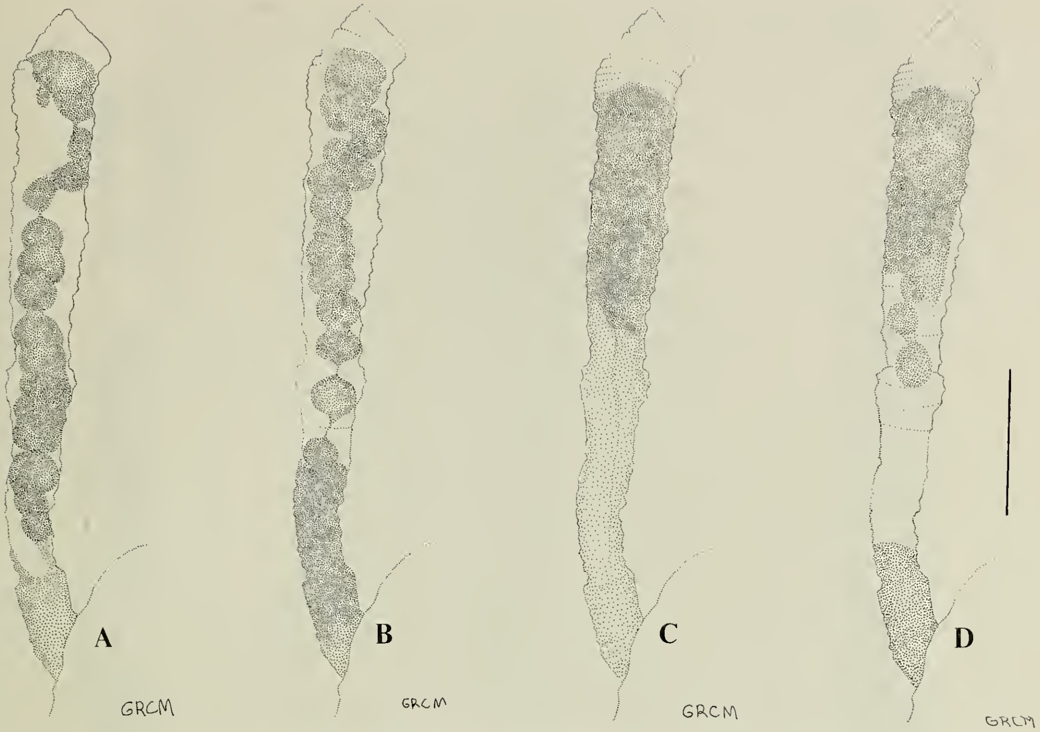

Fig. 6. Colony of *Linuche unguiculata* undergoing segmentation. A, planuloid formation (3.IV.97); B, planuloids almost distinct and the distal ones fused together (4.IV.97); C, regeneration of the column of the polyp starts by fusion of planuloids (dark areas) and the stretching of basal tissues (9.IV.97); D, contraction of the basal tissues, upon stimulation with a forceps, showing that the distal planuloids are entirely fused together (9.IV.97). Scale: 1.25 mm.

ner (1973) reviewed the known variation of the operculum in the scyphistomae of Coronatae. The only paper with a thorough account of the strobilation of *L. unguiculata* is that of Ortiz-Corp's et al. (1987). They observed the process in Puerto Rico, at temperatures of 25–28°C (December–May) and 28–30°C (June–November), for 7 yr. They noted strobilation once a year, sometimes within an operculate tube, with the production of free-swimming ephyrae. Werner (1979) also accounted for the annual strobilation of *L. unguiculata* under laboratory conditions. Werner (1979:94) hypothesized that for the colonial coronates "... their strobilation activities are genetically fixed to one distinct short season." He argued that the surplus of energy stored by the polyps is available for colony growth, in place of consecutive strobilation within one year the way solitary coronates are likely to do.

Jarms (1997) reported shortened life cycles of five species of Coronatae, the transformation of free ephyrae into planuloids and these into new polyps, due to unfavorable conditions of salinity, temperature or food supply. Planuloid formation by transformation of free ephyrae within the tube is known in the solitary *Nausithoe planulophora* (Werner 1971, Werner & Hentschel 1983, Jarms 1997) and *N. aurea* (Silveira & Morandini 1997), and by parthenogenesis in *Thecoscyphus zibrowii* (Werner 1984). A unique feature we have observed is the differing destiny of discs from the same strobila—one ephyra and many planuloids—with differing regulative mecha-

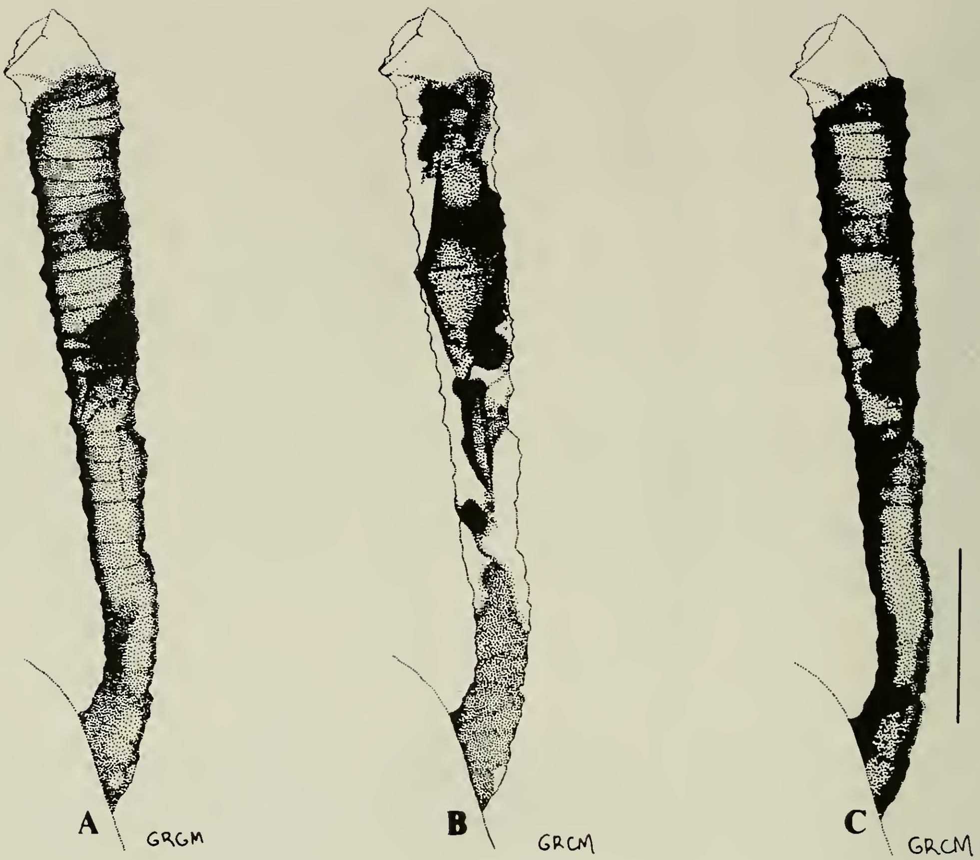

Fig. 7. Colony of *Linuche unguiculata* undergoing segmentation. A, the column of the polyp is almost entirely regenerated (13.IV.97); B, contraction of the tissues, upon stimulation with a forceps, to show that there is integration between the regenerated pieces, but that the column as a whole does not contract (13.IV.97); C, column totally regenerated, but the dark areas indicate the remains of fusing planuloids (14.IV.97). Scale: 1.25 mm.

nisms for each developing structure. Following the reasoning of Jarms (1997:275) on planuloid formation by *N. planulophora*, we believe the planuloids of *L. unguiculata* must be an alternative dispersive stage, since we have observed settlement and development of two new colonies. We hypothesize that segmentation is an advanced trait derived from the peculiar strobilation, with the addition of the operculum, perhaps the most derived response to the regulation of asexual reproduction in the species. *L. unguiculata* is a warm-water species (Mayer 1910, Kramp 1961, Ortiz-Corp's et al. 1987), and we have observed a new reproductive mechanism of the species to adapt to a subtropical area in which there is a marked influence of both warm and cold water masses (see Campaner 1985). The absence of ephyra and medusa from plankton and suprabenthic samples is thereby explained.

The ephyrae (Fig. 4) and the young medusa (Fig. 5) closely resemble the descriptions of the adult medusa of *L. unguiculata* (Mayer 1910, Ortiz-Corp's et al. 1987). The medusa illustrated in the present paper resembles the developmental stage that Mayer (1910:559) described "that the gonads appear when the medusa is about 5 mm wide." The arrangement of the gonads and the shape and coloration of the umbrella are

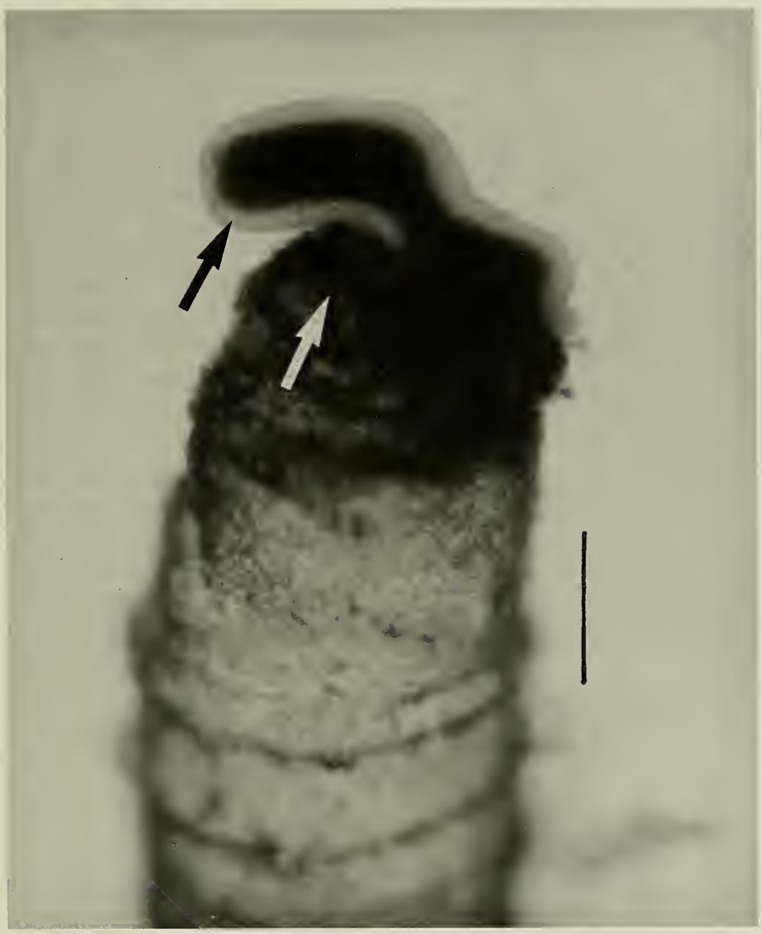

Fig. 8. Photomicrograph of the scyphistoma periderm tube of *Linuche unguiculata*, distal end and with operculum (white arrow). Note that one planuloid (black arrow) has emerged and rests upon the operculum. Scale: 0.3 mm.

Table 2.—Measurements of cnidae of cnidome of *Linuche unguiculata*. The range was taken from 20 nematocysts of each type at each stage, except the underlined measurements taken from only 9 nematocysts.

	Holotrichous isorhiza (μm)	Heterotrichous microbasic eurytele (μm)
Scyphistoma	10-6 × 6-4	17-14 × 14-11
		13-07 × 10-05
Ephyra	7-5 × 4	15-14 × 14-12
		13-09 × 12-08
Planuloid	7-6 × 5-4	17-14 × 14-12
		13-09 × 12-07

diagnostic for the species. The difficulty of obtaining the strobilae and the ephyrae-medusae reflects the prevailing asexual reproduction. The cnidome of scyphistoma, ephyra and planuloid are the same as recorded by Calder (1974) and Ortiz-Corp's et al. (1987) in medusae of *L. unguiculata*. The differences between our data may result from comparing different stages for the species. We followed Calder (1974) in separating the heterotrichous microbasic eurytele nematocysts into two size-classes, though they are almost one continuous size class.

There are some indirect indications, ei-

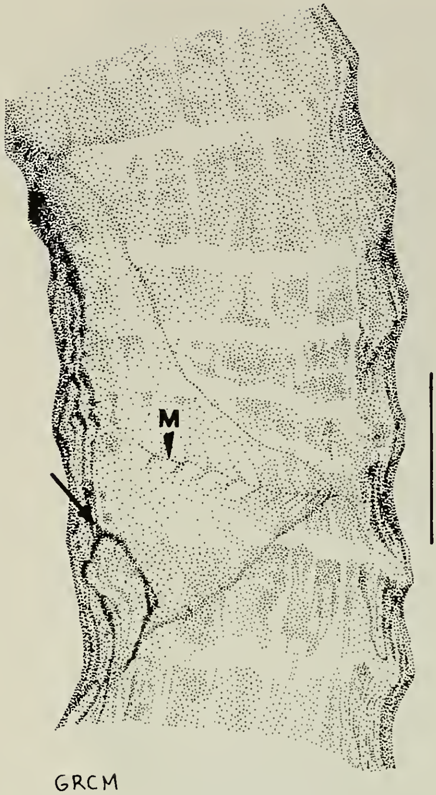

Fig. 9. Segment of periderm tube of *Linuche unguiculata* showing an internal cusp (since some had 2–3). Arrow points to the base of the outline of the cusp. Note that at the broad round margin (M) there are ridges. Scale: 0.3 mm.

ther in the swarming of the medusa (Larson 1982, Ortiz-Corp's et al. 1987, Halstead 1988), as well as in the outbreaks of their planulae (Russell & Tomchik 1993, Black et al. 1994), that in nature *L. unguiculata* strobilates seasonally (winter–spring) and the adult medusae occur in spring and early summer in the Caribbean, Atlantic coast of Florida, and the Bahamas. Although some authors report concentrations of medusae of *L. unguiculata* (Table 3), only two medical incidents (dermatitis) linked with the medusae of this species have been reported in the literature (Penner 1962). Black et al. (1994) associated seabather's eruption—SBE—with planulae of *L. unguiculata* in Florida. Russell & Tomchik (1993) and Black et al. (1994) summarized outbreaks of SBE in Florida. They argued that there may be an interval of up to 25 yr, between major outbreaks. Nevertheless, Williamson et al. (1996:308–310) stated that the dermatitis SBE, besides having other names, is caused by different organisms in distinct regions. We hypothesize that *L. unguiculata* is a species with a long life-cycle mainly resulting from the long duration of the scyphistoma stage. Under variable conditions, this warm-water species may present an efficient colonizing ability by the scyphistoma that undergoes asexual reproduction and propagation.

The oral disc regression-regeneration process we observed in operculate scyphistomae on many occasions has never been reported in any coronate. This mechanism may be considered analogous to observations on some leptolid polyps, e.g., *Thyroscyphus marginatus* (Harris 1990, and see revision in Crowell 1991). Tardent (1963) hypothesized that a regression-regeneration cycle in the hydranths of colonial leptolids would be a natural histophysiological rejuvenation mechanism for the colony, by extension a possible pattern for some species to secure perennation (sensu Cornelius 1992) in specific habitats. Nevertheless, it

Table 3.—Occurrence of swarms of medusae of *Linuche unguiculata* in Florida, the Caribbean and the Bahamas, from different sources.

Occurrence	Date	Author
Miami (Florida)	April 1950	Penner 1962
Sarasota (Florida)	July 1954	Penner 1962
Boca Grande (Florida)	July 1955	Penner 1962
Carrie Bow Cay (Belize)	Mar/Apr 1987; April 1988; Mar/Apr 1990	Larson 1992
The Bahamas	April/May 1989	Montgomery & Kremer 1995

remains an open question whether this process in laboratory observations really occurs under natural conditions (see revision in Hughes 1987).

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Acteonina permiana, a new species from the Permian Coyote Butte Formation, central Oregon (Mollusca: Gastropoda: Actaeonidae)

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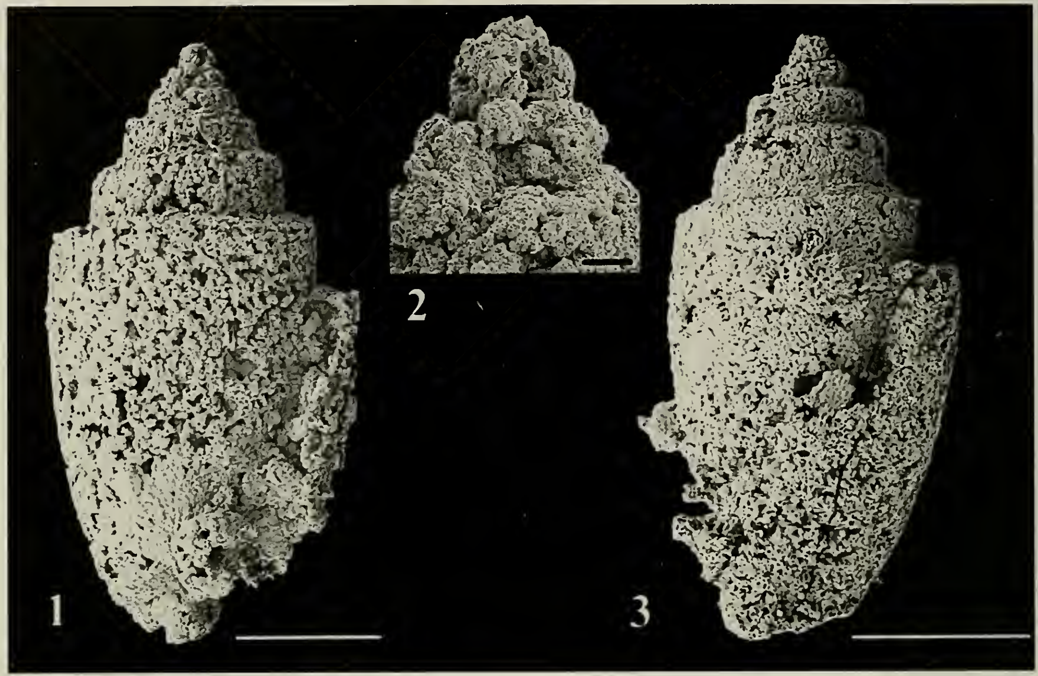
Abstract.—*Acteonina permiana*, is described from the Early Permian Coyote Butte Formation of Crook County, central Oregon. Occurrence of *Acteonina* indicates affinity with the Carboniferous to Permian Boreal faunal province, and implies that the Grindstone terrane need not have an "exotic" origin thousands of kilometers from the North American continent during the Permian.

Acteonina is among the rarest of all Upper Paleozoic gastropod genera. Knight (1932, 1936, 1941) counted only two known specimens, both from the Visean of Belgium. In their survey of Paleozoic opisthobranch gastropods, Kollmann & Yochelson (1976) point out that the genus, *Acteonina*, ". . . has not yet been found in North America in spite of careful search among large collections of Pennsylvanian and Permian gastropods." Acid etching of limestone samples from the Early Permian (Wolfcampian-Leonardina) Coyote Butte Formation of central Oregon has produced many new taxa (Hengstenberg et al. 1997), including four specimens of the new species, *Acteonina permiana.*

The presence of *Acteonina* in Oregon has important implications for western North American terrane paleogeography. The Coyote Butte Formation is part of the Upper Paleozoic–Mesozoic Grindstone terrane of central Oregon (Wardlaw et al. 1982), and occurs as chaotically intermixed limestone blocks within cherts and volcaniclastics. The limestone is interpreted as slide and slump blocks that became detached from a carbonate shelf and incorporated into deeper-water basinal clastics in a forearc basin (Blome & Nestell 1991). The exact dimensions of this basin, and specifically the longitudinal separation of this island arc from the North American mainland remain controversial, and distances of greater than 5000 km with southern hemisphere origins have been hypothesized (Jones 1990, Miller et al. 1992).

The Coyote Butte Formation fauna has been only partially described: brachiopods (Cooper 1957); fusulinids (Skinner & Wilde 1966), colonial rugose corals (Stevens & Rycerski 1983) and conodonts (Wardlaw et al. 1982). Acid etching reveals the presence of many undescribed gastropods, bivalves, chitons, rostroconchs, nautiloids, bryozoans, sponges, trilobites, ostracods and annelids. A detailed paleobiogeography, incorporating the paleoecological framework, is desirable, but much basic taxonomic work needs to be completed on these important taxa.

Of the described fauna, the fusulinids and corals have thus far been most useful for paleobiogeographic comparison. The colonial rugose corals are part of a "*Thysanophyllum* Belt" fauna that existed along the northern and western margins of Pangea, but Stevens and Rycerski (1983) suggested



Figs. 1–3. *Acteonina permiana*, new species, from the Coyote Butte Limestone, Crook County, Oregon. 1, Holotype USNM 498736. Bar is 1 mm; 2, Holotype USNM 498736, close-up of protoconch, showing heterostrophic larval whorl. Bar is 100 μm; 3, Paratype USNM 498737. Bar is 1 mm.

that the Coyote Butte fauna might have existed several hundred kilometers west of the margin based upon high Otsuka coefficient similarity with known exotic terranes. Fusulinids suggest a position at equatorial latitudes and many hundreds of kilometers west of the Permian North American margin (Ross and Ross 1983).

Presence of the only other species, *A. carbonaria*, in the plate-bound basins of Belgium suggests a northern hemisphere position for the Coyote Butte Formation and general affinity with the Carboniferous–Permian Boreal fauna. Biogeographic evidence from so small a sample size is tenuous, but corroborates preliminary paleomagnetic evidence (Harbert et al. 1995) of a northern hemisphere position for the Oregon Blue Mountains region. Long distance transport of the Grindstone terrane is not required for this distribution.

Systematic Paleontology

Family Actaeonidae d'Orbigny, 1842
Genus *Acteonina* d'Orbigny, 1850
type species *Acteonina carbonaria*
(DeKoninck, 1843)
Acteonina permiana, new species
Figs. 1–3

Diagnosis.—Very small (less than 4 mm length), shell outline like modern genus, *Conus*, with turret-stepped spire, elongate aperture, heterostrophic larval shell and columella with plica.

Description.—Small for genus; subcylindrical outline, superficially resembling *Conus*; flat whorl profile and rectangular sutures, producing a turreted spire; broad sutural ramp; narrow aperture, shallowly expanded at base; concave, plicate columella; heterostrophic larval whorl (Fig. 2).

Depository.—Four silicified specimens

are housed in the collections of the Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Type specimens include: USNM 498736 (holotype), USNM 498737 (paratype). The two other specimens (USNM 498738, USNM 498739) are fragments of turreted spires that also have the sutural ramp and five whorls.

Measurements.—USNM 498736 (holotype, Figs. 1, 2): length—4.10 mm, width—3.61 mm, whorl number—6. USNM 498737 (paratype, Fig. 3): length—2.15 mm, width—1.66 mm, whorl number—5.5.

Discussion.—The other species of the genus, *A. carbonaria*, is about two times the length of *A. permiana.* Whorl counts are the same for both species so we are not comparing juveniles of the Permian with adults of the Carboniferous. The acid etched residues from the Coyote Butte Fm. contain species from many different phyla that have variable lengths from several mm to several cm, so we are not biased by a size-sorted sample. *Acteonina carbonaria* also has a prominent collar-like ridge at the base of the parietal wall, which is absent or not preserved in A. *permiana.*

Location.—The fossil locality is in Crook County, Oregon, which may be found on the Twelvemile Reservoir, Oregon 7.5 minute U.S. Geological Survey quadrangle, 1981 edition. The UTM coordinate is 11TKU75826907. The geographic coordinates are 119°47′17″N, 97°44′10″W.

Age.—Early Permian (Wolfcampian to Leonardian) ages for the Coyote Butte Formation are suggested by: brachiopods (Cooper 1957), conodonts (Wardlaw et al. 1982), colonial rugose corals (Stevens & Rycerski 1983) and fusulinids (Skinner & Wilde 1966).

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Two new species of Spionidae (Polychaeta) from Tahiti, French Polynesia

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Abstract.—Two new species of Spionidae, *Scolelepis* (*Scolelepis*) *melasma* and *S.* (*S.*) *dicha* are described from the intertidal area of exposed Tahitian beaches. The species co-occur and are restricted to basaltic sandy beaches. *Scolelepis* (*S.*) *melasma* is characterized by the absence of an occipital tentacle, neuropodial unidentate, hooded hooks beginning on setiger 40–41, notopodial hooded hooks absent and branchiae fused basally. *Scolelepis* (*S.*) *dicha* also lacks an occipital tentacle, with neuropodial bidentate, hooded hooks beginning from setiger 26–32 and with posterior neuropodia having almost all hooded hooks, notopodal hooks absent, and branchiae fused basally.

During an ecological investigation of the intertidal fauna of exposed beaches in Tahiti, two extremely abundant species of spionids were collected. The polychaete fauna of French Polynesia or any other region of the South Pacific is poorly known and many of the species that have been described are incompletely known. While attempting to identify these spionids using the key of Blake & Kudenov (1978), it became apparent that they represented two new species, of the genus *Scolelepis* Blainville, 1828 and the subgenus *Scolelepis* sensu stricto as defined by Maciolek (1987).

The following abbreviations have been used in the text, AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; MNHN, Museum Nationale D'Histoire Naturelle, Paris; LACM, Los Angeles County Museum, Los Angeles; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Scolelepis (*Scolelepis*) *melasma*, new species

Fig. 1A–G, Table 1

Material examined.—French Polynesia, Tahiti, La Fayette Beach, 17°30.238′S, 149°27.377′W, intertidal, basaltic sand, 27 March 1995. Holotype (AM W23103), Paratypes: 2 (BMNH ZB 1996.518), 2 (MNHN UE413), 1 (USNM 170033), 10 (AM W23104), 1 (LACM Poly 1831, 1 (AM W23107).

Description.—Description based on holotype except where stated. Alcohol preserved material pale yellow, live material dark green in colour. Holotype posteriorly incomplete, 23.0 mm in length, 1.52 mm in width anteriorly, with about 92 segments. Paratype material varying in length from 20 to 30 mm and 1.52 to 3.04 mm in width anteriorly for 63 to 95 setigers, none of the type material is complete and the majority of the type material consists of ripe males and females.

Elongate pointed prostomium (Fig. 1A),

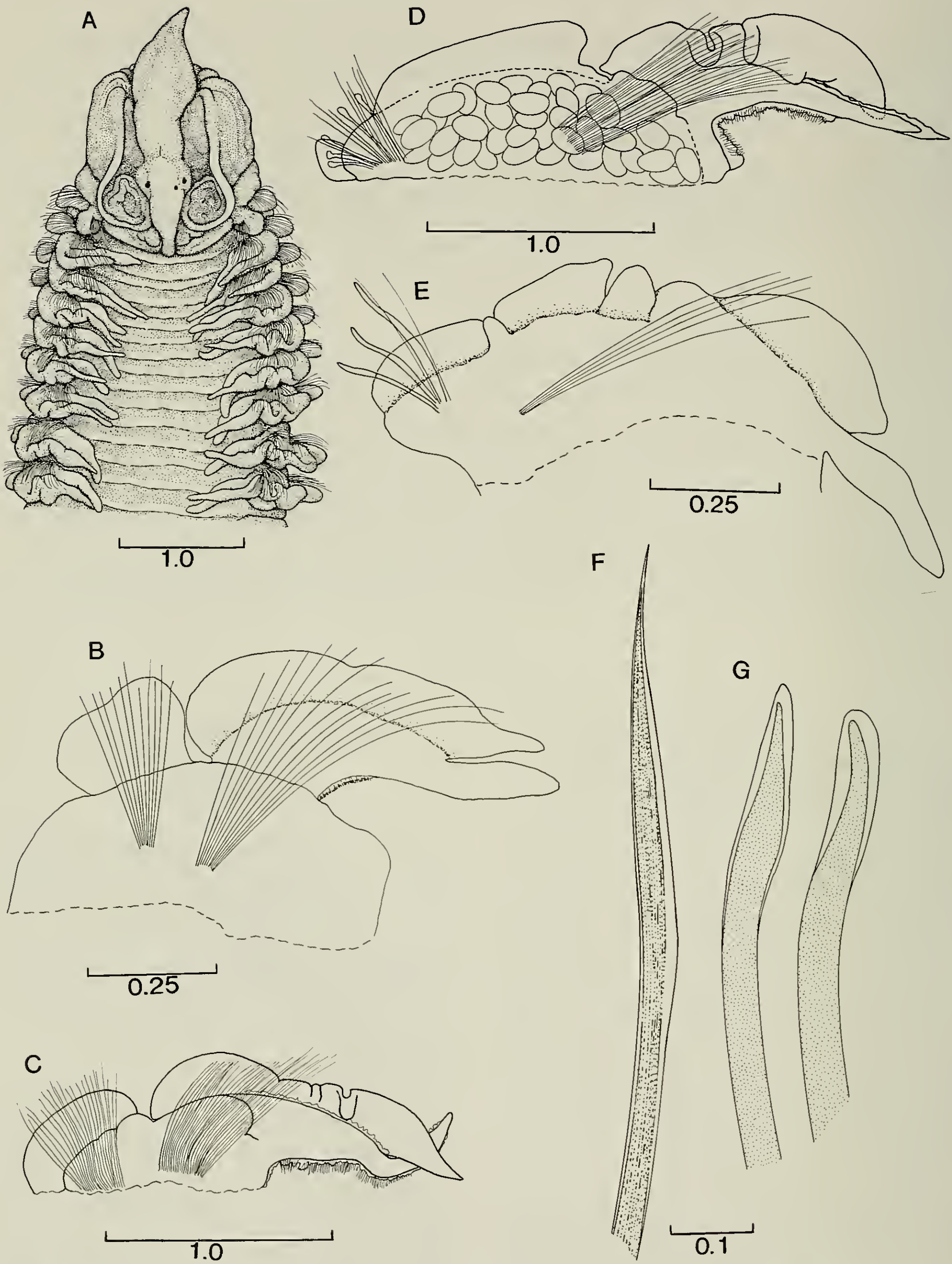

Fig. 1. *Scolelepis* (*Scolelepis*) *melasma* new species. Holotype (AM W23103). A. Dorsal view of anterior segments, B. Lateral view of parapodium of setiger 3, C. Lateral view of parapodium of setiger 20, D. Lateral view of parapodium of setiger 50, E. Lateral view of parapodium of setiger 85, F. Notoseta from setiger 3, G. Neurosetae from setiger 85.

Table 1.—Taxonomic characteristics of species in the subgenus *Scolelepis* (*Scolelepis*) described since Maciolek (1987).

Species	Occipital tentacle	Neuropodial hooks begin on setiger	Neuropodial hooks—with nos. of teeth	Notopodial hooks present or absent	Neuropodial notch present	Notosetae present on setiger 1	Branchial fusion	Comments
S. (S.) branchia Imajima, 1992	No	22	1	Absent	No	Yes	Fused basally	Accessory digitiform branchiae present from setiger 7, by setiger 30 present as 7 lobes, then decreasing
S. (*S.*) *brevibranchia* Hartmann-Schröder, 1991	Yes	15	2–3	Absent	Yes	No	Fused basally	Exact nos. of teeth difficult to determine from figures
S. (*S.*) *burkovskii* Sikorski, 1994	No	17–19	3	Absent	No	No	Fused basally	From the figures, clearly belongs to this subgenus although Sikorski (1994) did not designate subgenus
S. (*S.*) *crenulata* Hartmann-Schröder, 1991	Yes	34	2–3	Absent	No	Yes	Fused basally with notopodial lamellae with crenulated margins	Teeth above main fang very small and difficult to count
S. (*S.*) *denmarkensis* Hartmann-Schröder, 1983	No	36	3	Present	Yes	Yes	Fused for most of its length anteriorly, posteriorly only fused basally	Species overlooked by Maciolek (1987)
S. (*S.*) *dicha* n. sp.	No	26–32	2	Absent	Yes	No	Fused basally	Posterior neurosetae almost entirely hooded hooks
S. (*S.*) *matsugae* Sikorski, 1994	No	11–22	3	Present	Yes	No	Fused basally	Notopodial hooks begin on setigers 13–14. Sikorski (1994) did not designate subgenus
S. (*S.*) *lingulata* Imajima, 1992	Yes	21	1	Present	Yes	Yes	Fused basally	Neuropodial interramal lamellae on posterior setigers are lingulate and obliquely protruded
S. (*S.*) *melasma* n. sp.	No	40–41	1	Absent	Yes	Yes	Fused basally	
S. (*S.*) *planata* Imajima, 1992	Yes	19	3–4 pairs above main fang	?	Yes	No	Fused basally	Notosetal details not given
S. (*S.*) *sagittaria* Imajima, 1992	Yes	32	2–3	Present	Yes	Yes	Fused basally	Notopodial hooks from setiger 52
S. (*S.*) *variegata* Imajima, 1992	No	27	2	Absent	Yes	No	Completely fused until setiger 29, then only basally	

dorsal surface faintly tesselated, extending posteriorly to form inflated keel with two eye spots on one side and one on other side. Occipital papillae absent. Eye spots located just anterior to point of inflation. Peristomium expanded laterally to form pair of lateral wings enveloping the prostomium. Ventral mouth with raised glandular margins, pharynx not extended on holotype but partially everted on some type material. Palps detached on holotype but bases where previously attached clearly visible. Palps on paratypes extending to between setigers 10–12.

Setiger 1 with both noto- and neuropodia. Notopodia small rounded lobe with small bundle of capillaries, neuropodia, bluntly triangular lobe with capillaries. Setiger 2, with larger bluntly triangular neuropodial lobe and capillary setae, notopodium with small, rounded acicular lobe and laterally elongated postsetal lobe and a digitiform branchia attached basally, and numerous long capillary setae. Neuropodial and notopodial postsetal lobes increasing in size on subsequent setigers, margins of these lobes becoming thinner and crenulate. Similarly, the length of branchiae increasing on subsequent setigers and branchiae present on all remaining setigers of holotype. Anterior branchiae fused basally to notopodial lamellae. Fig. 1B–E illustrate the relative proportions of the parapodial lobes along the body.

All notopodial setae capillaries, with smooth tips and narrow wings (Fig. 1F), setiger 3 with about 20 capillaries and setiger 85 with about five capillaries. Notopodial hooded hooks absent. Neuropodial setae initially capillaries; setiger 3 with about 12 capillaries; from setiger 41, unidentate hooded hooks appear (Fig. 1G), 2–3 per fascicle; setiger 85 with two capillaries and three hooded hooks.

Segments well demarcated dorsally, with raised intersegmental ridges present, venter smooth with mid ventral glandular stripe.

Holotype a gravid female with numerous oocytes restricted to the parapodia and the area just adjacent to the parapodia, from about setiger 38 onwards (Fig. 1D), oocytes restricted to the lateral walls.

Variation.—In some paratypes a slight bulbous swelling occurs immediately below apex of the prostomium. The setiger on which neuropodial hooded hooks begin varies from 40 to 41. Posterior fragments collected indicate that the pygidium is a rounded cushion. Some ripe females with oocytes developed from setiger 34 and continuing to about setiger 85. Ripe males with spermatozoa also restricted to parapodial lobes from about setiger 35 to 90.

Remarks.—Maciolek (1987) reviewed the genus *Scolelepis* and based upon the structure of the hooded hooks, divided the genus into two subgenera, *Scolelepis* and *Parascolelepis.* The subgenus *Scolelepis* is characterized by falcate hooded hooks with 0–2 small apical teeth and a straight shaft, and the subgenus *Parascolelepis* is characterized by multidentate hooded hooks above a large main fang and curved shaft. Based upon these characters this new species from Tahiti belongs in the subgenus *Scolelepis.*

Maciolek (1987) tabulated the major characteristics of the 37 described species and three other described species having unidentate neuropodial hooded hooks, *S.* (*S.*) *knightjonesi* (de Silva, 1961 incorrectly quoted as 1965 by Maciolek 1987) described from Sri Lanka, *S.* (*S.*) *lamellicinata* Blake & Kudenov, 1978 from Australia and *S.* (*S.*) *lefebvrei* (Gravier, 1905) from Djibouti, Red Sea. However, of these, *S.* (*S.*) *knightjonesi* has an occipital papilla present that is lacking in *S.* (*S.*) *melasma.* The new species also has shorter palps than *S.* (*S.*) *knightjonesi*, which has palps extending to setiger 28 rather than setigers 10–12; in addition, the branchiae occur only laterally (Fig. 1A) and do not meet mid-dorsally, whereas on *S.* (*S.*) *knightjonesi* the branchiae overlap mid-dorsally. The new species can be easily distinguished from *S.* (*S.*) *lefebvrei* and *S.* (*S.*) *lamellicinata* as both these species have both noto- and neuropodial hooded hooks, whereas the new species has neuropodial hooks only present.

Since Maciolek's (1987) review several additional species of *Scolelepis* (*Scolelepis*) have been described and these are shown in Table 1, using the same characters as used by Maciolek, together with the two new species described here. Two of these recently described species of *Scolelepis* (*Scolelepis*) have unidentate neuropodial hooded hooks, *S.* (*S.*) *branchia* Imajima, 1992 and *S.* (*S.*) *lingulata* Imajima, 1992. The first of these species has accessory branchiae, which clearly distinguishes it from *S.* (*S.*) *melasma*, and the latter species has neuropodial hooded hooks from setiger 21, whereas the new species has them present from setiger 40–41.

Habitat and ecology.—The species occurs on all basaltic beaches in Tahiti which are found on both the east and west coasts of the island, on exposed beaches that are not protected by a barrier reef. The species lives in non-permanent mucous tubes and occurs in densities of 700–1000 m^2, in fine sandy sediments in the intertidal region of the beach; the tidal range is about 50 cm. All these beaches are fully exposed to oceanic waters and the worms occur in the surf zone. For more detailed ecological information see Frouin et al. (1998).

Etymology.—The specific name is a Greek word for "black", which refers to the black basaltic sediments in which this species occurs.

Distribution.—French Polynesia, Tahiti.

Scolelepis (*Scolelepis*) *dicha*, new species
Fig. 2A–G, Tables 1 & 2

Material examined.—French Polynesia, Tahiti, La Fayette Beach, 17°30.238′S, 149°27.377′W, intertidal, basaltic sand, 27 March 1995. Holotype (AM W23105), Paratypes: 1 (BMNH ZB 1996.519), 1 (MNHN UE 414), 1 (USNM 170034), 20 (AM W23106) and 1 (LACM Poly 1830).

Description.—Description based on holotype except where stated. Alcohol preserved material pale pink with scattered diffuse brown pigmentation on anterior dorsum and venter, most marked on prostomium. Palps detached but present with distinct brown pigmentation along one axis. Live material dark brown with blood vessels clearly visible around parapodia. Holotype complete, 15.2 mm long, 1.52 mm wide anteriorly, with about 70 segments. Paratype material varies from 15 to 20 mm long and 1.14 to 1.7 mm wide anteriorly for 70 to 75 setigers.

Prostomium pointed, simple elongated cone (Fig. 2A), peristomial wings poorly developed. Occipital papillae absent. Pharynx partially extruded, thin walled and faintly pigmented. Two pairs of eye spots arranged on either side of caruncle. Caruncle extending posteriorly, slightly raised forming an elongate occipital papilla on mid-axis of caruncle. On either side of caruncle scars indicating point of attachment of palps. On paratypes some of which have palps still attached, these extend to setiger 27.

Setiger 1 poorly developed, notopodia with small, rounded triangular lobe, notosetae absent, neuropodia with small conical lobe with few capillary setae pesent, branchiae absent.

Setiger 2 with elongate rounded notopodial lobe, and an elongate branchial lamella basally attached to notopodial lobe. Capillary notosetae numerous, forming a fan over the lobe. Neuropodia with semi-circular lobe and neurosetal capillaries arranged in a fan. Presetal lobes absent, both parapodial lobes postsetal in origin. Parapodial lobes and branchiae increasing in size on subsequent setigers (Fig. 2B), with margins of lobes thinner and margins of branchiae crenulated. Setiger 3 with about 12 notosetae and 10 neurosetae. Lobes and branchiae fully developed by setigers 3–4, branchiae not reaching mid dorsal line. Posteriorly, notopodial lobe becoming bilobed (Fig. 2C) but, by setiger 48 notopodial lobe almost entire again. Subsequently, the size of the parapodial lobes and branchiae declining although branchiae present almost to pygidium.

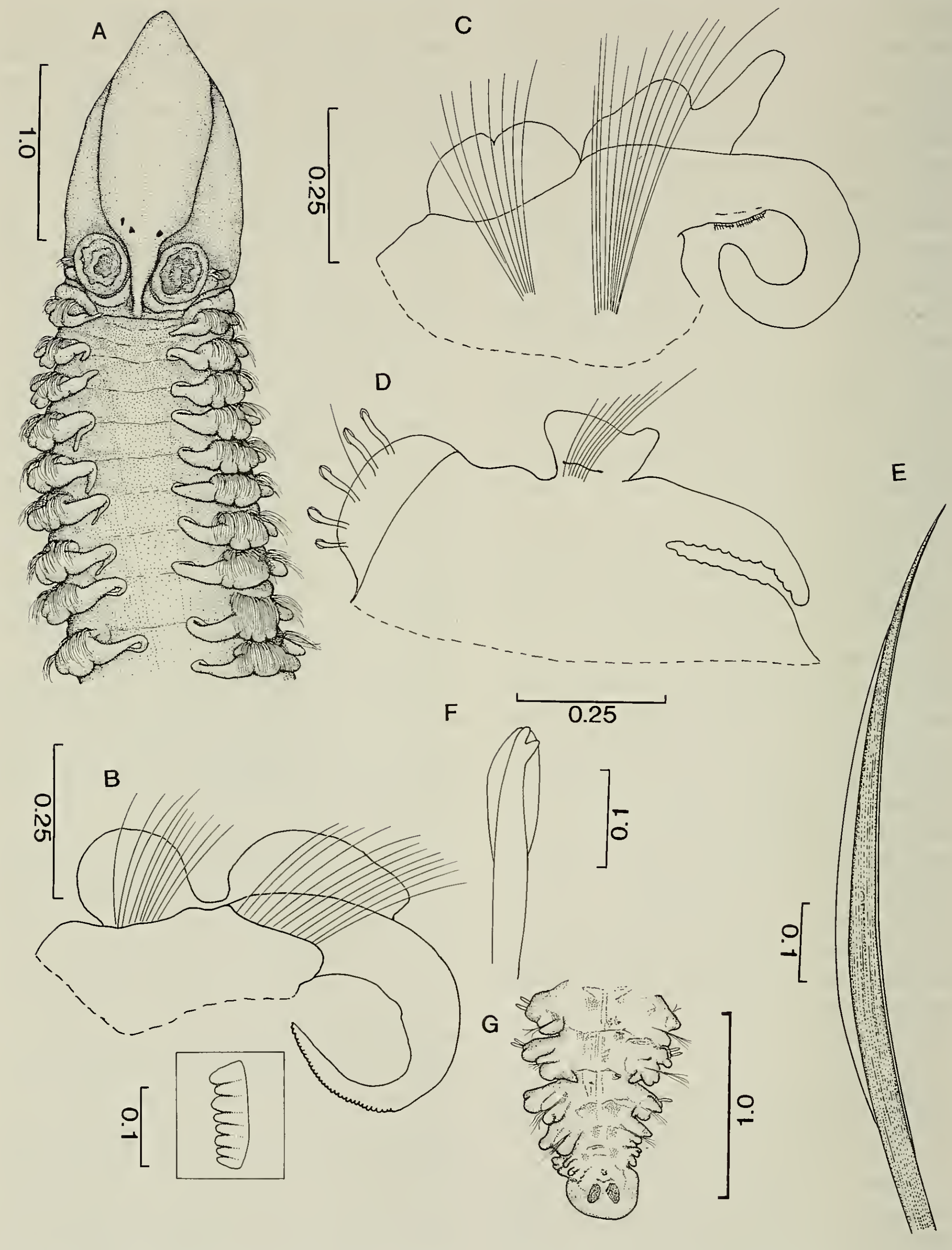

Fig. 2. *Scolelepis* (*Scolelepis*) *dicha* new species. Holotype (AM W23105). A. Dorsal view of anterior segments, B. Lateral view of parapodium of setiger 3, C. Lateral view of parapodium of setiger 21, D. Lateral view of parapodium of setiger 48, E. Lateral view of parapodium of setiger 85, F. Notoseta from setiger 3, G. Neuroseta from setiger 45, G. Dorsal view of pygidium.

Table 2.—The relationship between body length, maximum anterior width and the setiger on which neuropodial hooded hooks are first present on *S.* (*S.*) *dicha.*

Length (mm)	Width (mm)	Setigers present	Start of hooks (set no.)	Comments
8.33	1.31	31*	31	gravid
8.33	1.31	34	29	
11.90	0.60	51*	26	
11.90	1.43	44*	31	
13.10	1.43	42*	31	
14.88	1.19	38*	29	
15.48	1.19	64	29	
17.50	1.31	70	30	
18.45	1.31	70	30	
19.05	1.55	55*	32	gravid
19.64	1.31	69	31	gravid
20.24	1.90	47*	32	
21.43	1.67	71	31	gravid
21.43	1.43	63	30	
22.02	1.55	51*	32	gravid
23.81	1.19	71	31	
25.60	1.31	77*	31	
26.19	1.43	76	31	gravid
27.98	1.67	71	30	
47.62	2.38	71	31	

No. of individuals = 20.
* Indicates incomplete individual.

Notosetae capillaries throughout (Fig. 2E), broad bladed, narrow winged smooth tipped, with granular cores. Notosetal hooded hooks absent. Neurosetae initially capillaries replaced with bidentate hooded hooks (Fig. 2F), which first occur on setiger 31, with a mixture of capillaries and hooks, but rapidly thereafter majority of neurosetae hooded hooks, about 5–6 per parapodium (Fig. 2D).

Large part of dorsum uncovered with well demarcated, central longitudinal, dorsal glandular stripe. Segments are relatively poorly defined, suggesting that internal septa are not well developed. Venter smooth and internal body musculature clearly visible through body wall.

Holotype a gravid female with oocytes clearly visible from setiger 25, about 6–9 oocytes per setiger, but lacking from posterior segments.

Pygidium small rounded cushion with two patches of eye spots (Fig. 2G).

Variation.—The setiger on which neuropodial hooded hooks begin varies from 26 to 32 (Table 2) but on most individuals the hooks begin on setiger 29 or later. There is some evidence that with increasing size as measured by length, that the hooks begin later, suggesting some setal replacement with increasing length and presumably age. As many of the individuals were posteriorly incomplete, the maximum width anteriorly was also measured, but this showed less support for the relationship between increasing size as measured by width and the later development of neuropodial hooded hooks. Based on the 11 complete individuals which were measured, there was not a direct relationship between total length of animal and maximum anterior width. This may be real or perhaps a function of preservation techniques employed as in many polychaete species, the maximum anterior width can be used as a substitute for total length. Additional material would need to be examined to determine which was the valid interpretation.

The intensity of the pigmentation patterns varies within the paratype material. In a ripe male the gametes are clearly visible from setiger 35 and are then present almost until the pygidium.

Remarks.—As discussed above the genus *Scolelepis* has recently been reviewed by Maciolek (1987) and she erected two subgenera. *Scolelepis* (*S.*) *dicha* belongs to the subgenus *Scolelepis.* Based on the data presented by Maciolek (1987) and in Table 1, the following species in this subgenus possess bidentate neuropodial hooded hooks, notopodial hooded hooks absent, occipital papillae absent and notosetae absent on setiger 1, thus resembling *S.* (*S.*) *dicha: S.* (*S.*) *cantabra* Rioja, 1918, *S.* (*S.*) *vexillatus* Hutchings & Rainer, 1979, *S.* (*S.*) *variegata* Imajima, 1992, *S.* (*S.*) *williami* de Silva, 1961. Pettibone (1963) examined the type of *S.* (*S.*) *cantabra* and found that the occipital tentacle was lacking although Rioja had originally described it as being present, but she indicates that the holotype is damaged. However, regardless of this character, the setiger on which neuropodial hooks start is from setiger 20–25, whereas they start from setiger 26–32 in *S.* (*S.*) *dicha.* The new species can be separated from *S.* (*S.*) *vexillatus*, as the branchiae are always just fused basally, whereas in the latter species they are completely fused initially, only becoming partially free posteriorly from setiger 29. *Scoloplos* (*S.*) *williami* differs from the new species as the neuropodial hooded hooks begin on setiger 40, whereas in the new species they begin from setiger 26–32. Finally, *S.* (*S.*) *dicha* can be separated from *S.* (*S.*) *variegata* by the degree of fusion of the branchiae, in the new species they are only fused basally, whereas in *S.* (*S.*) *variegata* they are completely fused with the notopodial lamellae until setiger 29. Thus *S.* (*S.*) *dicha* can be easily distinguished from all these species on the basis of the setigers on which neuropodial hooded hooks begin and the degree of fusion of the branchiae and is therefore described as a new species.

Habitat and ecology.—The species occurs on the basaltic La Fayette beach in Tahiti and appears to be absent from other basaltic beaches that are found on both the east and west coasts of the island. The species lives in non-permanent mucous tubes and occurs in densities of 700–1000 m^2, in the upper intertidal region of the beach just below a line of rocks in fine sandy sediments; the tidal range is 50 cm. This beach is fully exposed to oceanic waters and is not protected by an offshore barrier reef. The species co-occurs with *Scolelepis* (*S.*) *melasma.* For more detailed ecological information see Frouin et al. (1998).

Etymology.—The specific name is a Greek word for "two" referring to the bidentate hooded hooks present in this species.

Distribution.—French Polynesia, Tahiti, La Fayette Beach.

Acknowledgments

We should like to thank Anna Murray for illustrating the anterior views of both species and Kate Attwood for preparing the plates.

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New species of bathyal and abyssal Sabellariidae (Annelida: Polychaeta) from near New Caledonia (southwest Pacific Ocean)

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Abstract.—Specimens described in this work were collected during the BIOCAL and BIOGEOCAL cruises (Biology and Geology of New Caledonia) in 1985 and 1987 conducted by the Museum National d'Histoire Naturelle (Paris, France). All of the 488 specimens collected from depths between 440 m and 1870 m belong to the subfamily Lygdaminae Kirtley, 1994, which is characterized by the presence of four parathoracic segments. Among these specimens, we recognize four genera, including *Bathysabellaria* Lechapt & Gruet, 1993 with two species, a new species of *Lygdamis* Kinberg, 1867, two new species of *Phalacrostemma* Marenzeller, 1895, and a new species of *Tetreres* Caullery, 1913. All of these species are set apart from other known species by the shape of the outer and inner paleae and by their geographic and bathymetric distributions. These collections illustrate the uniqueness and richness of the polychaete fauna of the Sabellariidae of this Pacific area.

Except for the relatively limited accounts of Hoagland (1920:627), Treadwell (1926: 191), Caullery (1944:54–66) from the Philippines and Indonesia, and that of Gibbs (1971:101–211) from the Solomon Islands, the benthic polychaete fauna from great depths of this geographic area remains poorly known, especially for the family Sabellariidae. The material on which this study is based was collected during the 1985 and 1987 cruises of the "Biology of New Caledonia" project, BIOCAL and BIOGEOCAL, respectively, conducted by the French National Museum of Natural History of Paris.

Specimens were collected with a Waren-type rock dredge (Stations DW) or with a beam trawl (Stations CP), fixed in a seawater formalin solution and stored in 70% ethanol. The material was received from the Centre National de tri d'Oceanographie Biologique, Brest, France, examined under low power magnification and selected morphological features were studied by scanning electron microscopy (SEM). All type material is deposited in the National Museum of Natural History, Paris (MNHNP).

Family Sabellariidae
Subfamily Lygdaminae Kirtley, 1994

The family Sabellariidae was subdivided by Kirtley (1994:14) into two subfamilies, the Sabellariinae with three parathoracic segments and the Lygdaminae with four parathoracic segments. All specimens considered here belong to the Lygdaminae, the genera being distinguished as follows:

1a. Compound (branched) feeding tentacles .... *Lygdamis*
1b. Simple (unbranched) feeding tentacles 2
2a. Operculum completely divided .... *Phalacrostemma*
2b. Operculum not completely divided ... 3

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† Deceased July 1997.

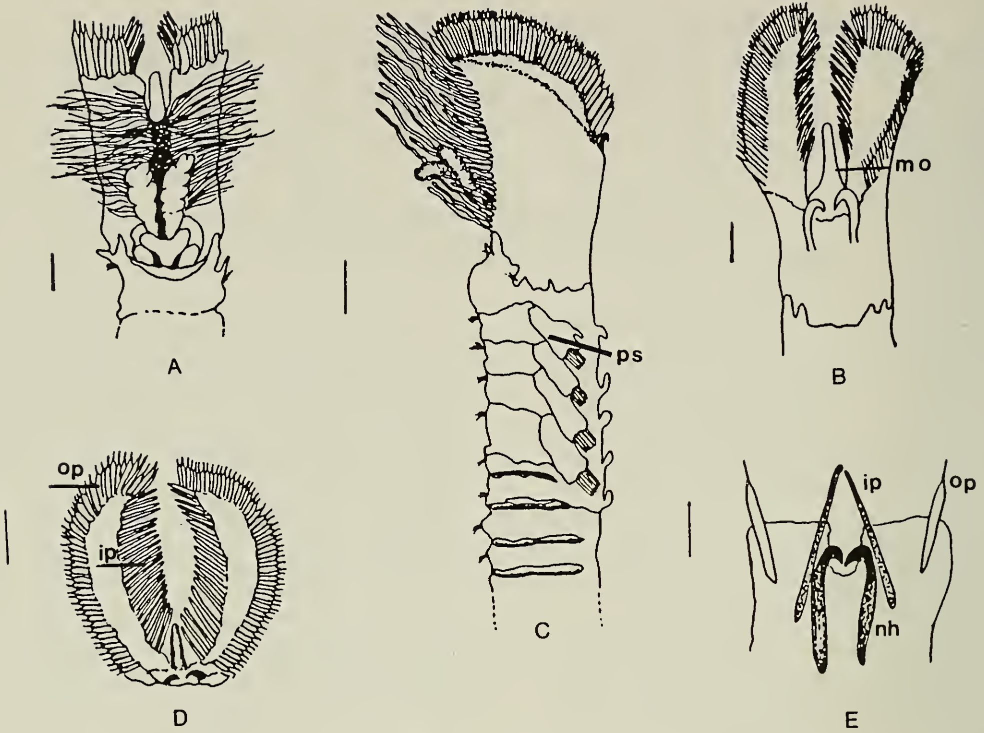


Fig. 1. *Lygdamis splendidus*, new species, (Holotype, MNHNP UC 356): A, ventral view of anterior end; B, dorsal view of anterior end; C, left lateral view; D, surface view of crown; E, cross-sectional diagram showing position of paleae and nuchal hooks on crown. Scale bars = 1 mm. Abbreviations: ip = inner paleae, mo = median organ, nh = nuchal hook, op = outer paleae, ps = parathoracic setiger.

3a. Operculum completely fused along ventral margin .... *Bathysabellaria*
3b. Operculum with deep indentation along ventral margin .... *Tetreres*

Genus *Lygdamis* Kinberg, 1867
Lygdamis splendidus, new species
Figs. 1, 2

Material examined.—Southwest off New Caledonia, BIOCAL cruise, station DW 66, 24°55′S, 168°21′E, 515 m, 3 Sep 1985, Holotype (MNHNP UC 356), Paratypes (MNHNP UC 357) (two specimens).

Description.—Holotype incomplete, missing posterior most segments and cauda; total length 13 mm, thoracic diameter 3 mm. Anterior end of opercular stalk completely divided into bilaterally symmetrical lobes (Fig. 1A, B). Opercular paleae of two kinds, in curved, dorsoventral rows (Fig. 1C, D). Outer paleae, 100–120 in number, 2 mm long, transparent, smooth, with distal ends terminating in fine tips (Fig. 2A, C); inner paleae, 36–40 in number, 3 mm long, yellow-gold, smooth, with slightly curved tips (Fig. 2B, D). Falcate dorsal nuchal hooks, tips recurved inward toward dorsal midline (Fig. 1E). With well-developed median organ arising from dorsal sagittal suture between opercular lobes (Fig. 1B). Twenty-five pairs of compound feeding tentacles on ventral margins of each side of opercular peduncle, pair of short prehensile prostomial tentacles arising from anterior margin of upper lip of stoma. Large U-shaped building organ with conical lobes on lat-

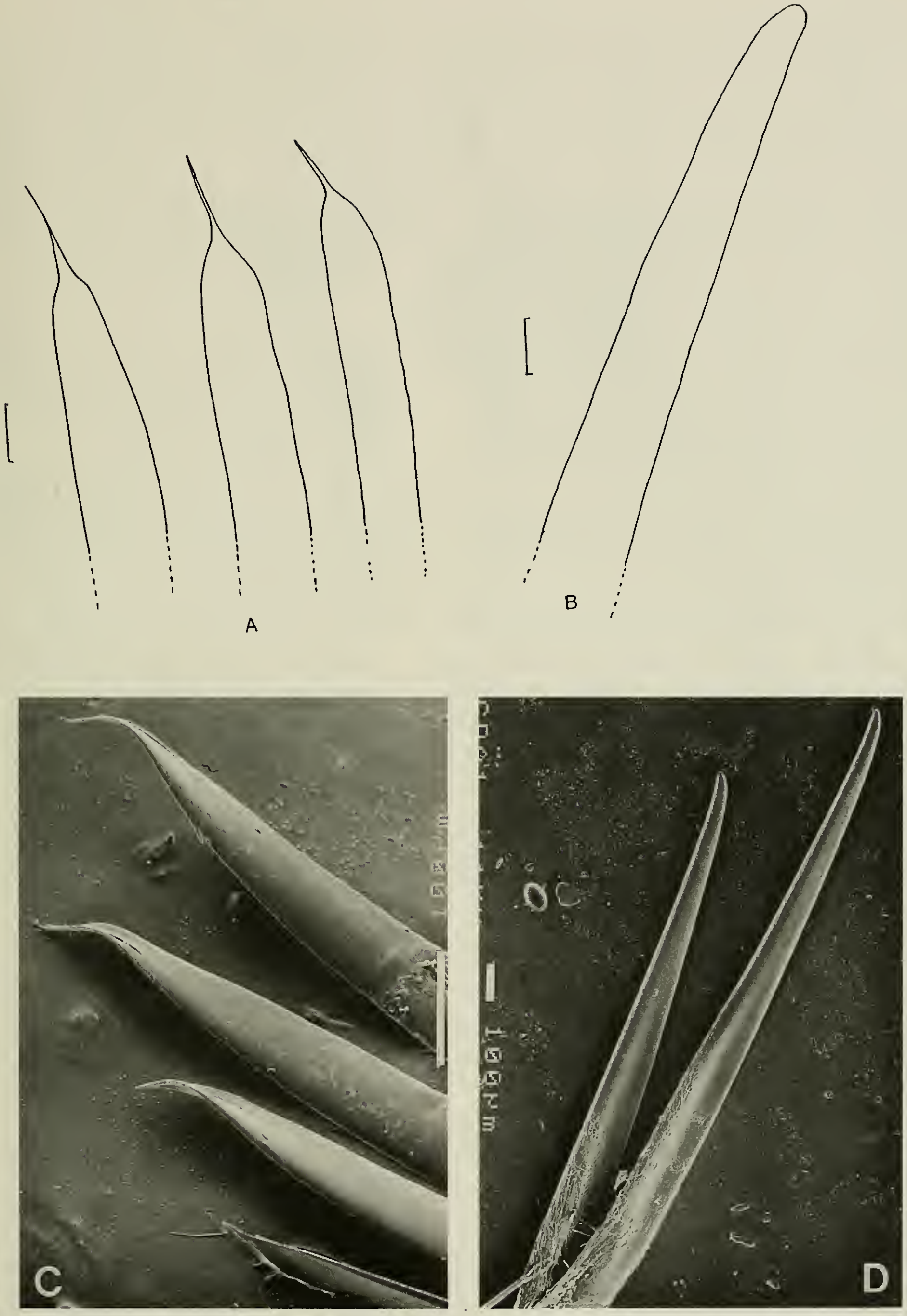


Fig. 2. *Lygdamis splendidus*, new species, (Holotype, MNHNP UC 356): A, outer paleae; B, inner paleae; C, SEM of outer paleae; D, SEM of inner paleae. Scale bars = 0.1 mm for A, B and 100 µm for C, D.

eral margin, with conical cirrus with small bundle of short, ventral, finely serrate capillary setae. Setiger 2 with same bundle of finely serrate capillary setae. Four parathoracic segments (Fig. 1C) with small cirri on distal dorsal margin of notopodial sheaves; 7–8 paired, stout setae with lanceolate distal tips and spinous, capillary companion setae with curved tips in transverse row on each notopodial sheave. Neuropodial setae similar, but smaller in size and fewer in number. Dorsal branchiae on parathoracic segments. Abdominal segments with bundles of long, spinous neurosetae and uncinigerous notopodial tori. Cauda not observed. No tubes.

Etymology.—The specific name, from Latin *splendidus* = magnificent, refers to its very beautiful appearance.

Remarks.—*Lygdamis splendidus* is clearly distinguished from other species of *Lygdamis* by the shape of the outer paleae, tapering to fine distal tips, the shape of inner paleae, and total number of paleae; moreover, of all *Lygdamis* species, *L. splendidus* occurs at the greatest depth. *L. indicus* Kinberg, 1867 and *L. gilchristi* (McIntosh, 1922) appear to be most similar to *L. splendidus* but differ in the shapes of the inner and outer paleae and by their geographical and bathymetric distributions (Fig. 3).

Key to the species of *Lygdamis* [after Kirtley (1994:117–118)]

1a. Outer paleae with smooth lateral margins 4

1b. Outer paleae with lateral margins not smooth 2

2a. Outer paleae with serrate lateral margins, with slightly concave inner surfaces (A, Fig. 3) (West Africa, 77 m) . . . . *L. robinsi*

2b. Outer paleae with lateral margins not serrate 3

3a. Outer paleae with complex ornamentation, with irregular, wavy, transverse lines across middle portion of blade, inner paleae with fine, marginal decoration (B, Fig. 3) (West Africa, 22 m) . . . . *L. kirkegaardi*

3b. Without complex ornamentation on outer paleae 4

4a. Distal ends of outer paleae straight, nearly bilaterally symmetrical 5

4b. Distal ends of outer paleae curved, conspicuously asymmetrical 8

5a. Outer paleae with narrow distal spines terminating in narrow, delicate spike; nuchal hooks with weakly recurved tips (C, Fig. 3) (Indonesia, 36 m) . . . . *L. indicus*

5b. Outer paleae with distal tips tapering to very long spike; nuchal hooks with strongly recurved tips; inner paleae with slightly curved tips (D, Fig. 3) (New Caledonia, 515 m) . . . . *L. splendidus*, new species

5c. Outer paleae converge slowly to sharp tips; inner paleae converging abruptly to symmetrical short, sharp tip (E, Fig. 3) (South Africa, 75 m) . . . . *L. gilchristi*

6a. Outer paleae with blade margins almost parallel through middle portion, terminating in narrow mucronate tips; inner paleae with gently bent tips (F, Fig. 3) (Australia, 70 m) . . . *L. augeneri*

6b. Outer paleae narrowing continuously from middle portion to tips 7

7a. Distal ends of outer paleae slightly asymmetrical; inner paleae with bent distal ends; nuchal hooks strongly recurved, with sharp tips (G, Fig. 3) (Australia, 64 m) . . . . *L. giardi*

7b. Outer paleae moderately expanded through middle portion and tapering slowly to sharp distal point; inner paleae tapering slowly to dull point; nuchal hooks with strongly recurved sharp tips (H, Fig. 3) (England) . . . . *L. muratus*

8a. Outer paleae with distal tip as flat projection from cylindrical paleal blade 9

8b. Outer paleae with distal tip as cylindrical continuation of paleal blade . . 12

9a. Middle portion of outer paleae expanded, distal ¼ constricted and slightly curving (l, Fig. 3) (Madagascar) . . . . *L. malagasiensis*

9b. Distal ¼ of outer paleae not abruptly constricted 10

10a. Distal tip of outer paleae very narrow, rounded at distal end of blade, with elongate, sigmoidal spike; inner pale-

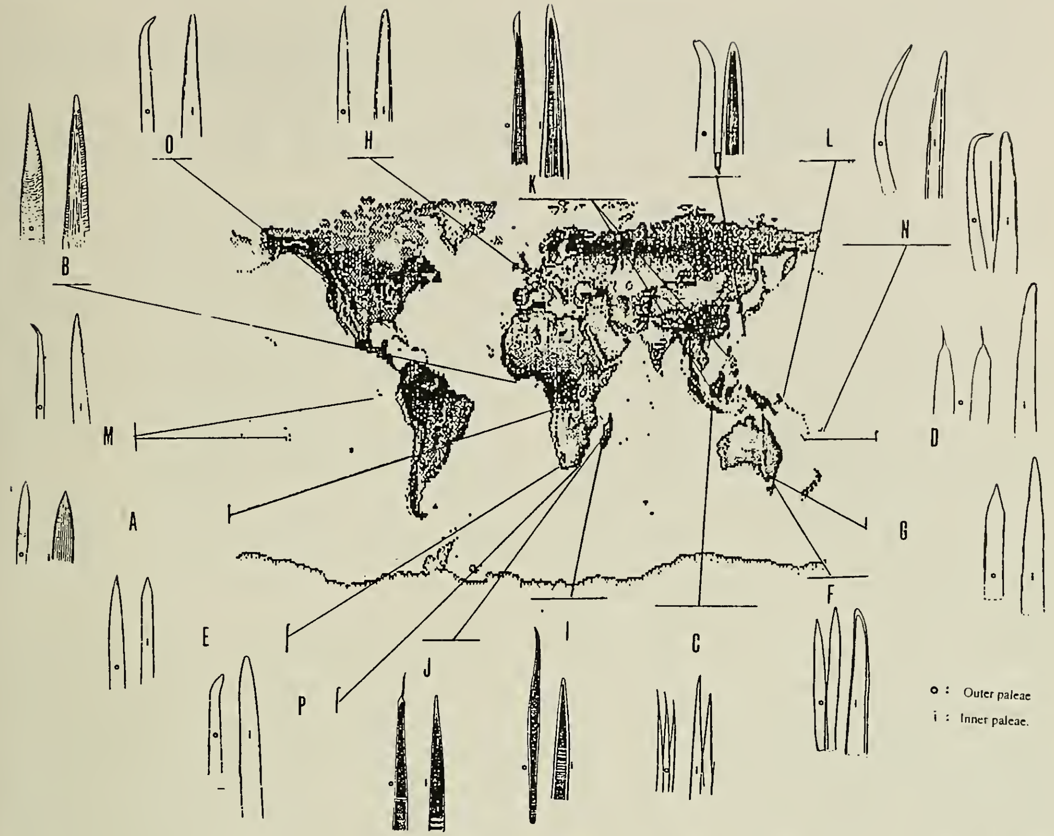


Fig. 3. Shapes of outer paleae and inner paleae of species of the genus *Lygdamis* with geographical observations. A = *L. robinsi*, B = *L. kirkegaardi*, C = *L. indicus*, D = *L. splendidus*, new species, E = *L. gilchristi*, F = *L. augeneri*, G = *L. giardi*, H = *L. muratus*, I = *L. malagasiensis*, J = *L. bhaudi*, K = *L. ehlersi*, L = *L. gibbsi*, M = *L. nesiotes*, N = *L. laevispinis*, O = *L. rayrobertsi*, P = *L. dayi*, Q = *L. curvatus*.

ae with narrow tips (J, Fig. 3) (Madagascar) .... *L. bhaudi*

10b. Distal tip of outer paleae without sigmoidal spike 11

11a. Outer paleae with narrow, curved distal tip (K, Fig. 3) (Indonesia, Philippines, 45 m) .... *L. ehlersi*

11b. Outer paleae with wide, curved distal tip; tip of nuchal hook bent about 90° from axis of shaft (L, Fig. 3) (Solomon Islands, coral reef) ...... *L. gibbsi*

12a. Distal tips of outer paleae conical, sigmoidal in outline 13

12b. Distal tips of outer paleae not sigmoidal in outline 14

13a. Outer paleae with sigmoidal tip, curved inward about 30° from vertical axis of shaft toward center of crown; nuchal hooks very large, strongly bent to blunt tips (M, Fig. 3) (East Pacific Ocean, coral reef) .... *L. nesiotes*

13b. Outer paleae with sigmoidal tip, curved inward about 80° from vertical axis of shaft toward center of crown; nuchal hooks relatively small, strongly bent, short, stout, with sharp tip (N, Fig. 3) (South Central Pacific Ocean) .... *L. laevispinis*

14a. Tip of outer paleae with stout, short abruptly pointed tips; nuchal hooks elongate, large, strongly bent (O, Fig. 3) (Florida, Gulf of Mexico, 328 m) .... *L. rayrobertsi*

14b. Tips of outer paleae short, blunt 15

15a. Inner paleae with fine transverse markings (P, Fig. 3) (South Africa) . . . *L. dayi*
15b. Inner paleae stout, tapering to dull point; outer paleae with stout, rounded tips (Q, Fig. 3) (Bonin Islands) . . . . *L. curvatus*

Genus *Phalacrostemma* Marenzeller, 1895
Phalacrostemma tenue, new species
Figs. 4, 5

Material examined.—Southeast off New Caledonia, BIOCAL cruise, station CP 62, 24°19′S, 167°48′E, 1395 m–1410 m, 2 Sep 1985, Holotype (MNHNP UC 358), Paratypes (MNHNP UC 359) (two specimens).

Description.—Holotype 4 mm long; diameter of opercular crown 1.5 mm. Anterior end of opercular stalk completely divided into two bilaterally symmetrical halves (Fig. 4A, B). Each side of crown with 16–17 outer paleae; 2–3 inner paleae in dorsal position. Outer paleae with transverse striations and expanded distal margins, with regular distal denticles forming fringe (Figs. 4C, 5A, B). Inner paleae smooth, tips blunt with regularly spaced transverse ridges (Fig. 4D). Two nuchal hooks on each side of anterior dorsal midline of stalk, each curving to an acute tip.

Robust median organ arising from between dorsal inner margins of stalk. Pair of long prehensile prostomial tentacles arising from anterior margin of upper lip of stoma, with 4 simple, ciliated feeding tentacles on each side of buccal cavity.

First setiger with bundle of ventral pectinate capillary setae. Second setiger with conical cirrus with bundles of pectinate setae. Four parathoracic segments, each with neuropodial sheaves of setae with pectinate distal margins; notopodial sheaves with 5–7 setae with oar-shaped denticulate and acute distal tips, with companion capillary setae. Eight abdominal setigers with bundles of long, slender and spinous capillary neurosetae, and uncinigerous notopodial tori, uncini with 7–8 teeth in double row. Lacking cauda. No tubes.

Paratypes 4 mm long with three abdominal setigers. Only two inner paleae on right side of stalk, 18 outer paleae on left side of stalk.

Etymology.—The specific name, from Latin *tenuis* = thin, refers to its very small size.

Remarks.—*Phalacrostemma tenue* is closely related to *P. lechapti* Kirtley, 1994, formerly described as *P. cidariophilum* Fauvel, 1914 (not Marenzeller, 1895), but the arrangement of spinous fringes on the outer paleae and the parathoracic notosetae (Table 1) clearly distinguish these two abyssal forms, one from the Atlantic (Fauvel 1914: 273), the other from the Pacific.

Phalacrostemma profundum, new species
Fig. 6

Material examined.—Loyauté Basin, zone Z2, BIOGEOCAL cruise, station CP 317, 20°48′S, 166°53′E, 1630 m, 2 May 1987 (one specimen); off southwest Lifou, zone SB2, BIOGEOCAL cruise, station CP 265, 21°04′S, 167°04′E, 1870 m, 18 Apr 1987 (two specimens with tubes), Holotype (MNHNP UC 360), Paratype (MNHNP UC 362); off southwest New Caledonia, zone SB5, BIOGEOCAL cruise, station CP 214, 22°44′S, 166°28′E, 1665 m, 9 Apr 1987 (one specimen), Paratype (MNHNP UC 361).

Description.—Holotype 12 mm long, including opercular crown; diameter of opercular crown 2 mm, thoracic diameter 1.8 mm. Short opercular stalks well divided into two symmetrical halves with outer paleae 2 mm long (Fig. 6A, B). Each half of crown with 30–40 outer paleae spirally arranged, some paleae moved backward in relation to external row. These outer paleae tapered, ringed, without spinous ornamentation (Fig. 6D, E). Along dorsal edge of each crown, 2–3 yellow, smooth, inner paleae with distal apex slightly curved (Fig. 6C). Crown margins with 13–14 long bifid pericoronal palpi. Four pairs of curved dorsal hooks. A small median organ present between dorsal inner margins of stalk. Pair of large, deeply

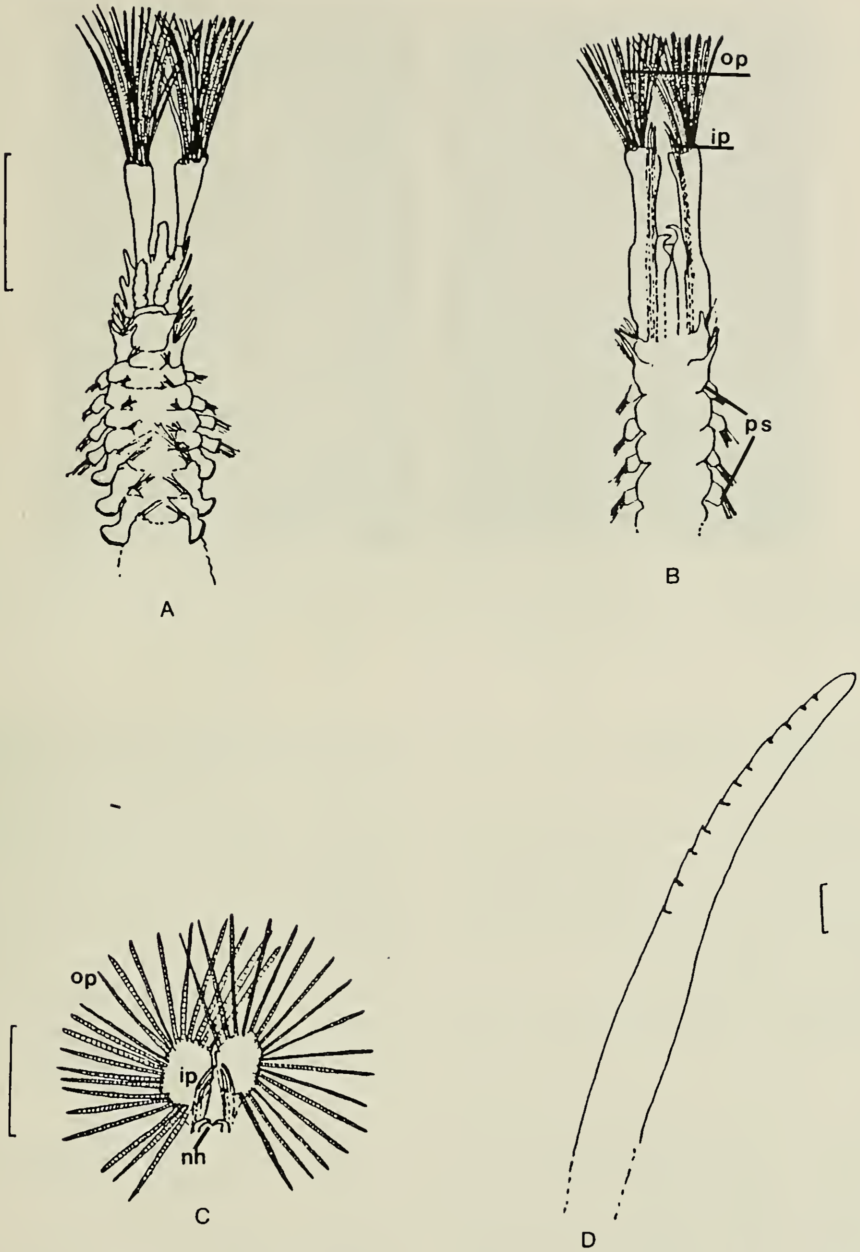


Fig. 4. *Phalacrostemma tenue*, new species, (Holotype, MNHNP UC 358): A, ventral view of anterior end; B, dorsal view of anterior end; C, surface view of crown; D, inner paleae. Scale bars = 1 mm for A–C and 0.1 mm for D. See Fig. 1 for key to abbreviations.

grooved, peristomial tentacles arising from anterior margin of stoma. Four feeding tentacles on each anterior lateral margin of buccal cavity. Large glandular, U-shaped building organ with marginal bundles of short spinous capillary setae. Setiger 2 with bundles of spinous capillary setae and short triangular cirri.

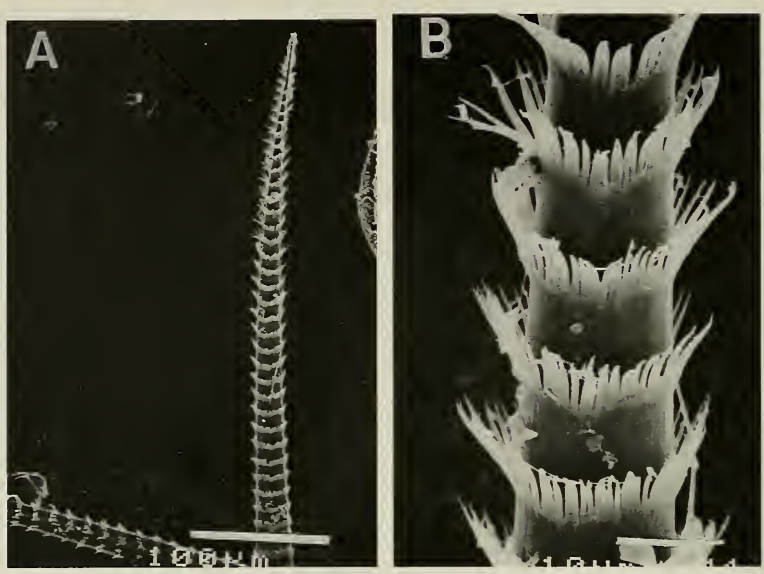


Fig. 5. *Phalacrostemma tenue*, new species, (Holotype, MNHNP UC 358): A, SEM of outer paleae; B, SEM of outer paleae magnified. Scale bars = 100 μm for A and 10 μm for B.

Four parathoracic segments with slightly spinous neuropodial capillary setae and bundles of 6–7 tapering bristly notopodial setae with smooth capillary companion setae. Abdominal segments with spinous capillary neurosetae, notopodia with comblike uncini with 8–9 rows of teeth. Cauda absent. Tubes composed of sand grains.

Etymology.—The specific name, from the Latin *profundus* = deep, refers to the great depths from which it occurs (1720 m on average).

Remarks.—Phalacrostemma profundum, new species, is distinguished from *P. cidariophilum* Marenzeller, 1895 and from other species of this genus by the smooth outer paleae and the shape of the inner paleae and by its geographical distribution (Table 1).

Genus *Bathysabellaria* Lechapt & Gruet, 1993

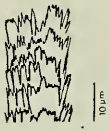
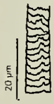
Characteristics of this genus include an opercular stalk completely fused; blades of outer paleae broad, stout, inner surfaces slightly concave, terminating in acuminate tips, blades with basal transverse ridge, rotated around longitudinal axis of shafts; inner paleae twice as long as outer paleae, inner surface slightly concave, outer surfaces expanded, gently curved toward center of crown, with 3–4 simple, small, filamentous ciliated feeding tentacles on each side of buccal cavity; two relatively small preoral tentacles; nuchal spines straight, cylindrical, with very slightly curved distal tips; four parathoracic segments (Lechapt & Gruet 1993).

Bathysabellaria neocaledoniensis Lechapt & Gruet, 1993
Fig. 7

Material examined.—Southwest Pacific Ocean: off New Caledonia, BIOCAL cruise, stations DW 44, 22°47′S, 167°14′E, 440 m–450 m, 30 Aug 1985, 24 specimens, DW 77, 22°15′S, 167°15′E, 440 m, 3 Sep 1985, one specimen.

Description.—Opercular paleae of two kinds: outer paleae in concentric row along anterior periphery of crown surface, 28 in number, bright yellow-gold, smoothly ta-

Table 1.—Some characteristics of species of *Phalacrostemma* Marenzeller, 1895.

SPECIES		Characteristics of outer paleae	Aspect of outer paleae	Number of outer paleae	Characteristics of inner paleae	Geographic occurence	Depth sampling
P. abyssalis	Kirtley, 1994	With short distal fringe with simple ornamentation		10	no data	Flores Sea (Indonesia)	794 m
P. cidariophilum	Marenzeller, 1895	Smooth distal margins slightly inclined from horizontal		8	Flattened, straight with gently rounded tips	Adriatic, Mediterranea	485 m–1298 m
P. dorothyae	Kirtley, 1994	Thecae of middle part of blade with short finely denticulate fringe forming crescentic distal margin		no data	Irregular, slightly inflated thecae with distal margins	Florida	350 m
P. gloriae	Kirtley, 1994	Thecae of middle portion with shorter and fewer denticles with slightly undulatory horizontal trace		no data	Thecae well developed with distal margins producing zig-zag pattern	Gulf of Mexico	230 m
P. gwendolynae	Kirtley, 1994	Distal fringe with expanded delicately attenuate distal extension		no data	no data	Carribean Sea	228 m
P. lechapti	Kirtley, 1994	Distal of outer paleae with irregularly distally expanded rows of alternately wide and narrow marginal extensions, with both long and short, pectinate, distal tips		no data	With conspicuous thecae and with deep groove along proximal median portion	Azores	880 m–1440 m
P. paulinae	Kirtley, 1994	Distal portion with expanded distal regular denticles forming distal fringes		no data	no data	West Atlantic	2160 m
P. perkinsi	Kirtley, 1994	Middle portion without distinct dentition and very weakly expanded distal margins		no data	no data	Bahamas Islands	1360 m
P. setosa	(Treadwell, 1906)	Distal portion without conspicuously expanded, with distal margins forming horizontal zig-zag pattern.		no data	no data	Hawaï Islands	300 m–700 m
P. tenera	(Augener, 1906)	Incomplete description	—	no data	no data	Barbados	365 m
P. profundum	this work	Tapering, ringed without spinous ornamentaion		30/40	Smooth with distal portion lightly incurved	Off New Caledonia	1700 m
P. tenue	this work	Longitudinal striations and expanded distal margins with regular distal denticles forming fringes		16/17	Smooth blunted tips with regularly spaced transverse markings	Off New Caledonia	1400 m

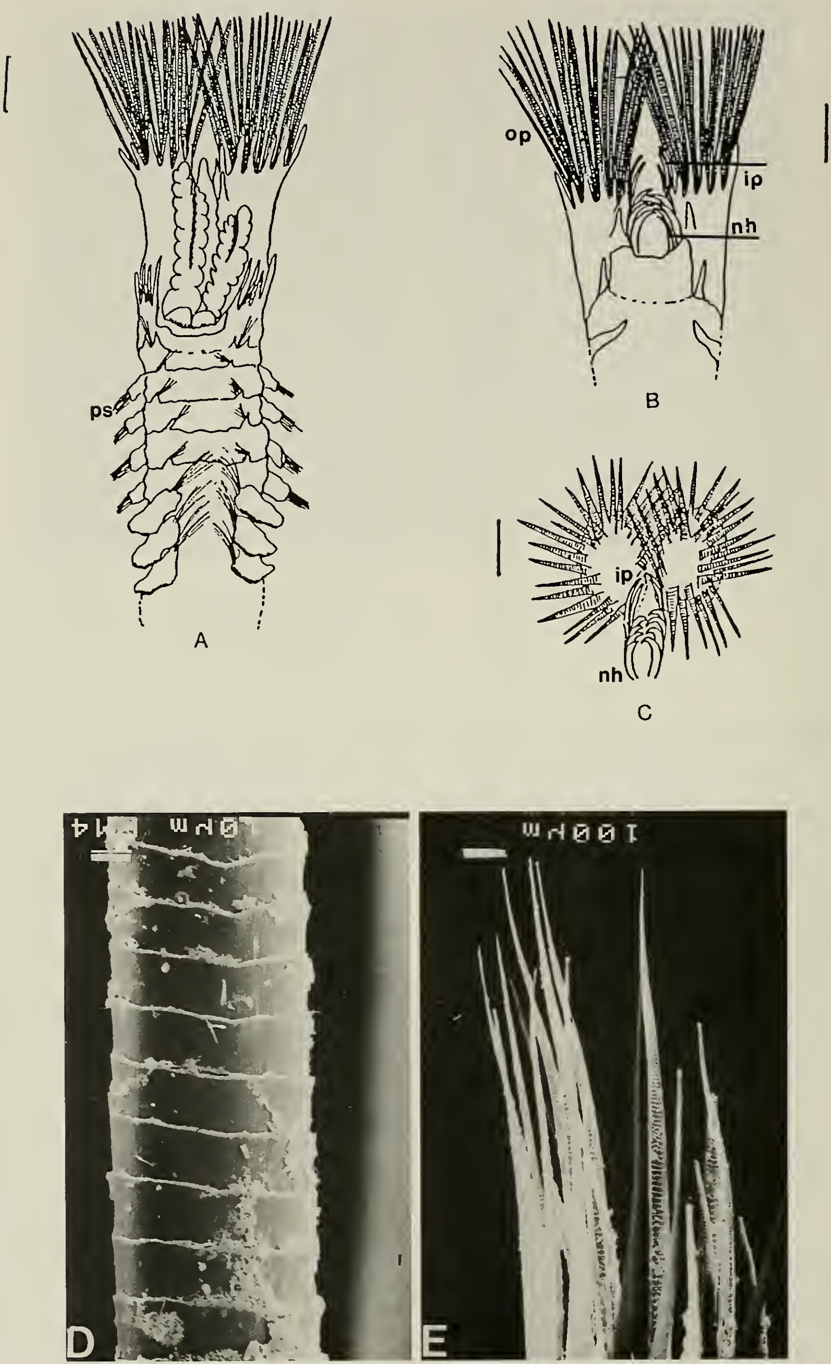


Fig. 6. *Phalacrostemma profundum*, new species, (Holotype, MNHNP UC 360): A, ventral view of anterior end; B, dorsal view of anterior end; C, surface view of crown; D, SEM of outer paleae magnified; E, SEM of outer paleae. Scale bars = 1 mm for A–C, 10 μm for D and 100 μm for E. See Fig. 1 for key to abbreviations.

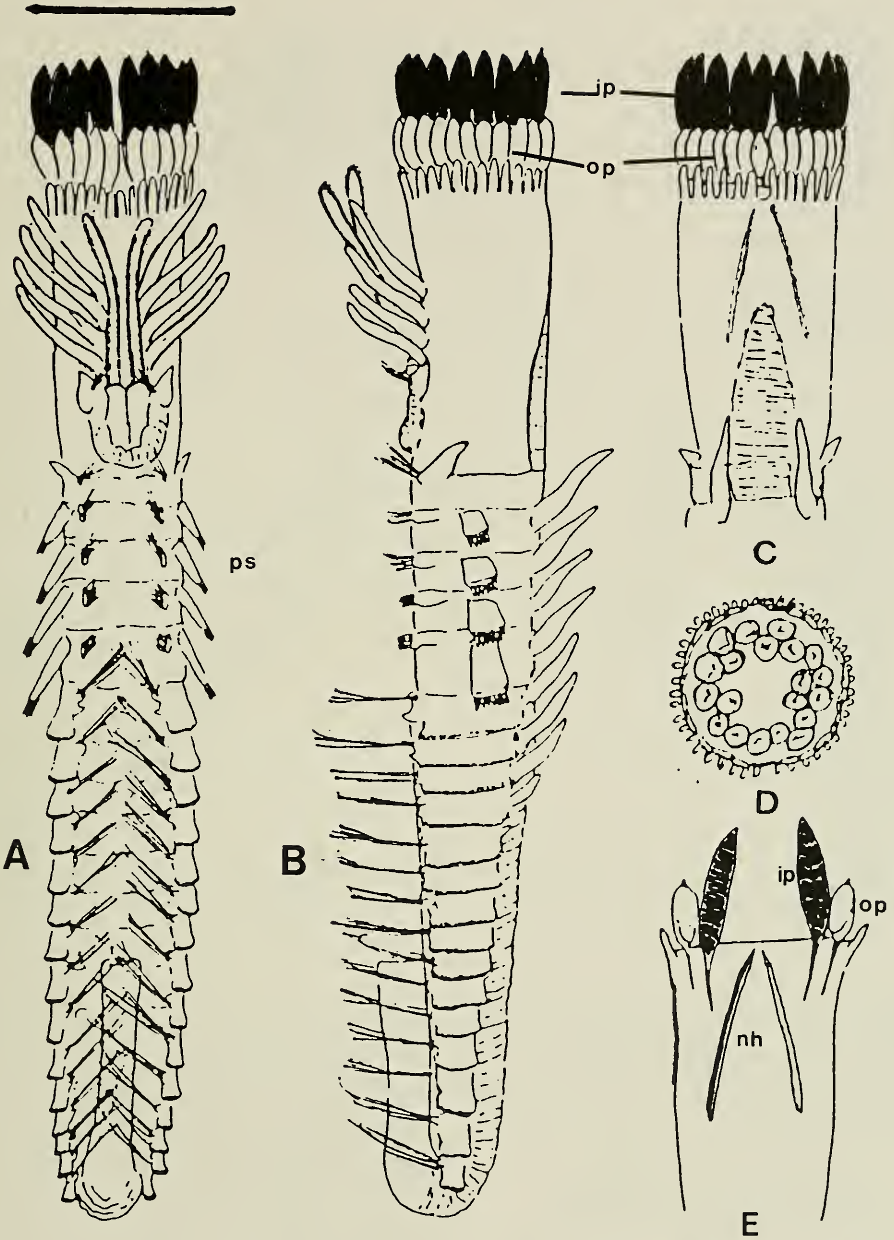


Fig. 7. *Bathysabellaria neocaledoniensis:* A, ventral view; B, left lateral view; C, dorsal view of anterior end; D, view of anterior surface of crown; E, cross-section of anterior end of crown showing position of opercular setae and nuchal spines. Scale bar = 2 mm. See Fig. 1 for key to abbreviations.

pered distal margin, and frayed or broken tips; inner paleae in single irregularly crowded row, 11 in number, erect, twice as long as outer paleae (Fig. 7A–E); blades inflated, terminating in slightly bent, mucronate tips, with basal concavity and numerous fine transverse serrations, with simple pair of golden, acicular nuchal spines on each side of dorsal midline of opercular stalk.

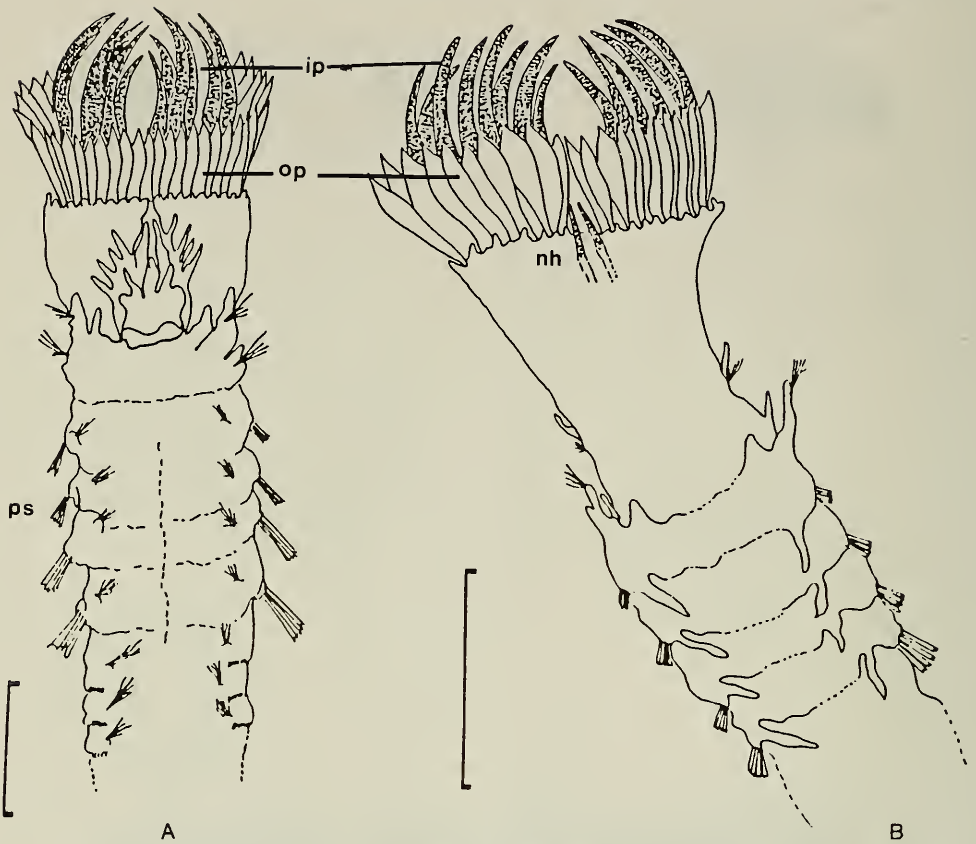


Fig. 8. *Bathysabellaria spinifera:* A, ventral view of anterior end; B, dorsal view of anterior end. Scale bars = 1 mm.

Agglutinated tubes composed of small sand grains and *Globigerina* tests.

Remarks.—Known only from the localities reported herein.

Bathysabellaria spinifera
Lechapt & Kirtley, 1996
Fig. 8

Material examined.—Off New Caledonia, BIOCAL cruise, stations DW 36, 23°08′S, 167°11′E, 650 m–680 m, 29 Aug 1985, 11 specimens; DW 33, 23°10′S, 167°10′E, 675 m–680 m, 29 Aug 1985, 3 specimens; DW 46, 22°53′S, 167°17′E, 570 m–610 m, 30 Aug 1985, 145 specimens; DW 51, 23°05′S, 167°45′E, 680 m–700 m, 30 Aug 1985, 287 specimens and MUSORSTOM IV cruise (N/O *Vauban*), station DW 222, 22°57′S, 167°33′E, 410 m–440 m, 30 Sep 1985, 2 specimens.

Description.—Opercular crown with two kinds of paleae: outer paleae bright yellow, blades smoothly tapered, with fine serration, 33–51 in number in various specimens and disposed in a complete circle around periphery of crown without any interruption or ventral indentation (Fig. 8A, B); inner paleae golden brown, arranged in two or three concentric rings, not in a spiral whorl; blades spiniform, distally curved, with inflated base and numerous fine serrations, one or two short inflated paleae inserted between long curved paleae, 20–30 in external row, 10 to 20 in the internal row. Two

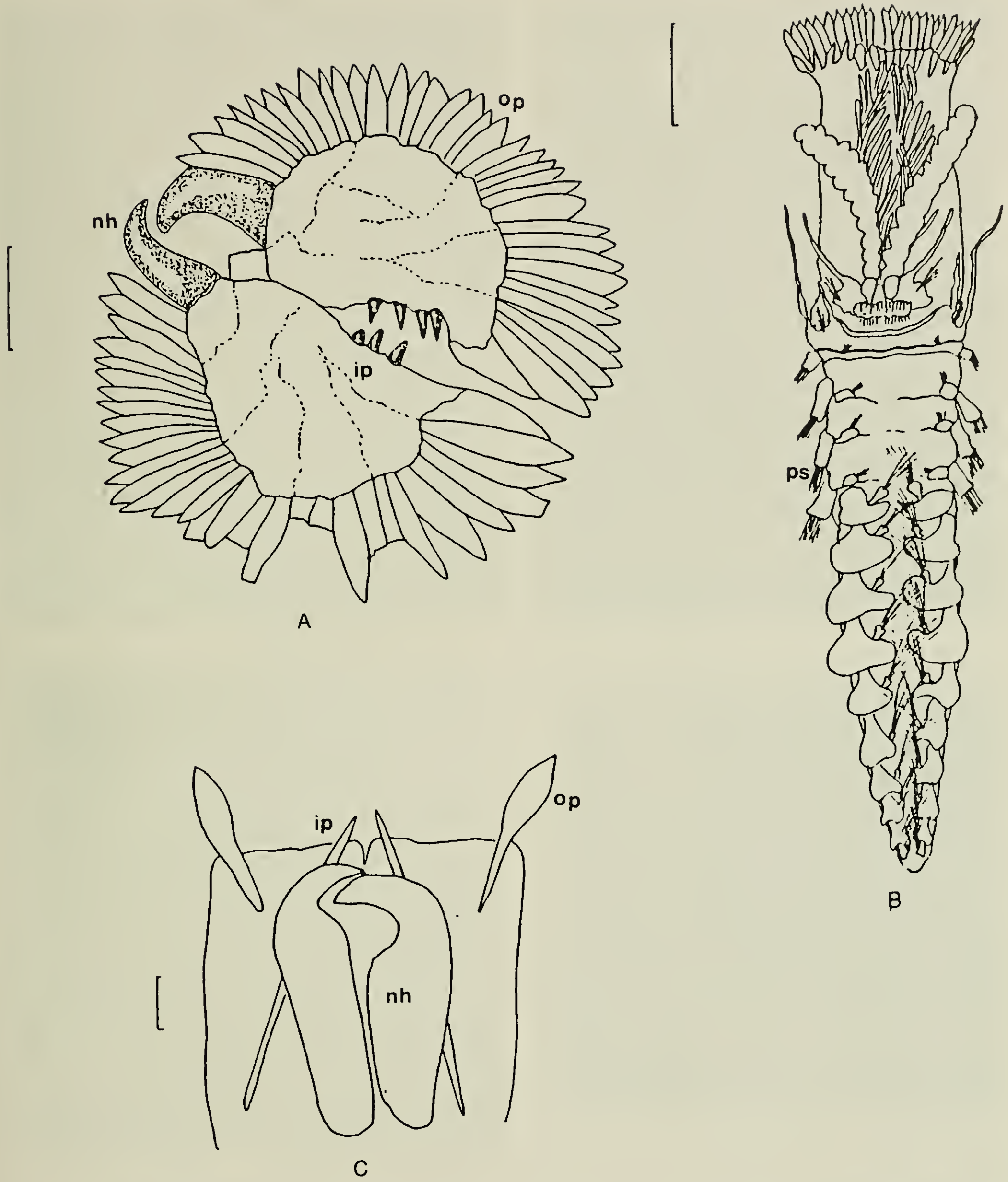


Fig. 9. *Tetreres robustus*, new species, (Holotype, MNHNP UC 363): A, view of surface of crown; B, ventral view; C, cross-section of anterior end of crown showing position of opercular setae and nuchal spines. Scale bars = 1 mm for A, C and 10 mm for B.

straight, golden, cylindrical, acicular nuchal spines with slightly curved distal tips on each side of the dorsum of the opercular stalk.

No tubes were sampled.

Remarks.—Bathysabellaria spinifera, only from the localities reported herein (Lechapt & Kirtley 1996), is characterized by a greater number of individuals (400 specimens) and a wider bathymetric distribution than the other species of the genus, *B. neocaledoniensis.*

Genus *Tetreres* Caullery, 1913

Tetreres robustus, new species

Figs. 9–10

Material examined.—Southeast off New Caledonia, BIOCAL cruise, stations DW 44, 22°47′S, 167°14′E, 440 m–450 m, 30 Aug 1985, 2 specimens (Holotype MNHNP UC 363); DW 77, 22°15′S, 167°15′E, 440 m, 5 Sep 1985, 5 specimens (Paratypes MNHNP UC 365); blocks with burrows inside (UC 364).

Description.—Holotype 35 mm long with 19 setigers (incomplete specimen). Thoracic diameter 8 mm, opercular crown 8 mm in diameter. Opercular stalk partially divided along dorsal midline (Fig. 9A). Outer paleae, 70–80 in external series, yellow gold, smooth, with distally spatulate blades (Figs. 9A, B, 10A, B); inner paleae, 3–4 on each side, parallel to midline of crown, 6 mm long (Figs. 9A, 10D). Pair of large dorsal nuchal hooks bent outward at right angles to longitudinal axis of blades and shaft with tips pointing inward toward prostomium (Figs. 9C, 10C).

Opercular stalk with 25–30 long, conical papilli; relatively short peristomial tentacles, 12 in number, and 2 long paired lateral lips. Building organ with accessory setigerous cirri on each side. Series of 4 elongate, triangular cirri along either side of setiger 2; inferior cirri with tiny bundles of fine, spinous capillary setae. Four parathoracic segments with fin-like notopodia, each with 7–9 stout setae with lanceolate tips and companion capillary setae. Neuropodia with similar setae, fewer in number (4–6), with pair of dorsal branchiae on each parathoracic segment.

Abdominal segments with neuropodial cirri with bundles of long capillary setae, some long, smooth capillary setae, and strongly spinous capillary setae. Notopodial uncini with 8–9 teeth in double rows.

All specimens were collected inside burrows of 6–7 mm in diameter, in large blocks made of *Globigerina* tests (UC 364).

Etymology.—The specific name, from the Latin *robustus* = robust, refers to its great size.

Remarks.—*Tetreres robustus*, new species, is characterized by the number and shape of the outer paleae and belongs to the group of species whose outer paleae possess elongate, flattened blades.

Key to the species of *Tetreres*

1a. Outer paleae with elongate flattened blades 2
1b. Outer paleae without flattened blades 4
2a. Nuchal hooks with short distal tips (Indian Ocean, 896 m) . . . . *T. sandraae*
2b. Nuchal hooks with long distal tips . . 3
3a. Blades of outer paleae with attenuate distal spike 8
3b. Blades of outer paleae without attenuate distal spike 6
4a. Cylindrical outer paleae with distal prolongation 5
4b. Cylindrical outer paleae without distal prolongation (Indonesia, 330 m) . . . . *T. superbus*
5a. Distal tip of outer paleae short, flattened, with filiform plume (Philippine Islands, 1470 m) . . . . . . *T. philippinensis*
5b. Blades of outer paleae short, flattened, without filiform distal tip (Antarctica, 3803 m) . . . . *T. maryriceae*
6a. Blades of outer paleae taper abruptly to slightly flattened tip 7
6b. Blades of outer paleae taper gradually to acute tip 8
7a. Blades of inner paleae with internal fusiform outline (Western Atlantic, 4825 m) . . . . *T. varians*
7b. Blades of inner paleae without internal fusiform outline (Hawaiian Islands, 589 m) . . . . *T. baileyae*
8a. Margins of blades of outer paleae almost parallel 9
8b. Margins of blades of outer paleae not parallel 10
9a. Outer paleae with acute extended tip (Antarctica, 4758 m) . . . .*T. cassidyi*
9b. Outer paleae with dyssimetrical acute tip (Southeast Pacific Ocean, 440 m) . . . . *T. robustus*, new species

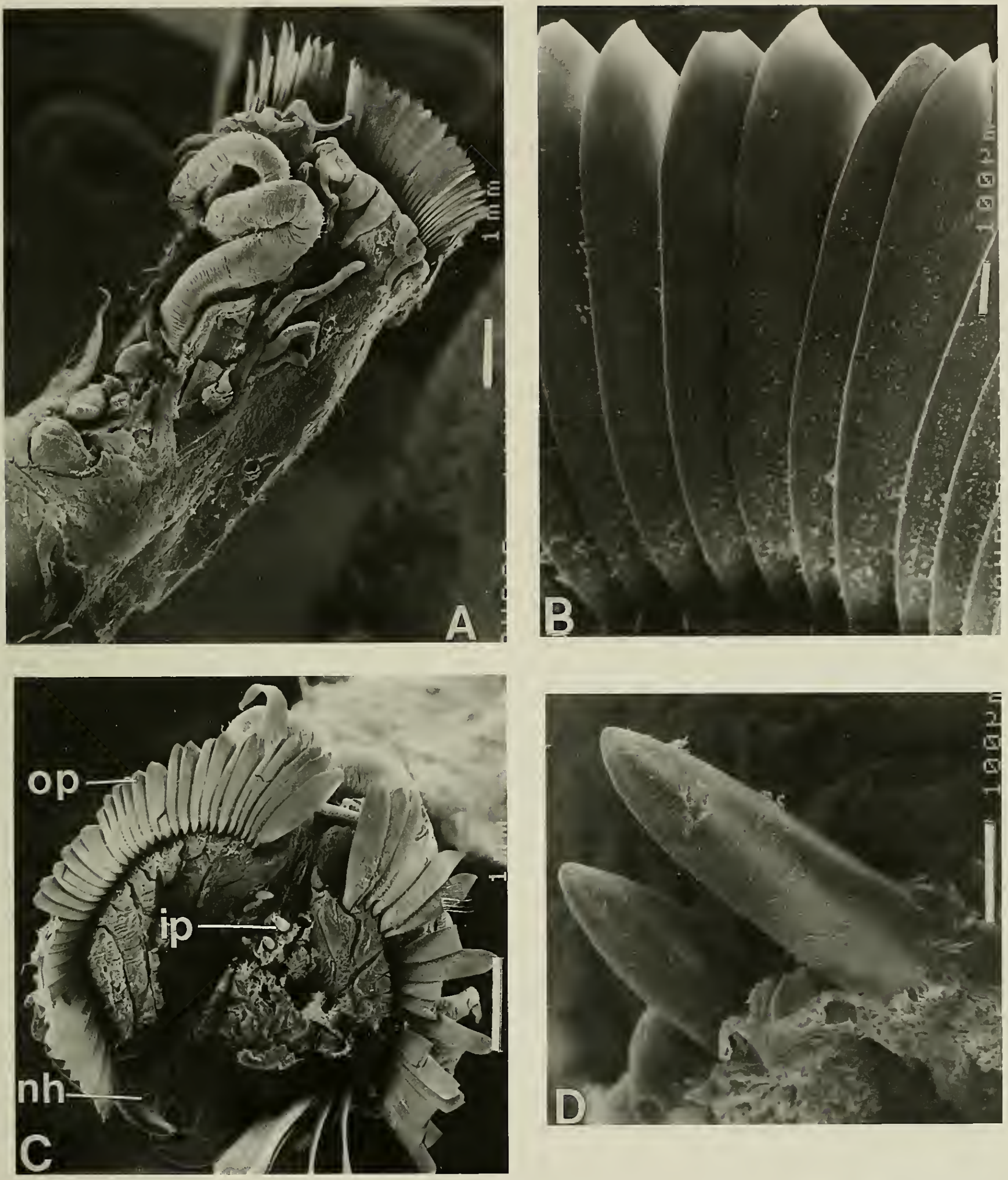


Fig. 10. *Tetreres robustus*, new species, (Holotype, MNHNP UC 363): A, SEM of anterior end; B, SEM of outer paleae; C, SEM of surface of crown; D, SEM of inner paleae enlarged. Scale bars = 1 mm for A, C and 100 μm for B, D. See Fig. 1 for key to abbreviations.

10a. Margins of blades of outer paleae wide through distal one-half (East Central Pacific Ocean, 3850 m) .... *T. jirkovi*

10b. Margins of blades of outer paleae wide through middle portion, with conspicuous transverse thecal bands across surface (Northwest Atlantic Ocean, 4825 m) .... *T. perryi*

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Two new species of *Nereis* (Polychaeta: Nereididae) from Todos Santos Bay, Ensenada, Baja California, México

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Abstract.—The nereidid fauna of Todos Santos Bay was studied. In this paper we describe two species of *Nereis* that are new to science. *Nereis fauchaldi* belongs to the species group with the dorsal ligule expanded in posterior parapodia, and homogomph falcigers with smooth blades. *Nereis imajimai* belongs to the species group with the dorsal ligule short in posterior parapodia, and homogomph falcigers with short and dentate blades.

Nereididae is one of the polychaete families with a broad distribution. Members of this family are found at all latitudes and from the intertidal to abyssal depths; however, they are found more frequently in shelf depths. Terminology of parapodial structures follows Hutchings & Reid (1990).

Baja California, Mexico, is a state with two different coasts bordering two different water masses, the Gulf of California (Cortes Sea) on the eastern side, and the Pacific Ocean on the western side. Nereidid polychaetes have been little studied on the Pacific side. Only a few species have been reported by Hartman (1952, 1963), Treadwell (1923), Berkeley & Berkeley (1958) and Reish (1963). In the present work we describe two new species of *Nereis* from Todos Santos Bay, located in the Pacific coast of Baja California, 100 km south of the U.S.A.-Mexico border. The study is based on samples from 47 stations collected between 31°40′ to 31°55′N and 116°36′ to 116°50′W, carried out by the O/V *Francisco de Ulloa* from CICESE.

The material reported was obtained with a Van Veen grab (0.1 m^2), during the cruise "BAHIA-10-94" off the Ensenada coast in October 1994. Type specimens are deposited in the Polychaetological Collection of the Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, México (UANL); others are in the Centro de Investigación Cientifica y de Educación Superior de Ensenada, B.C., México (CICESE).

Nereis fauchaldi, new species
Fig. 1a–f

Material examined.—Stn. 26 (1) (Holotype, UANL 3945), [116°44′N, 31°47′W], 210 m depth.

Additional material.—Western coast of Baja California, Sebastian Vizcaino Bay, dredge (6 Jul 1989) Stn. F-10, (1) [28°07′N, 115°00′W], 85 m depth (UANL 3946); Shrimp trawl (6 Jul 1989) Stn. 2 (1) [28°47′N, 114°34′W], 84 m depth (UANL 3947).

Description.—The holotype is an incomplete specimen, without evident pigmentation pattern, 12 mm long, 1.5 mm wide including parapodia, with 40 setigers. Prostomium pentagonal, two digitate frontal antennae, shorter than palps. Eyes large, anterior pair oval, posterior pair round. Palps biarticulate, thin, palpostyles conical. Peristomium longer than next two seg-

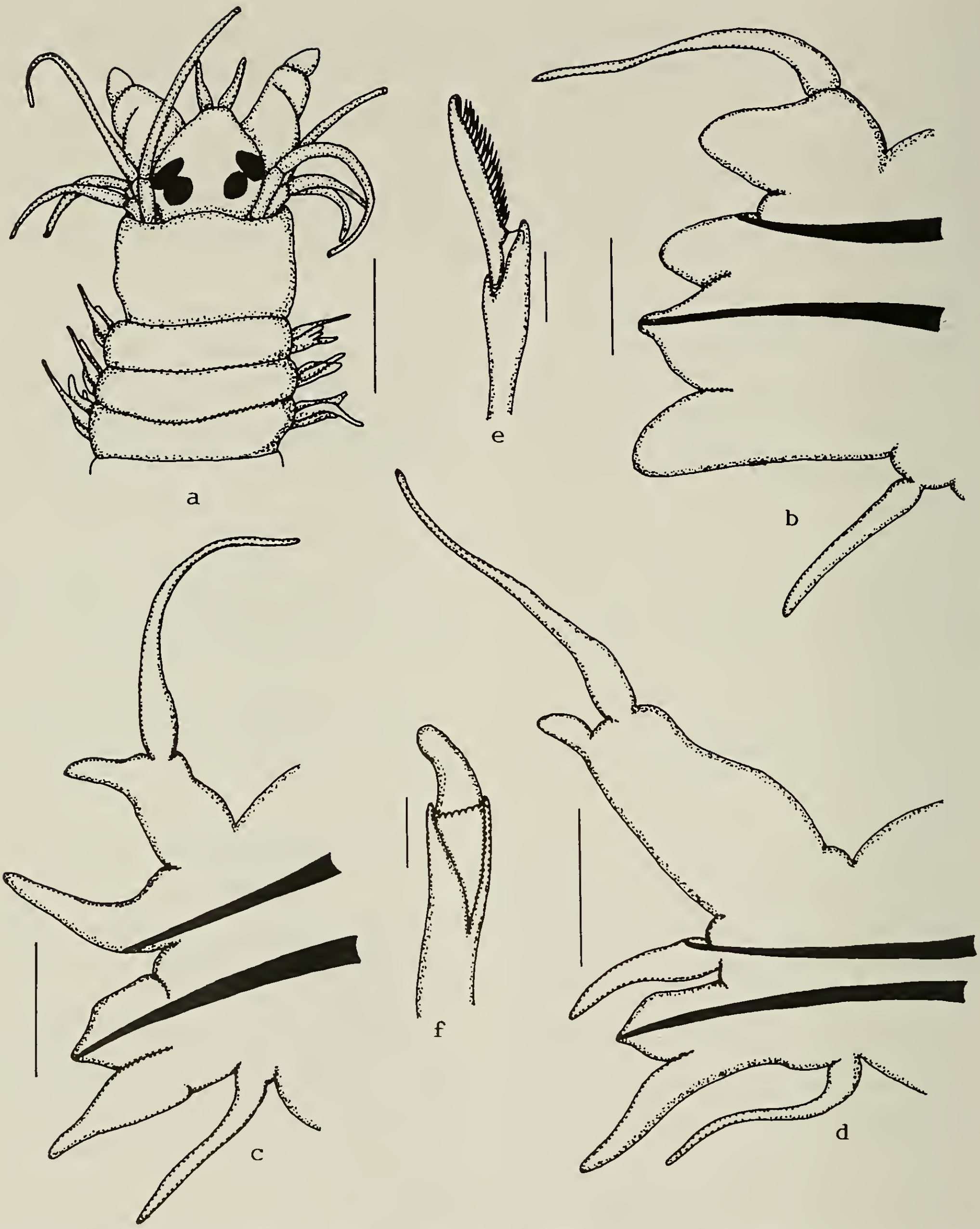

Fig. 1. *Nereis fauchaldi*, new species: a, anterior end, dorsal view; b, 9th setiger, anterior view; c, 26th setiger, anterior view; d, 39th setiger, anterior view; e, neuropodial heterogomph falciger of setiger 9; f, notopodial homogomph falciger of setiger 28. Scale bars: a = 1 mm; b–d = 150 μm; e–f = 15 μm.

ments, with four short tentacular cirri, longest reaching setiger 3 (Fig. 1a).

Pharynx with brown jaws, each with 6 teeth; paragnaths as: I = 2 cones; II = 12 cones in 2 oblique rows; III = 14 cones in oval group; IV = 20 cones in crescent shape; V = 0; VI = 8 cones in circle; VII–VIII = 70 small cones in 3 rows near oral aperture, and 7 larger cones in one distal row.

Parapodia of first two setigers uniramus, thereafter biramous. Anterior notopodia with dorsal and median ligule distally conical, superior lobe rounded. Neuropodium with postsetal lobe short, end mammiliform, ventral ligule distally rounded. Dorsal cirri inserted medially on dorsal ligule; ventral cirri inserted basally (Fig. 1b). Median and posterior parapodia with long dorsal ligules. Median and ventral ligule elongate, narrow, postsetal lobes expanded distally. Dorsal cirri inserted subdistally, ventral cirri inserted basally, shorter than dorsal cirri (Fig. 1c, d).

Anterior notosetae slender homogomph spinigers in supracicular position. Supracicular neurosetae similar to notosetae, and a single heterogomph falciger; infracicular setae heterogomph spinigers and falcigers, each falciger with long blade and thin, moderately long serrations, distal part of blade strongly bent (Fig. 1e). Median and posterior supracicular notosetae homogomph falcigers, starting in setiger 14; blade short and distally blunt, without serrations; shaft with crenulate distal membrane (Fig. 1f). Supracicular neurosetae of median parapodia homogomph spinigers and heterogomph falcigers; infracicular setae heterogomph spinigers. Posterior neuropodia each with one heterogomph falciger in supracicular position; and one heterogomph falciger and spiniger in infracicular position.

Pygidium unknown.

Remarks.—*Nereis fauchaldi*, new species, belongs to the group of species characterized by having posterior parapodia with greatly expanded dorsal ligules. This group includes *N. angelensis* Fauchald, 1972, *N. anoculis* Hartman, 1960, *N. anoculopsis* Fauchald, 1972, *N. fossae* Fauchald, 1972, *N. heterocirrata* Treadwell, 1931, *N. ligulata* Hilbig, 1992, *N. nichollsi* Kott, 1951, *N. piscesae* Blake & Hilbig, 1990, *N. profundi* Kirkegaard, 1959, *N. sandersi* Blake, 1985 and *N. vexillosa* Grube, 1851. All of these species, except *N. vexillosa*, have been found in deep waters. These species may be separated into two groups: species with dentate homogomph falcigers; and those with smooth homogomph falcigers. *Nereis fauchaldi*, new species, belongs to the second group, together with *N. angelensis* and *N. fossae*. These species differ in paragnath arrangement and insertion of dorsal cirri. The types of *Nereis angelensis* Fauchald, 1972: holotype (LACM-AHF 1060) and *Nereis fossae* Fauchald, 1972: holotype (LACM-AHF 1058), paratypes (LACM-AHF 1059) (12 specimens) were reviewed. *Nereis angelensis* has the following paragnath arrangement: Area I = 2 in line, II = 17 in 3 irregular rows, III = 24 in 4–5 rows, IV = 18–20 in cresent shape, V = 0, VI = 3 in line right side, 3 in triangle left side, VII–VIII = 35 in one irregular line; *N. fossae* has Area I = 2 in line, II = 15 in 2 rows, III = 28 in oval shape, IV = 18 in cresent shape, V = 0, VI = 3 in line, VII–VIII = 6 in one irregular line; *N. fauchaldi* has Area I = 2 cones, II = 12 cones in 2 rows, III = 14 cones in oval group, IV = 20 cones in cresent shape, V = 0, VI = 8 cones in group, VII–VIII = 70 small cones in 3 rows near the oral aperture, and 7 larger cones on one distal row. *Nereis angelensis* has dorsal cirri inserted basally, while *N. fossae* has dorsal cirri inserted medially, and *N. fauchaldi* has dorsal cirri inserted subdistally.

Etymology.—The species is named after Kristian Fauchald in recognition of his valuable contributions to the systematics of the polychaetes of western Mexico.

Distribution.—*Nereis fauchaldi* is known from its type locality, Todos Santos Bay, Baja California, Mexico, and from Sebastian Vizcaino Bay, western Baja California.

Nereis imajimai, new species

Fig. 2a–g

Material examined.—Stn. 1, [116°38′N, 31°50′W], 25 m depth, (8 specimens) (UANL 3948), Stn. 4, [116°39′N,

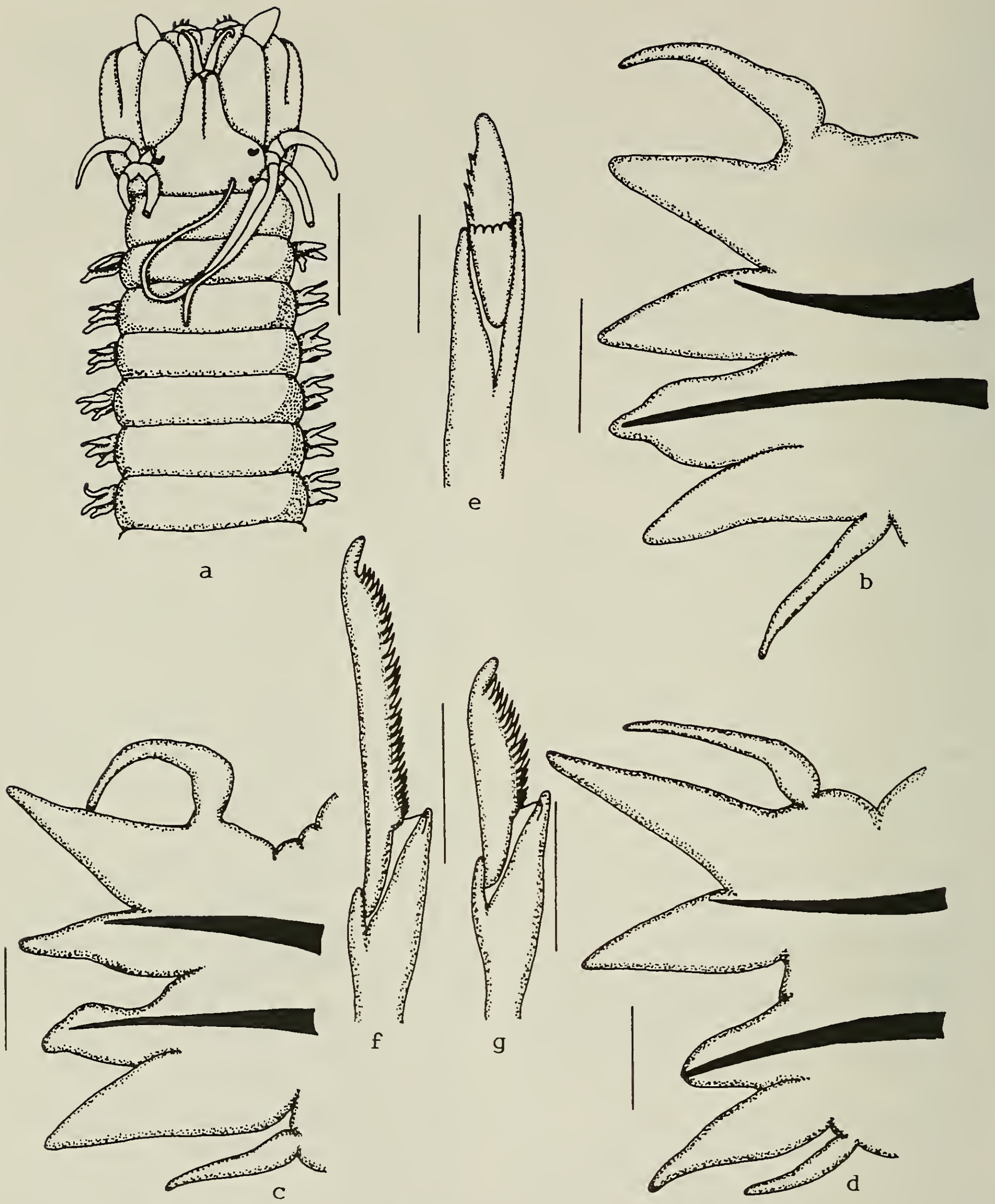

Fig. 2. *Nereis imajimai*, new species: a, anterior end, dorsal view; b, 10th setiger, anterior view; c, 30th setiger, anterior view; d, 53rd setiger, anterior view; e, notopodial homogomph falciger of setiger 30; f, neuropodial heterogomph falciger in upper infracicular position of setiger 30; g, neuropodial heterogomph falciger in middle infracicular position of setiger 30. Scale bars: a = 1 mm; b–d = 150 μm; e = 15 μm; f–g = 10 μm.

31°47′W], 20 m depth, (3 specimens) (UANL 3951), Stn. 13, [116°40′N, 31°50′W], 24 m depth, (10 specimens) (CICESE), Stn. 14, [117°40′N, 31°51′W], 19 m depth, (4 specimens) (CICESE), Stn. 22, [116°42′N, 31°46′W], 51 m depth, (1 specimen) (CICESE), Stn. 26 (Holotype, UANL 0000), [116°44′N, 31°47′W], 210 m depth.

Additional material.—West coast of Baja California, 4 Sep 1990, stn. H-8, [27°56′N, 114°54′W], 66 m depth (2 specimens) (UANL 3981).

Description.—The holotype is an incomplete specimen, yellowish in color, 15 mm long and 1 mm wide including setae, with 54 setigers. Prostomium longer than wide, with pair of cirriform antennae. Eyes small, anterior pair reniform, posterior pair round. Biarticulated palps, with conical palpostyles. Tentacular ring slightly longer than setiger 1, four pairs of tentacular cirri, longest reaching posteriorly to setiger 5 (Fig. 2a).

Pharynx with pair of brown jaws, and with six teeth; paragnaths as: Area I = 0, II = 2 right, 3 left in one row, III = 6 in group, IV = 6 right, 9 left in cresent shape, V = 0, VI = 3 in triangle, VII–VIII = 55 in 3–4 rows.

Setigers 1–2 uniramous, biramous thereafter. Anterior notopodia with dorsal and median ligules triangular, subequal; neuropodia with postsetal lobes distally digitiform, ventral ligules subulate. Dorsal and ventral cirri inserted basally, similar in length (Fig. 2b). Median and posterior parapodia with dorsal and median ligules thin, triangular in shape, dorsal ones longer. Dorsal cirri longer than ventral cirri (Fig. 2c, d).

Anterior parapodia with supracicular notosetae slender homogomph spinigers. Supracicular neurosetae heterogomph falcigers with long finely serrated blades, and homogomph spinigers; infracicular neurosetae slender heterogomph spinigers and falcigers, falcigers similar to supracicular ones. Middle notopodia with homogomph falcigers, with short blade and four coarse teeth along edge, crenulate membrane along distal margin of shafts (Fig. 2e); supracicular neurosetae homogomph spinigers, infracicular neurosetae heterogomph falcigers with long blades and fine serrations, similar to those of anterior parapodia (Fig. 2f), and heterogomph falcigers with short blades (Fig. 2g). Posterior parapodia each with notopodial supracicular homogomph falciger. Supracicular neurosetae homogomph spinigers and one heterogomph falciger; infracicular setae heterogomph spinigers.

Pygidium unknown.

Remarks.—*Nereis imajimai*, new species, belongs to a small group of species that possesses short dorsal ligules in posterior parapodia, homogomph falcigers with short, dentate blades, and no paragnaths on Areas I and V. Other species in this group include *N. apalie* Wilson, 1985 and *N. cirriseta* Hutchings & Turvey, 1982, both known from Australia. *N. imajimai* differs from these species in paragnath arrangement. *Nereis apalie* has paragnaths only on Areas IV = 4 right, 2 left and Area VI = 1; *N. cirriseta* has conical paragnaths arranged as: II = 7 in 2 oblique rows, III = 1 minute cone centrally, IV = 9–10 irregularly in oblique crescent shape, VI = 5 in small oval patch, VII–VIII = 7 in single, evenly spaced transverse row.

Etymology.—The species is named after Minoru Imajima in recognition of his valuable contributions on the systematics of the Nereididae.

Type locality.—Todos Santos Bay, Stn. 26 [116°44′N, 31°47′W], 210 m depth.

Distribution.—*Nereis imajimai* is known from Todos Santos Bay, Ensenada, Baja California, Mexico and the west coast of Baja California.

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Marphysa belli (Polychaeta: Eunicidae) and two related species, *Marphysa oculata* and *M. totospinata*, a new species, with notes on size-dependent features

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Abstract.—Three morphologically related species, *Marphysa belli*, *Marphysa oculata* and *Marphysa totospinata* are described or re-described based on a morphometric study. The morphological differences among these species are discussed. The developmental patterns of antennae, branchiae and setae are emphasized.

Since the establishment of *Marphysa belli* in 1833 by Audouin and Edwards from the French side of the English Channel, this species has been widely reported from other regions of the world, such as Plymouth, England (McIntosh 1910), New England region of the U.S.A. (Pettibone 1963), and the Gulf of Mexico (Treadwell 1921, Gathof 1984). *Marphysa belli* is unique in having both compound falcigers and compound spinigers in the anterior region and in having well-developed branchiae restricted to a short anterior region. With a large number of specimens at hand, this study examines the validity of the cosmopolitan distribution of *M. belli* and the correlation between the variation of certain morphological characters and body size (width) of the specimens.

All specimens were observed with stereo and compound light microscopes. Sketches for the illustrations were made using a camera lucida. The statistical figures were produced with the program Origin. For the correlation coefficients, the confidence limits were set at 0.05.

Marphysa belli Audouin & Edwards, 1833
Figs. 1a–j, 2–6

Material examined.—Gulf of Mexico, off Florida, USNM 090007 (*n* = 2). Atlantic Coast of U.S.A.: USNM 9166 (*n* = 1), USNM 28955 (*n* = 1), USNM 56988 (*n* = 2), USNM 109810 (*n* = 2), USNM 109817 (*n* = 1), USNM 109820 (*n* = 4), USNM 109823 (*n* = 1), USNM 109825 (*n* = 7), USNM 109829 (*n* = 1), USNM 109830 (*n* = 2), USNM 109831 (*n* = 3), USNM 109838 (*n* = 1), USNM 109843 (*n* = 4), USNM 109844 (*n* = 3), USNM 120624 (*n* = 1), USNM 145277 (*n* = 1), USNM 145280 (*n* = 1), USNM 145281 (*n* = 1), USNM 145282 (*n* = 2), USNM 145283 (*n* = 1), USNM 145284 (*n* = 1), USNM 145287 (*n* = 1), USNM 145290 (*n* = 1), and USNM 145294 (*n* = 1). English Channel, France, St. Malo area, Lancieux: NMW.Z.1991.067.2 (*n* = 2, Natural History Museum of Wales). English Channel, France, Bay of Seine: LA073A (*n* = 10, Natural History Museum of Paris) and LAW3A (*n* = 5, Natural History Museum of Paris). The following description is mainly based on a specimen from the Woods Hole region of Massachusetts (USNM 28955).

Abbreviations.—For the prostomial appendages, AI indicates the lateral palps, AII the paired inner lateral antennae and AIII the single median antenna. Species descriptions, including the jaw formulae, are pre-

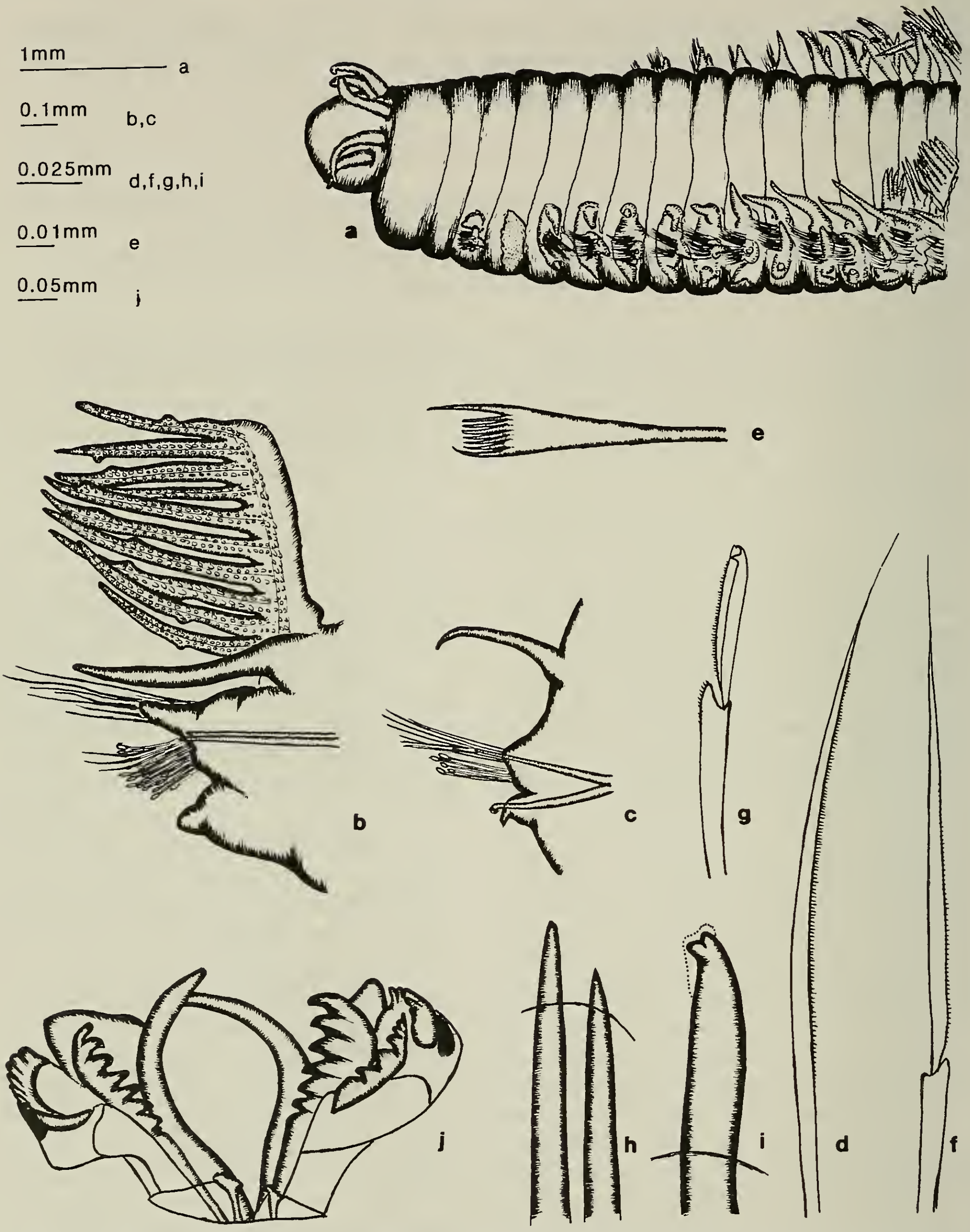

Fig. 1. *Marphysa belli*: a, anterior end, lateral view (USNM 28955); b, 14th parapodium; c, 91st parapodium; d, limbate seta; e, pectinate seta; f, compound spiniger; g, compound falciger; h, aciculae; i, subacicular hook; j, maxillae (USNM 109830).

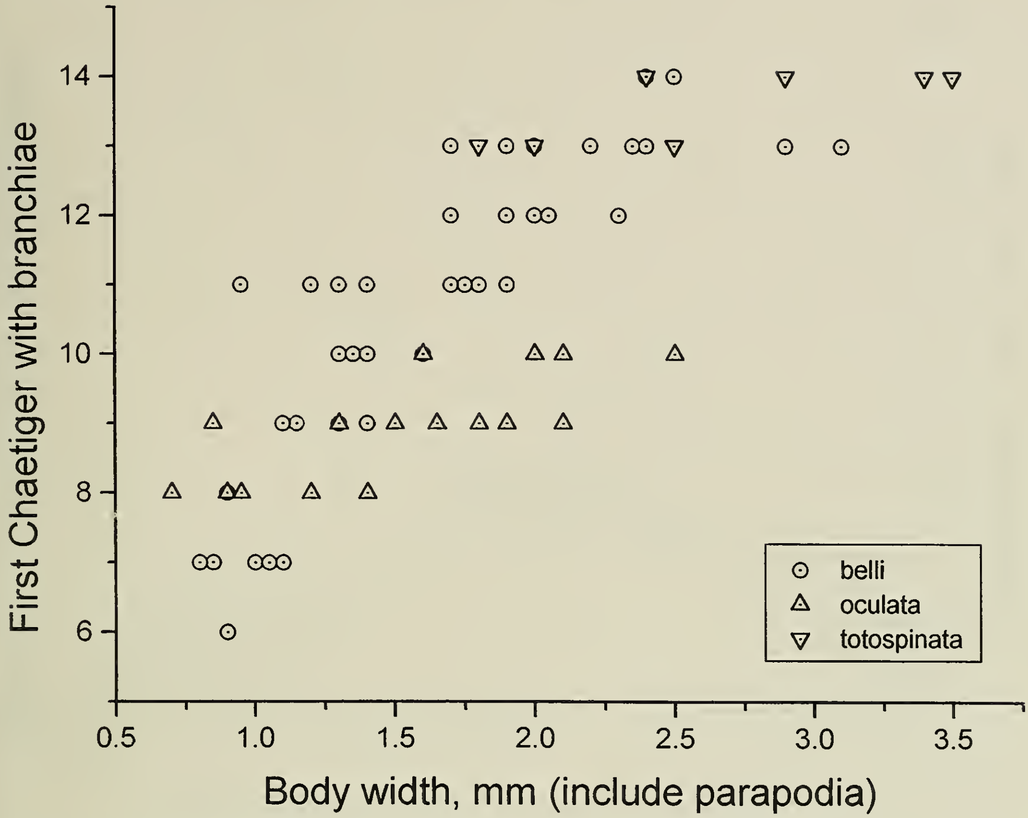

Fig. 2. Size-dependent variation of the first chaetiger with branchiae in *M. belli* (*n* = 48), *M. oculata* (*n* = 18) and *M. totospinata* (*n* = 7).

sented in a format similar to that of Fauchald (1982).

Description.—Specimen complete, with 245 chaetigers. Two pairs of anal cirri; dorsal pair long, reaching last 6 chaetigers. First 10 chaetigers measure 3.0 mm in length, widest region measures 2.3 mm.

Prostomium (Fig. 1a) distally rounded and entire, slightly narrower and shorter than, and ½ depth of, peristomium. Two palps and three antennae, slightly wrinkled, same size; palps and lateral antennae slightly close to each other. Length of AI:AII: AIII = 1:1.2:1.5; AIII extending just past anterior end of prostomium; AII reaching edge of anterior end of prostomium. No eyes observed (eyes observed in other specimens, see discussion below). First ring of peristomium about ⅔ of total peristomial length (dorsal view). No peristomial cirri.

First parapodia smaller than others. Dorsal cirri long throughout body, slender in posterior region. Dorsal cirri always longer than ventral cirri. Postsetal lobe very long in anterior parapodia (Fig. 1b), becoming smaller beginning at first chaetiger (32nd) with subacicular hook (Fig. 1c).

Pectinate branchiae present from 12th–27th parapodia; 12th parapodia with 7 filaments, 27th parapodia with 6 filaments, as many as 12 filaments observed on 18th parapodia. Individual branchial filaments longer than dorsal cirri (Fig. 1b).

Serrated limbate setae (Fig. 1d) longest of those situated on dorsal side of parapodia. Pectinate setae (Fig. 1e) present from anterior parapodia, with 5–9 teeth; tooth on one edge longer, more stout than others, tooth on other edge slightly longer than others. One to eight compound spinigers (Fig.

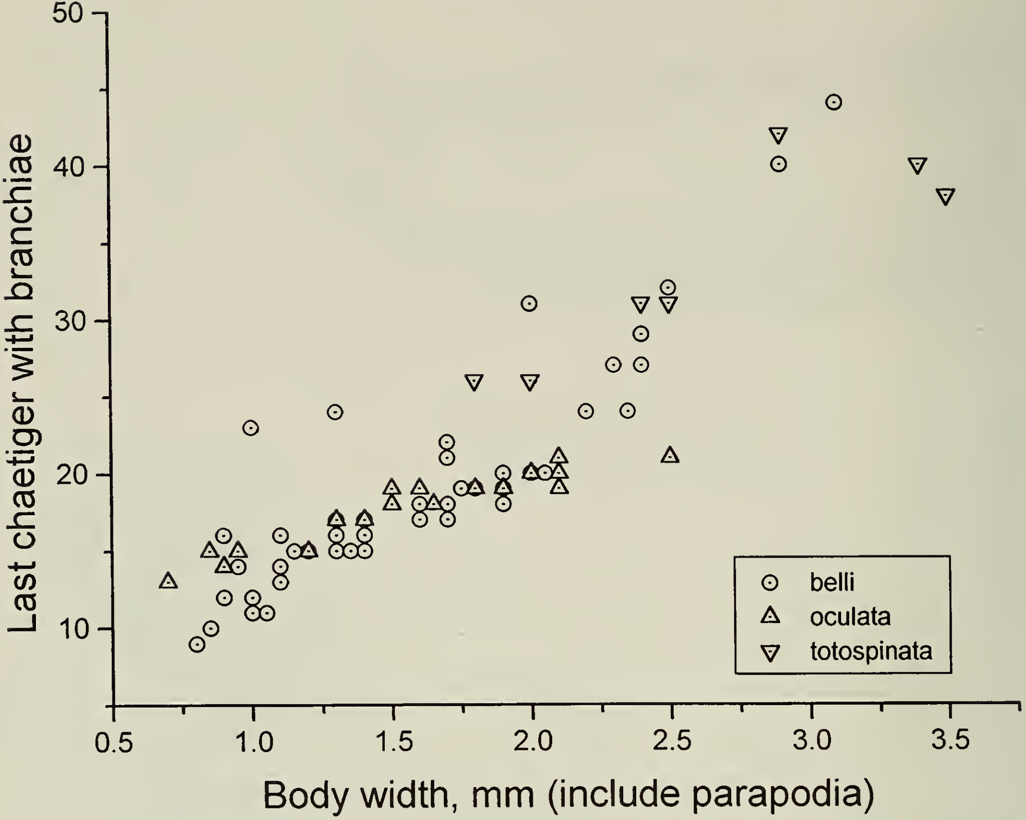

Fig. 3. Size-dependent variation of the last chaetiger with branchiae in *M. belli* (*n* = 49), *M. oculata* (*n* = 18) and *M. totospinata* (*n* = 7).

1f) present from first to about 55th parapodia, situated on posteroventral side of parapodia, with shaft and one side of blade serrated. Compound falcigers (Fig. 1g) present throughout body, arranged in about 3 rows on anteroventral side of parapodia; blade bidentate, with serrated hood and shaft; compound falcigers at least twice as numerous as compound spinigers in any chaetiger in which both kinds of setae occur. Aciculae (Fig. 1h) 2–3 in number in anterior region, becoming single from anterior-middle region; honey color, becoming darker towards posterior end; blunt-headed anteriorly, sharper in posterior region. Subacicular hook (Fig. 1i) bidentate with hood, present from 32nd parapodia, always single, except for replacement; honey to dark honey color.

Maxillary formula (Fig. 1j): 1+1, 6+6, 0+6, 8+4, 1+1 (USNM 109820); 1+1, 7+6, 0+6, 8+4, 1+1 (USNM 109830); 1+1, 8+7, 0+8, 9+4, 1+1 (USNM 109831); 1+1, 8+7, 0+7, 9+5, 1+1 (LAW3A); 1+1, 7+6, 0+6, 7+5, 1+1 (LA073A).

Remarks.—The beginning of branchiae (Fig. 2), the ending of branchiae (Fig. 3), the maximum number of branchial filaments (Fig. 4), the ending of the compound spinigers (Fig. 5) and the beginning of the subacicular hook (Fig. 6) are all size-dependent features (see Table 1). The ending of compound spinigers occurs several chaetigers posterior to the beginning of the subacicular hook.

Of 63 specimens examined, only six are complete. Four complete larval specimens, USNM 109818 (49 chaetigers, 0.8 mm

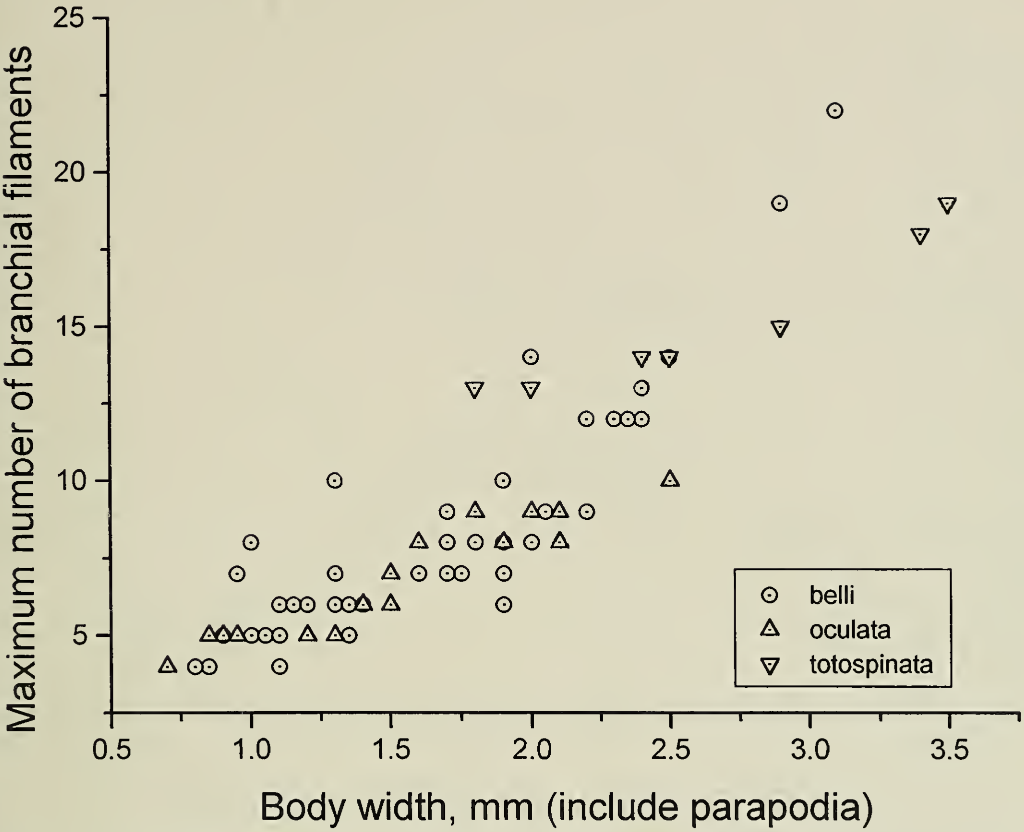

Fig. 4. Size-dependent variation of the maximum number of branchial filaments in *M. belli* (*n* = 49), *M. oculata* (*n* = 17) and *M. totospinata* (*n* = 7).

wide), USNM 109817 (70 chaetigers, 0.9 mm wide), USNM 145290 (58 chaetigers, 0.85 mm wide) and USNM 145294 (88 chaetigers, 1.05 mm wide), have only three antennae developed; the lateral palps (AI) have not appeared. Three other incomplete specimens (USNM 56988, 145280, 109820), have a body width of 0.9–1.05 mm and also have only three antennae developed. One complete specimen, USNM 109825 (77 chaetigers, 1.1 mm wide), has three antennae and two palps developed; two other small incomplete specimens, USNM 109825 (1.2 mm wide) and USNM 145277 (1.1 mm wide), also have antennae and palps. These observations suggest that *M. belli* does not develop its palps until it reaches about 80 chaetigers and a body width around 1.1 mm.

One pair of very light-colored reniform eyes was observed in most of the specimens from the Atlantic coast of the U.S.A., such as in USNM 109820. For specimens from the French coast of the English Channel, those collected two decades ago, eyes are not observed. All recently collected specimens have distinctive eyes. It is likely that the absence of eyes in preserved specimens of *M. belli* is an artifact of prolonged preservation.

When one of us (HL) visited the Natural History Museum in Paris, the type specimen of *M. belli* from the Island of Chausey was not available. However, many specimens from around the type locality, such as St. Malo, which is in the same bay as the type locality, were examined. Audouin & Edwards' (1833) original description is

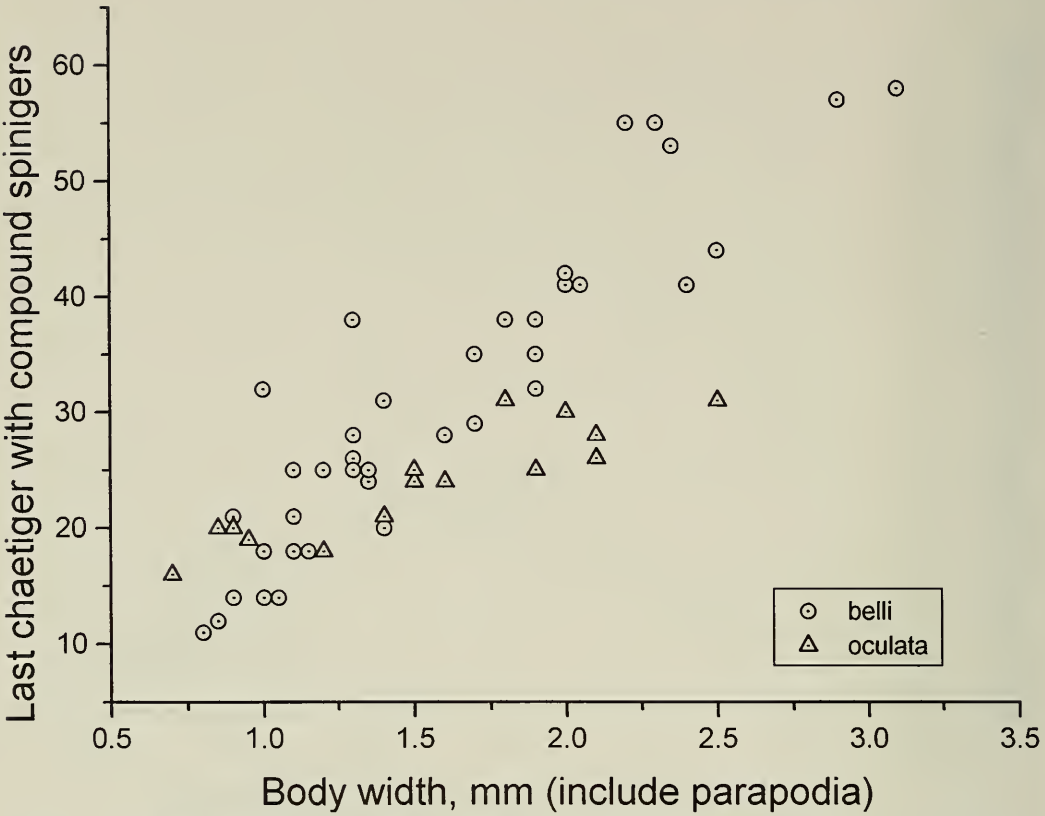

Fig. 5. Size-dependent variation of the last chaetiger with compound spinigers in *M. belli* (*n* = 40) and *M. oculata* (*n* = 15).

very simple, and it does not contradict the features we observed in these specimens.

Geographic distribution.—*M. belli* has a wide geographic distribution. It not only occurs on the French side of the English Channel but is also found along much of the Atlantic coast of the U.S.A. (Massachusetts, Delaware, Georgia) and from one station in the Gulf of Mexico, off Florida.

Marphysa oculata Treadwell, 1921
(Char. emend.)
Figs. 2–6, 7a–j, 8

Material examined.—North Atlantic Ocean, Gulf of Mexico, USA, off Florida, Dec 1982 or Jun 1983 (USNM 129779), 25°17′48″N, 81°39′48″W, SOFLA, 14 m, STA 52, *n* = 12; USNM 129706, *n* = 2; USNM 130127, *n* = 1; USNM 130256, *n* = 2; USNM 130368, *n* = 6; USNM 130484, *n* = 1. The following description is based mostly on the catalogued specimen USNM 129779.

Description.—Specimen complete, with 120 chaetigers. First 10 chaetigers measure 2.1 mm in length, widest region (with parapodia) measures 2.2 mm. Two pairs of anal cirri; long dorsal pair reaching last 5 chaetigers; small ventral pair only ⅓ length of dorsal pair.

Prostomium distally round and entire (Fig. 7a); slightly narrower than peristomium, subequal in length and less than ½ depth of, peristomium. Three antennae (AII and AIII) and two palps (AI), irregularly slightly wrinkled, evenly spaced, short, similar in thickness. Length of AI:AII:AIII = 1:1.3:1.4. AII and AIII extending to near

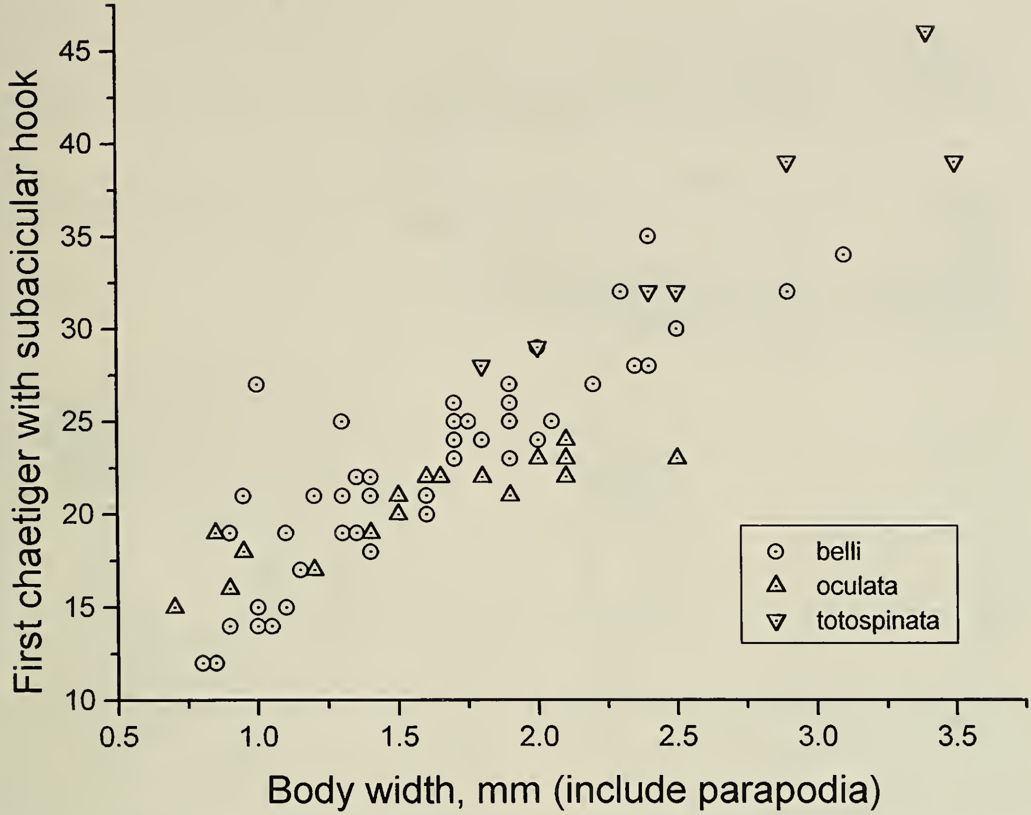

Fig. 6. Size-dependent variation of the first chaetiger with subacicular hook in *M. belli* ($n = 49$), *M. oculata* ($n = 17$) and *M. totospinata* ($n = 7$).

anterior end of prostomium. One pair of large, black oval eyes outside of AII and posterior to AI, partly covered by peristomium. First ring of peristomium ⅔ (dorsally) to ¾ (ventrally) of total peristomial length. No peristomial cirri.

First chaetiger equal in length to second ring of peristomium, following chaetigers broader and longer. First parapodia smaller than others. Dorsal cirri long throughout body, always longer than ventral cirri. Postsetal lobe long in anterior parapodia (Fig. 7b), absent from chaetigers with subacicular hook. Ventral cirri digitiform throughout body, becoming smaller from about first chaetiger lacking prominent postsetal lobe.

Pectinate branchiae present from 10th to 19th parapodia, with 9 filaments, individual filaments slightly longer than dorsal cirri. Limbate setae (Fig. 7c) longest, finely serrated on one edge. Pectinate setae (Fig. 7d) present in anterior body region, with 7–11 teeth, tooth on one edge longer, more stout than others, tooth on other edge slightly longer than others. Compound falcigers bidentate (Fig. 7e, f), present from 16th parapodia, shaft and base of hood serrated. Compound spinigers (Fig. 7g) serrated on blade and shaft, present on first to 27th parapodia, 20 or more compound spinigers on 10th parapodia. Aciculum (Fig. 7h) with blunt head; yellow to very light honey in color; up to 3 aciculae present from 6th to 8th parapodia, only 1 aciculum present from 14th parapodia to posterior end. Subacicular hook (Fig. 7i) bidentate, with hood, distal tooth small and directed obliquely, proximal tooth directed laterally; yellow to very light honey in color; present from 23rd parapodia, always single, except for replacement.

Table 1.—Correlations between body width (X, mm) and the morphometric characters (Y), which is expressed by linear regression "Y = AX + B," in *Marphysa belli* (n = 49), *M. oculata* (n = 17) and *M. totospinata* (n = 7). *SD* is standard deviation. *R* is coefficient. The morphometric characters are: the first chaetiger with branchiae (FB), the last chaetiger with branchiae (LB), the maximum number of branchial filaments (MB), the first chaetiger with subacicular hook (SH), the last chaetiger with compound spiniger (CS) and the first chaetiger with compound falciger (CF).

Y	A ± *SD*	B ± *SD*	*R*
M. belli FB	5.30 ± 0.51	3.27 ± 0.30	0.85
M. belli LB	1.15 ± 1.56	11.23 ± 0.92	0.87
M. belli MB	−1.30 ± 0.81	5.81 ± 0.48	0.87
M. belli SH	8.46 ± 1.22	8.80 ± 0.72	0.87
M. belli CS	−1.55 ± 2.43	20.60 ± 1.43	0.92
M. oculata FB	7.18 ± 0.39	1.17 ± 0.24	0.78
M. oculata LB	10.70 ± 0.62	4.50 ± 0.38	0.95
M. oculata MB	1.57 ± 0.50	3.46 ± 0.31	0.95
M. oculata SH	13.16 ± 0.96	4.61 ± 0.58	0.90
M. oculata CS	11.56 ± 1.75	8.03 ± 1.08	0.90
M. oculata CF	−5.40 ± 1.96	10.96 ± 1.21	0.93
M. totospinata FB	11.90 ± 0.63	0.63 ± 0.23	0.78
M. totospinata LB	9.77 ± 5.51	8.95 ± 2.03	0.89
M. totospinata MB	5.85 ± 1.31	3.51 ± 0.48	0.96
M. totospinata SH	10.70 ± 4.66	9.20 ± 1.72	0.92

Maxillary formula (Fig. 7j): 1+1, 6+5, 0+5, 7+4, 1+1 (USNM 129779); 1+1, 6+5, 0+5, 9+3, 1+1 and 1+1, 7+6, 0+6, 6+4, 1+1 (USNM 130368).

Remarks.—According to morphometric data, the size-dependent morphological variation is distinctive in this species.

Antennae: we have a complete specimen with 71 chaetigers which possesses three antennae but lacks the lateral pair of palps (AI), whereas several other specimens with about 84 chaetigers possess the lateral palps. These observations suggest that the palps of *M. oculata* do not develop until it reaches about the 80-chaetiger stage. This estimation is comparable to the palp developmental pattern of *Marphysa belli.* The palp development of these two species of *Marphysa* is much later when compared to that of *Eunice wui* (Lu & Fauchald 1998), whose palps emerge after the worm reaches about 30 chaetigers in size. However, both *Eunice* and *Marphysa* of the Eunicidae develop their lateral palps much later than species in the Onuphidae. For example, *Notonuphis antarctica* (our observations), *Nothria elegans* (Blake 1975), *Mooreonuphis jonesi* (Fauchald 1982) and *Kinbergonuphis simoni* (Hsieh & Simon 1987) have developed the lateral palps when they are only 5 chaetigers in size. It appears that the pattern of development of the palps is more uniform among the Onuphidae when compared to the Eunicidae.

Branchiae: before the development of the palps, the branchiae are already well developed. During the development of the worm, the starting chaetiger with branchiae changes from the 8th parapodia to the 10th parapodia (Fig. 2, Table 1); the ending chaetiger with branchiae changes from the 13th parapodia to the 21st parapodia (Fig. 3, Table 1); the number of branchiae changes from only 6 pairs to 12 pairs; the maximum number of branchial filaments changes from 4 to 10 (Fig. 4, Table 1).

Compound falcigers (Fig. 8, Table 1): their number is always less than that of the compound spinigers in any given segment in which both occur. In young worms (0.7 mm wide), compound falcigers are present in all chaetigers. When the worm grows, compound falcigers are lost from a certain number of anterior chaetigers. The loss

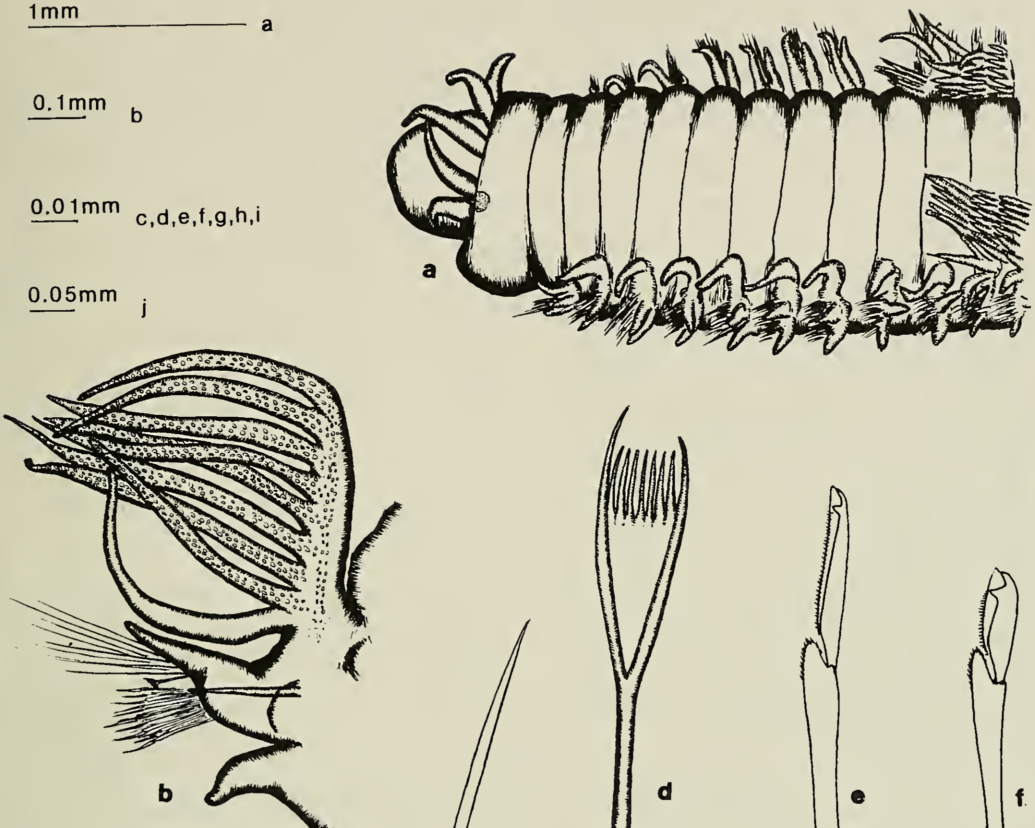

Fig. 7. *Marphysa oculata*: a, anterior end, lateral view (USNM 129779); b, 15th parapodium; c, limbate seta; d, pectinate seta; e, f, compound falcigers; g, compound spiniger; h, aciculum; i, subacicular hook; j, maxillae.

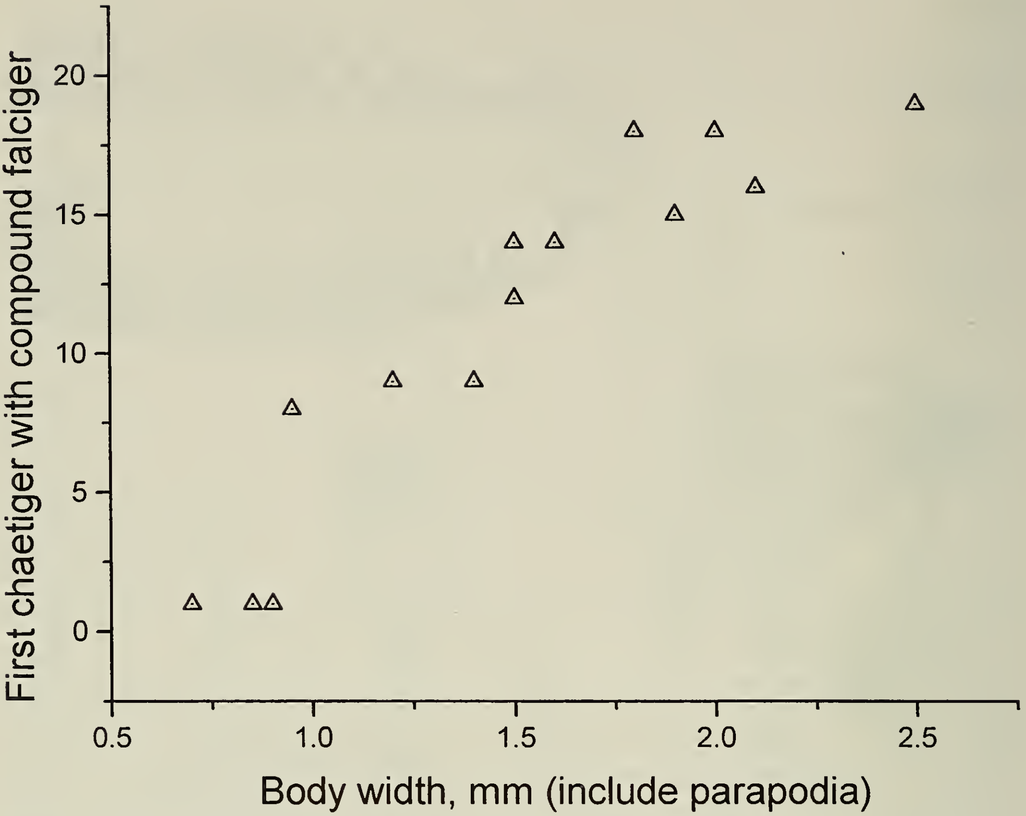

Fig. 8. Size-dependent variation of the first chaetiger with compound falcigers in *M. oculata* (n = 15).

starts at about chaetiger 8 and proceeds from there in both directions. For a 2.5 mm wide worm, compound falcigers are absent in the first 19 parapodia.

Compound spinigers (Fig. 5, Table 1): the ending position of the compound spinigers is size-dependent and varies from the 16th chaetiger to the 31st chaetiger.

Subacicular hook (Fig. 6, Table 1): the first occurrence of a subacicular hook changes from the 15th parapodia to the 24th parapodia. It always occurs several chaetigers after the ending of the branchiae and several chaetigers before the ending of the compound spinigers.

The sensory organ reported by Hayashi & Yamane (1994) for *Marphysa sanguinea* is also observed on the ventral base of dorsal cirri (22rd parapodia) of *M. oculata* (USNM 130127).

Treadwell (1921) described a single incomplete specimen from Key West Harbor, Florida (close to our collection site) as *Marphysa belli*, variety *oculata* based on the presence of eyes in his specimen versus the absence of eyes in European specimens, though he mentioned with contradiction that "Since the presence or absence of eyes does not in itself seem to me of specific importance, I have regarded this as merely a varietal difference." As indicated earlier, the eye condition of *M. belli* is likely related to preservation. Treadwell's description on *M. belli*, variety *oculata* totally agrees with our specimens, especially for the setal distribution, i.e., compound spinigers are the main compound setae in the anterior region. Thus, we believe that they belong to the same species. Unfortunately, Treadwell (1921) did not mention the consistent differences between his species and *M. belli.* In the anterior body region, there are at least twice as many compound falcigers than compound spinigers in *M. belli*, whereas in *M. oculata* the compound spinigers are at least twice as common as the compound falcigers, or the compound falcigers may be absent in some anterior parapodia. Only after the observation of many specimens (*M. oculata*, *n* = 24; *M. belli*, *n* = 63) did this morphological difference between the two species become obvious, thereby warranting a separate species status for *M. oculata.*

Marphysa totospinata, new species
Figs. 2–4, 6, 9a–h

Material examined.—Atlantic coast, Ireland, Mayo, near Blacksod Bay (Holotype: NMW.Z.1988.069.84, and 6 paratypes: NMW.Z.1988.069.84 and NMW.Z.1988.069.84).

Description.—Specimen complete, with 322 chaetigers. Two pairs of anal cirri; longer dorsal pair reaching last 4 chaetigers. First 10 chaetigers measure 3.4 mm in length, widest region measures 5.9 mm.

Prostomium distally round and entire (Fig. 9a), slightly narrower than, same length and ½ depth of, peristomium. Three antennae (AII and AIII) and two palps (AI), slightly irregularly wrinkled, same size, evenly spaced; length of AI:AII:AIII = 1:1.2:1.4; all extend past anterior end of prostomium, AI reaching first ring of peristomium, AII reaching second ring of peristomium, AIII reaching anterior end of first chaetiger. One pair of light brown reniform eyes between AI and AII. First ring of peristomium about ⅔ of total length (dorsal view). No peristomial cirri.

Anterior four chaetigers thick and cube-shaped; becoming flatter dorsoventrally from fifth chaetiger. First parapodia smaller than others. Dorsal cirri long, finger-shaped from beginning, becoming slender in posterior region; dorsal cirri always longer than ventral cirri. Ventral cirri with oval base in anterior chaetigers, becoming slender posteriorly. Postsetal lobe long in anterior parapodia until about 65th parapodia, length comparable to dorsal and ventral cirri in some chaetigers. Sensory organ similar to that described by Hayashi & Yamane (1994) for *Marphysa sanguinea* and *M. oculata* also observed on ventral base of dorsal cirri of 286th parapodia (Fig. 9b).

Pectinate branchiae present from 14th–40th parapodia. Twelveth parapodia with 11 filaments, as many as 18 filaments observed on 27th parapodia. Individual branchial filaments slightly longer than dorsal cirri. Branchiae completely cover dorsal region of worm.

Serrated limbate setae longest of those situated on dorsal side of parapodia. Pectinate setae (Fig. 9c) present from anterior parapodia; with 8–9 teeth, tooth on one edge longer, more stout than others, tooth on other edge slightly longer than others. Compound falcigers (Fig. 9d) present throughout body, with serrated hood and serrated shaft; more than 20 compound falcigers arranged in several rows on anteroventral side of parapodia, fewer in number on posterior side. Compound spinigers (Fig. 9e) present from beginning till very posterior end, such as on parapodium 286 (Fig. 9b); serrated on shaft and one side of blade; 6–7 compound spinigers arranged in a line on posteroventral side of parapodia, decreasing to 1–2 in number in posterior region. Compound falcigers at least twice as numerous as compound spinigers in anterior parapodia. Aciculae (Fig. 9f) 3–4 in anterior region, single or occasionally double from middle-anterior region; honey color, becoming darker in posterior region; blunt-headed, with sheath. Subacicular hook (Fig. 9g) from 46th parapodia, single in 75% of parapodia, double in those remaining; honey to dark honey color; bidentate with hood.

Maxillary formula (Fig. 9h): 1+1, 7+6, 0+7, 8+5, 1+1 in one paratype (NMW.Z.1988.069.86).

Remarks.—The beginning (Fig. 2) and

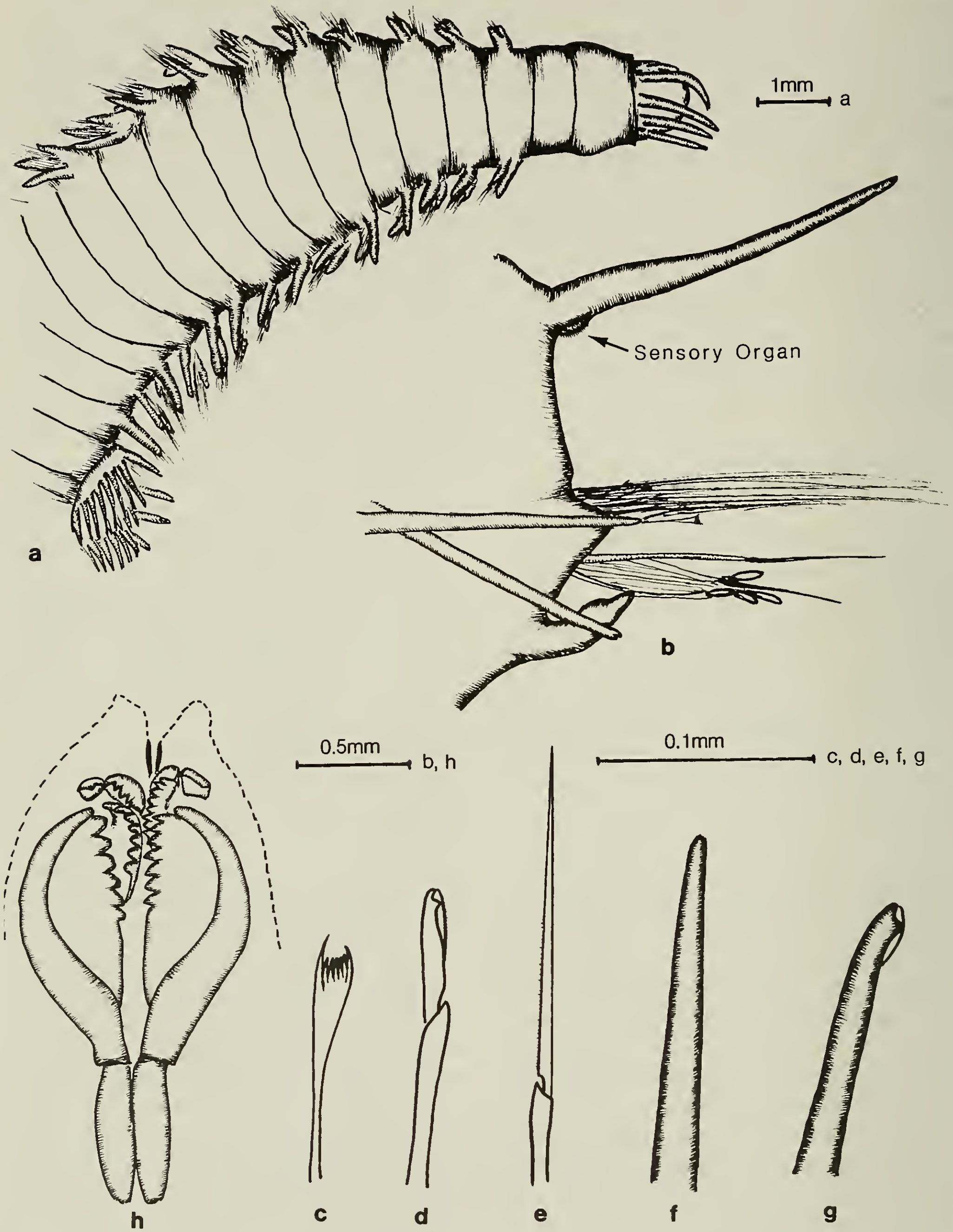

Fig. 9. *Marphysa totospinata*, new species: a, anterior end, dorsal view (NMW.Z.1988.069.84); b, 286th parapodium; c, pectinate seta; d, compound falciger; e, compound spiniger; f, aciculum; g, subacicular hook; h, maxillae (NMW.Z.1988.069.86).

ending (Fig. 3) position of branchiae, the maximum number of branchial filaments (Fig. 4) and the starting position of the subacicular hook (Fig. 6) of *M. totospinata* are all size-dependent characters (see Table 1). This species ($n = 7$) is consistently different from *M. belli* ($n = 63$) and *M. oculata* ($n = 24$) in its setal arrangement: in the anterior parapodia, compound spinigers are the dominant setal type in *M. oculata*, whereas in *M. totospinata* compound falcigers are more numerous; in *M. belli*, compound spinigers occur on less than ¾ of the anterior parapodia, whereas in *M. totospinata* compound spinigers are present nearly throughout the entire body.

McIntosh (1910) described a specimen of *M. belli* from the Plymouth region. According to his description, compound spinigers exist from the beginning to the posterior end of the worm. If this is the case, his specimen should belong to *M. totospinata*.

Etymology.—The species is named for its special morphological character, which is the occurrence of compound spinigers throughout the body length.

Discussion

The branchial and setal patterns are size-dependent morphological characters in *Marphysa belli* and its two related species, *M. oculata* and *M. totospinata*. Among the 15 sets of correlations calculated at a confidence limit of 0.05 (Table 1), the range of coefficients (R) is between 0.78 and 0.96 (average = 0.89). The general morphological variations fall in a similar range between *M. belli* and *M. oculata* and between *M. belli* and *M. totospinata*, for a similarly sized specimen. Slight morphometric differences exist between *M. oculata* and *M. totospinata*. For example, in a specimen of *M. oculata* that is 2.5 mm wide, its branchiae begin on the 10th parapodia and end on the 22nd parapodia, and its subacicular hook emerges from the 23rd parapodia, whereas for a similarly sized specimen of *M. totospinata*, its branchiae begin on the 13th parapodia and end on the 32nd parapodia, and its subacicular hook emerges from the 32nd parapodia. Though only relatively small sized specimens of *M. oculata* and large sized specimens of *M. totospinata* were available for the present study, several specimens of both species have overlapping size ranges. In addition, both species show distinctive features when compared to similarly sized specimens of *M. belli*, whose size ranged from small (larva) to large specimens. These observations support the suggestion that *M. oculata* is not the juvenile stage of *M. totospinata*. The arrangement of compound setae is the major difference among these species. If additional specimens of *M. belli* from other areas of the world, such as the Mediterranean, South Africa and Indochina, can be examined, it is possible that new sister species can be separated. This species group potentially provides a good case for further biogeographic study.

Key to the *Marphysa belli* group

1. At least twice as many compound falcigers than compound spinigers in anterior parapodia 2
1′. At least twice as many compound spinigers than compound falcigers in anterior parapodia .... *M. oculata*
2. Compound spinigers limited to anterior ⅓ body region or less .... *M. belli*
2′. Compound spinigers present along nearly the entire body .... *M. totospinata*

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Pseudechiniscus asper, a new Tardigrada (Heterotardigrada: Echiniscidae) from Hokkaido, northern Japan

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Abstract.—A new semi-terrestrial tardigrade species of the family Echiniscidae, *Pseudechiniscus asper*, is described from a single male collected from Hokkaido, northern Japan. This species can be readily distinguished from the known congeners by a combination of the following characters: almost the entire surface of all dorsal plates is covered with coarse cuticular granulation; the subtriangular projection is present at position D; paired lobes on pseudosegmental plate are roundly triangular and tipped with papillate projection; and, each internal claw is armed with a spur.

In autumn of 1988, the second author collected lichen samples to obtain the tardigrades around Lake Shikotsu in southwestern Hokkaido, northern Japan. Tardigrade specimens extracted from the lichen samples were fixed with 5% formalin, and mounted on glass slides with Hoyer's medium. Cover slips were sealed by Paraffin-Balsam. Close examination was performed using a phase contrast and Nomarski differential interference microscope (ZEISS Axiophoto) and illustrations were depicted with the aid of camera lucida.

After a review of the literature, it was concluded that one of the specimens represents a new species belonging to the genus *Pseudechiniscus* of the family Echiniscidae, which is described and illustrated as *Pseudechiniscus asper*, new species. Terminology is mainly that used in Dastych & Kristensen (1995) and Kristensen (1987).

Pseudechiniscus asper, new species
Figs. 1–2

Type material.—Holotype: Four-clawed adult male; Shikotsuko-onsen, Chitose, southwestern Hokkaido, northern Japan (141°24′N, 42°46′E); ca. 250 m; extracted from a foliose lichen, *Phaeophyscia imbricata*, on trunk of *Acer japonicum*, 9 Oct 1988, K. Utsugi leg. Holotype is deposited in the National Science Museum, Tokyo (NSMT), under the registered number NSMT-Tg 44.

Diagnosis.—Small size. Dorsal plates covered with coarse cuticular granulation. Scapular plate and segmental paired plates II and III each with segmental lateral plates. Subtriangular projection at position D. Paired lobes on pseudosegmental plate roundly triangular, tipped with papillate projection. Internal claws each with a spur.

Description.—Body length 166 μm excluding leg IV, width 83 μm; body width : body length, 1:2. Eyespot not detected, body color evenly translucent in Hoyer's medium.

Dorsal plates well developed and conspicuous. Delineation of dorsal plates and subdivision within a plate each comprised of cuticular ridge. Almost entire surface of

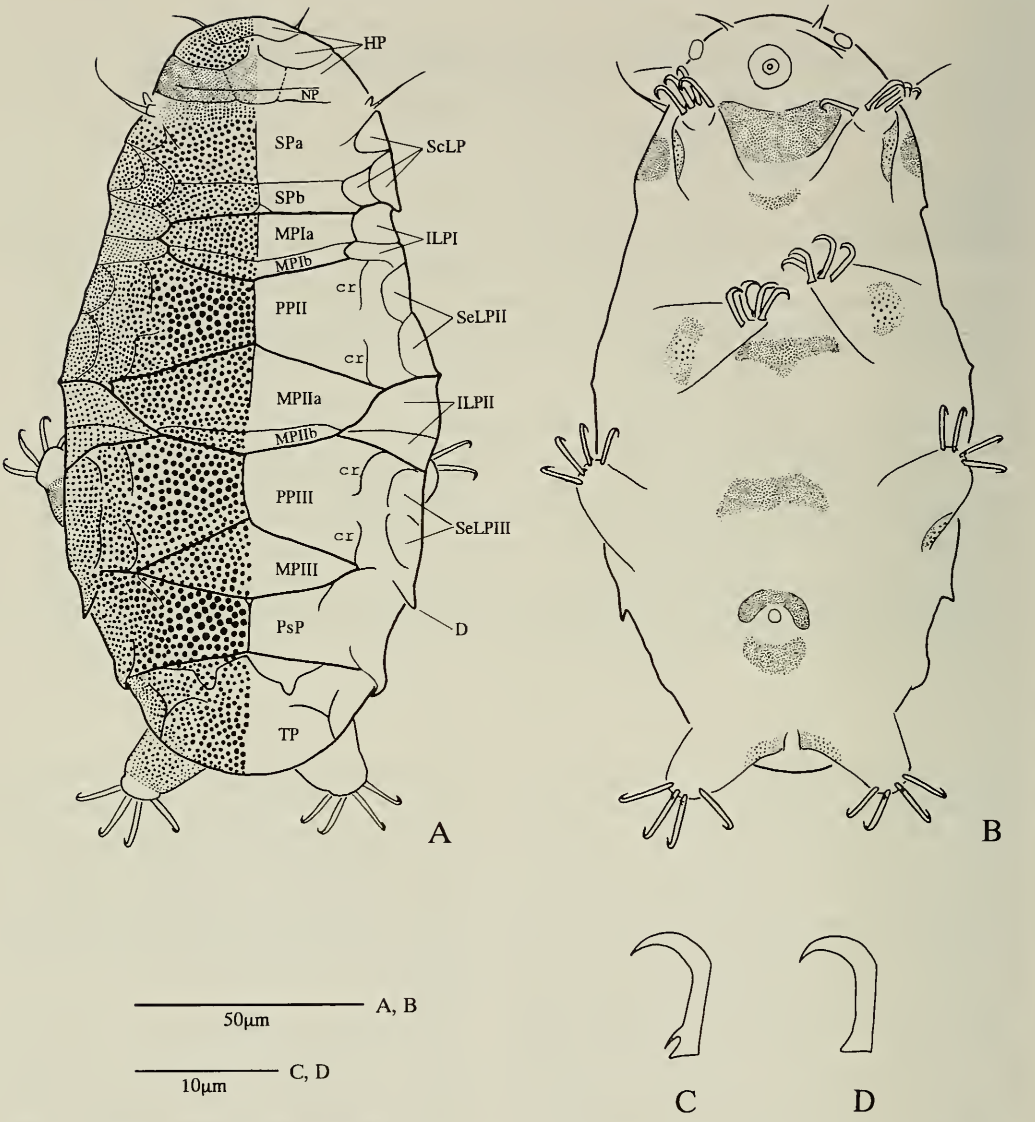

Fig. 1. *Pseudechiniscus asper*, new species, holotype male (NSMT-Tg 44), Hokkaido, N Japan: A, Habitus, dorsal view; B, Habitus, ventral view; C, Internal claw of leg II; D, External claw of leg II. Abbreviations: cr = cuticular ridge; D = subtriangular projection at position D; HP = head plate; ILPI, ILPII = intersegmental lateral plates I–II; MPI, MPII, MPIII = median plates I–III (a: anterior, b: posterior); NP = neck plate; PPII, PPIII = segmental paired plates II–III; PsP = pseudosegmental plate; ScLP = scapular segmental lateral plates; SeLPII, SeLPIII = segmental lateral plates II–III; SP = scapular plate (a: anterior, b: posterior); TP = terminal plate.

all dorsal plates covered with coarse, uniformly distributed granules which consist of hemispherical cuticular thickenings; posterior half of head plate and neck plate only with very fine, densely distributed punctations which consist of pillar structures of epicuticle; and small region around primary papilla and cirrophore of cirrus A devoid of any sculpture. Granules larger on segmental paired plates II and III, and pseudosegmental plate, ca. 1.5 µm in diameter; granules medium in size on anterior half of head

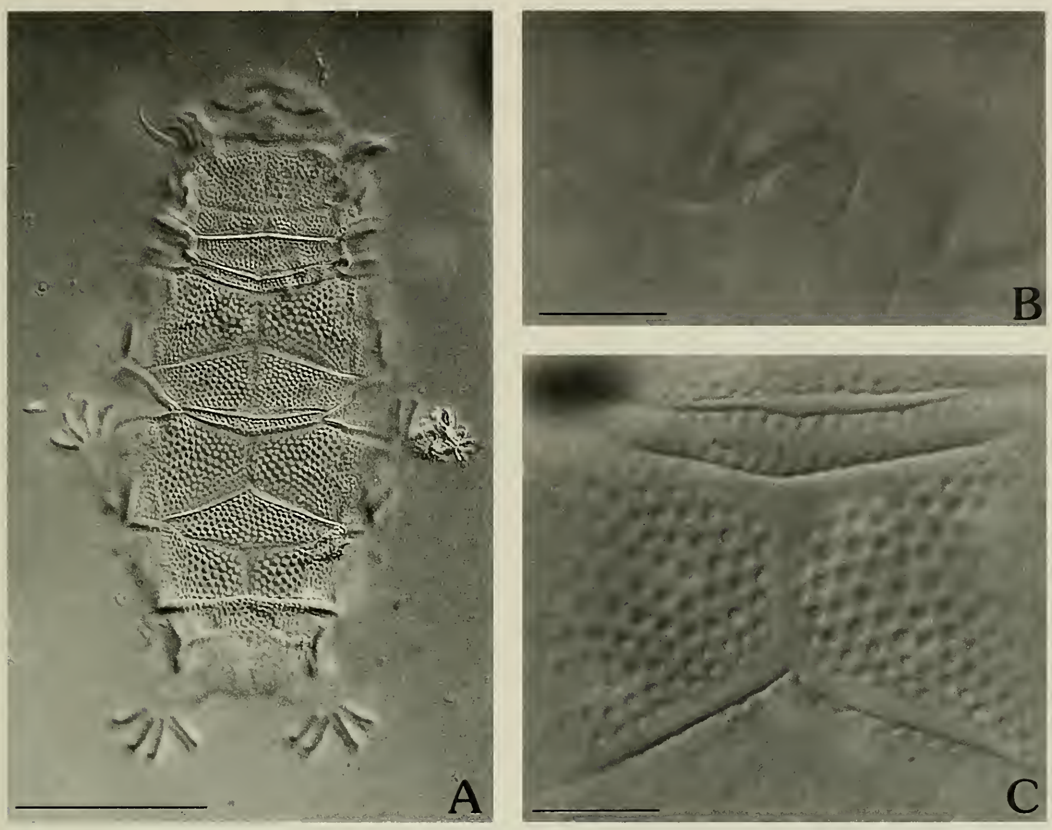

Fig. 2. *Pseudechiniscus asper*, new species, holotype male (NSMT-Tg 44), Hokkaido, N Japan, differential interference contrast photomicrographs: A, Habitus, dorsal view; B, Internal claw of leg II; C, Detail of segmental paired plate III. Scales = 50 μm (A), 10 μm (B, C).

plate, scapular plate, median plates, and terminal plate, ca. 0.9 μm in diameter; granules smaller on most anterior part of scapular plate, and intersegmental lateral plates I and II, ca. 0.5 μm in diameter. Granules larger in central region of each plate than those in peripheral region of same plate. Space between granules smooth, without striae.

Head plate (HP) well-defined, gently faceted, subdivided into smaller pieces by smaller anterior and larger posterior W-shaped sculptures; ridge of large W-shaped sculpture effaced in its middle. Most posterior points of large W-shaped sculpture and minuscule indentations of neck plate interconnected by rather shallow, inconspicuous cuticular furrow which is dilated anteriorly.

Neck plate (NP) narrow but appreciable; almost entire neck plate overlapping most posterior part of head plate; posterior edge of neck plate with a pair of vague, minuscule indentations.

Scapular plate (=plate I; SP) well developed, inconspicuously subdivided at mid-dorsal line of body, shallowly subdivided into anterior and posterior subrectangular parts (SPa, SPb); anterior part fairly larger than posterior part. Three pairs of scapular segmental lateral plates (ScLP) separated from central main part; anterior segmental lateral plate connected with anterior central part; two pairs of posterior segmental lateral plates arranged transversely, connected with posterior central part.

Median plate I (MPI) distinctly subdivided into anterior and posterior parts (MPIa, MPIb); anterior part subrectangular, fairly larger, somewhat wider than posterior part, inconspicuously but completely subdivided at middorsal line of body; posterior part separated from anterior part as a transverse strip, concave dorsally, undivided at middorsal line of body; anterior and posterior edges of median plate I slightly and moderately angulated at middorsal line of body respectively.

Intersegmental lateral plate I (ILPI) subdivided into anterior and posterior parts; anterior part wider than posterior part; proximal edge of two parts obtuse.

Segmental paired plate II (PPII) well developed, with two pairs of lateral segmental plates (SeLPII); posterior segmental lateral plate somewhat larger than anterior segmental lateral plate; central main part of segmental paired plate II with cuticular ridges (cr) laterally; ridges effaced centrally forming separate anterior and posterior lines. Cuticular ridge, which is made up by posterior edge of segmental plate II and anterior edge of intersegmental lateral plate II, forming blunt swelling in its most distal part.

Median plate II (MPII) larger than median plates I and III, distinctly subdivided into anterior and posterior parts (MPIIa, MPIIb); anterior part fairly larger and wider than posterior part, weakly subdivided at middorsal line of body; posterior part forming a narrow transverse strip, concave dorsally, undivided at middorsal line of body; anterior and posterior edges of median plate II angulated at middorsal line of body.

Intersegmental lateral plate II (ILPI) subdivided into anterior and posterior parts; anterior part larger than posterior part; proximal points of two parts acute.

Segmental paired plate III (PPIII) well developed, similar to segmental paired plate II in size and shape, with two pairs of lateral segmental plates (SeLPIII); anterior and posterior lateral segmental plates incompletely separated; central main part of segmental paired plate III with cuticular ridges (cr) laterally; ridges effaced centrally forming separate anterior and posterior lines. Projection at position D (D) subtriangular, broad-based, ca. 9 μm long.

Median plate III (MPIII) well-defined, rhomboid, undivided; anterior and posterior edges of median plate III moderately and poorly angulated at middorsal line of body, respectively.

Pseudosegmental plate (PsP) distinctly and wholly subdivided at middorsal line of body; paired lobes roundly triangular; each tipped with papillate projection, 8 μm high, 17 μm wide; lobes slightly conjoined middorsally with each other; posterior edge of pseudosegmental plate weakly arcuate but not sinuate. Posterior edge of pseudosegmental plate covering anterolateral side of terminal plate swollen in appearance.

Terminal plate (TP) with remarkable, long cuticular ridge posterolaterally, thus having a strongly facetted appearance, and with very blunt cuticular ridge on its middorsal line of body.

Subcephalic plate thin but comparably conspicuous, situated below mouth opening; anterior edge moderately marked but effaced in its middle, distinctly arcuate; lateral edge well marked, arcuate, dilated anteriorly; posterior edge scarcely marked, arcuate. Dense patches of cuticular granulation situated between each pair of legs I–III, and circum-genital region; each granule similar to that on dorsal plates, but much smaller; granules on central part of each patch somewhat larger than those on peripheral part; patch above gonopore with weakly developed edge, thus having a plate-like appearance, other patches without perceptible edge; patches between legs increasing in size posteriorly. Net pattern on ventral surface below subcephalic plate throughout but barely visible.

Leg plates developed on outer surfaces of legs I–III and dorsal surface of leg IV; each leg plate covered with granules similar to those on dorsal plates; granules larger but sparse on central part of leg plate, smaller but dense on peripheral part. Plate of leg IV without dentate collar. Sensory organ absent from legs I–III, not detected on leg IV.

Internal and external cirri and secondary clava situated ventrally. Internal and external cirri filamentous, without true cirrophore but with swollen base, without anchor-shaped bifurcation at tip; external cirrus longer than internal cirrus, 12 μm long and 8 μm long, respectively. Secondary clava hemispherical, situated nearer to external cirrus than to internal cirrus.

Primary clava and cirrus A situated anterolaterally on scapular plate; primary clava papillate, situated just beneath base of cirrus A, ca. 1.5 μm long; cirrus A filamentous, short, with normal subconical cirrophore but without bifurcation at tip, ca. 20 μm long, 12% of body length.

Claw normally curved distally, thickened basally; internal claw slightly longer than external claw on all legs; claws of leg I–III ca. 9 μm long; claws of leg IV longer than claws of other legs, ca. 11 μm. External claw on all legs without spur; each internal claw on all legs with a distinct, moderately curved spur directed toward base of claw; spur located at a height approximately ¼ as long as claw length; apex of spur not reaching base of claw.

Mouth opening situated ventrally. Buccal tube and stylet support weakly sclerotized, thus hardly discernible. Pharyngeal bulb ovoid, 14 μm long, 11 μm wide; outer cuticular lining inside pharyngeal bulb clearly thicker than bar-shaped placoid.

Male gonopore simple, being a slightly raised ring; anus normal, situated between leg IV of both sides.

Etymology.—From the Latin word *asper* (rough), referring to the general appearance of dorsal plates in the present new species.

Remarks.—In *Pseudechiniscus asper*, described in this paper, the single specimen collected is male. *Pseudechiniscus* males are very rare and have been reported only two times, viz. Dastych (1987) as *P. alberti* and Kristensen (1987) as unidentified species. Kristensen (1987) stated that *Pseudechiniscus* species with males are found limnic or in other stable biotopes and that this is related to the thin sclerotization of the dorsal plates and the absence of the leg plates. It might be true in the species studied by Kristensen (1987), but it is remarkable that both *P. alberti* from Canada and *P. asper* from Japan were found in unstable environments such as terrestrial moss or lichen and have thick dorsal plates. Additional data are required to reveal the relationship between environmental habitat and the mode of reproduction.

Kristensen (1987) stated that all *Pseudechiniscus* species are provided with the sensory organ on leg I. However, there are some species lacking this character, e.g., *P. juanitae* in Maucci (1986), *P. suillus* in Ramazzotti & Maucci (1983), Dastych (1989), and Kathman & Dastych (1990), *P. victor* in Maucci (1986), and *P.* cfr. *suillus* in McInnes (1995). Also, in *P. asper* the sensory organ on leg I is absent.

The sensory organ on leg IV, which is usually developed as a papilla or spine on its outer surface in *Pseudechiniscus* (Kristensen 1987), is not detected in the new species. This character is sometimes hard to observe, depending on the direction of the specimen on the glass slide, and we could not decide whether this character is absent or present in *P. asper.*

The large size of granules on dorsal plates, the presence of a subtriangular projection at the position D, and the presence of segmental lateral plates in the scapular plate and segmental paired plates II–III distinctly separate the new species from species such as *Pseudechiniscus brevimontanus* Kendall-Fite & Nelson, 1996, *P. nataliae* Biserov & Maucci *in* Biserov, 1986, *P. ramazzottii* Maucci, 1952, *P. scorteccii* Franceschi, 1952. *P. asper* bears some resemblance to *P. occultus* Dastych, 1980 from Poland, especially in the general appearance of the granulation on the dorsal plates, but can be readily distinguished from it mainly by the absence of the posterior lobe on the scapular plate, the absence of a spurs on the external claws of leg IV, and the absence of anchor-shaped bifurcations of cephalic cirri and cirrus A. The last character was omitted in the original description of *P. occultus* (Dastych 1980) but later emended as presented in Dastych (1987, 1988).

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Parapetalophthalmus suluensis, a new genus and species (Crustacea: Mysidacea: Petalophthalmidae) from the Sulu Sea

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Abstract.—A new genus, *Parapetalophthalmus*, is established for the new species *P. suluensis*, collected from the Sulu Sea. It is closely related to *Pseudopetalophthalmus*, but easily distinguished from this genus by the sixth to eighth thoracopods in which the endopods are small, 1- or 2-segmented rudiments.

During a cruise to southeastern Asian seas (KH-72-1) by the R/V *Hakuho Maru* of the Ocean Research Institute, University of Tokyo, mysid specimens belonging to the family Petalophthalmidae were collected from the Sulu Sea. They resemble species of the genus *Pseudopetalophthalmus* in appearance, but are distinctly different from it by the rudimentary endopods on the sixth to eighth thoracopods. *Parapetalophthalmus suluensis*, new genus, new species, is established for these specimens.

The type specimens are deposited in the National Science Museum, Tokyo (NSMT), Japan.

Parapetalophthalmus, new genus

Diagnosis.—Body slender. Carapace very short, leaving posterior 5 or 6 thoracic somites exposed dorsally; rostrum very short, rounded, without acute process, flanked by pair of small denticles. Eye developed and elongate; cornea spherical, broader than stalk; eyestalk elongate, without papilla. Antennular peduncle very long, slender. Antennal scale lanceolate, proximal ⅔ of outer margin naked, ending in 1 jointed spine, distal ⅓ of outer margin setose; apex and inner margin setose. Mandibular palp long, powerful and prehensile; third segment short and robust, with 9 long spines. Thoracopods: first pair without exopod, endopod terminating in claw, with inner lobe on ischium; second pair without exopod, endopod robust, terminating in strong, curved claw, with quadrangular, large, inner lobe on ischium; third to fifth pairs with endopod slender, without terminal claw; sixth to eighth pairs with endopod rudimentary. Pleopods of male biramous, natatory; of female biramous, exopod very slender, endopod fused with sympod. Uropod: exopod 2-segmented, proximal segment with outer margin naked except for 2 spines and 1 seta at distal end, margin of distal segment setose; endopod without spines but with setae, statocyst absent. Telson rectangular; apex with 9 spine groups and 8 plumose setae between them, each spine group composed of 3 spines with middle spine longest, spines of outermost group barbed, longer, stouter, articulated at base.

Type species.—*Parapetalophthalmus suluensis*, new genus, new species.

Etymology.—The generic name is derived from the close resemblance to *Pseudopetalophthalmus* and *Petalophthalmus*; it is a masculine gender.

Remarks.—The new genus is closely re-

Table 1.—Morphological differences between *Pseudopetalophthalmus* Bravo & Murano, 1997, and *Parapetalophthalmus,* new genus.

	Pseudopetalophthalmus	*Parapetalophthalmus*
Eyestalk	With small papilla	Without papilla
Third segment of mandibular palp	With 7 long and strong setae	With 9 long and strong setae
Endopods of 3rd to 5th thoracopods	Terminating in a strong claw	Terminating in 2 short setae
Endopods of 6th to 8th thoracopods	Long and multi-segmented	Reduced to 1- or 2-segmented, small rudiment

lated and morphologically similar to *Pseudopetalophthalmus*, which was recently established by Bravo & Murano (1997). The most distinctive difference between the two genera is found in the thoracopods. In *Pseudopetalophthalmus* the endopods of the third to eighth thoracopods are long, multisegmented, and bearing a terminal claw, whereas in the new genus those of the sixth to eighth thoracopods are small, 1- or 2-segmented rudiments, and those of the third to fifth thoracopods terminate in 2 setae but not in a claw.

Parapetalophthalmus and *Pseudopetalophthalmus* can also be separated by differences in the eyestalk and mandibular palp. In the new genus the eyestalk is not armed with a papilla, and the third segment of the mandibular palp is armed with 9 long spines as compared to 7 in *Pseudopetalophthalmus*. Morphological differences between *Pseudopetalophthalmus* and *Parapetalophthalmus* are summarized in Table 1. The new genus also resembles *Petalophthalmus*, but is easily distinguished from it by characteristics of the rostrum, antennal scale, mandibular palp, thoracic endopods, and telson.

Parapetalophthalmus suluensis, new species
Figs. 1–4

Type specimens.—Holotype (NSMT-Cr 12168), adult male (13.0 mm); allotype (NSMT-Cr 12169), adult female (11.4 mm); paratypes (NSMT-Cr 12170), 1 immature female (9.1 mm), 1 juvenile (5.2 mm); Sulu Sea, 08°12.7′N, 117°59.6′E to 08°11.8′N, 117°58.4′E, 285–306 m, plankton net installed in mouth of 3-m beam trawl, 26 May 1972.

Description.—Body slender. Carapace very short, leaving posterior 5 or 6 thoracic somites exposed dorsally; frontal margin broadly rounded, upturned, not forming definite rostral projection, leaving eyes completely uncovered; small blunt process on either side of margin (Fig. 1A, B); anterolateral corner rounded.

Eye well developed, extremely elongate, projecting laterally, slightly less than 3 times as long as width of cornea; cornea functionally normal, much wider than eyestalk; eyestalk narrow, broadened distally in distal half, without papilla (Fig. 1A, B).

Antennular peduncle slender, 3-segmented. In male first segment longer than succeeding 2 segments together, with tuft of setae on outer dorsal surface at distal end and distal fourth, 1 small spine on dorsal surface near distal end; second segment half as long as first, about 3 times as long as broad, with tuft of setae on outer dorsal surface at distal end, inner margin with 7 setae arranged at regular intervals; third segment shortest, less than 1.5 times as long as broad, armed with 4 setae arranged at regular intervals on inner margin and with 2 setae at inner distal corner. Outer flagellum twice wider than inner, projecting anterolaterally and then anteriorly, with many fine setae on proximal part of inner margin (Fig. 1A). In female antennular peduncle more slender than that of male; second segment about 5 times as long as broad; third segment about 3 times as long as broad. Outer

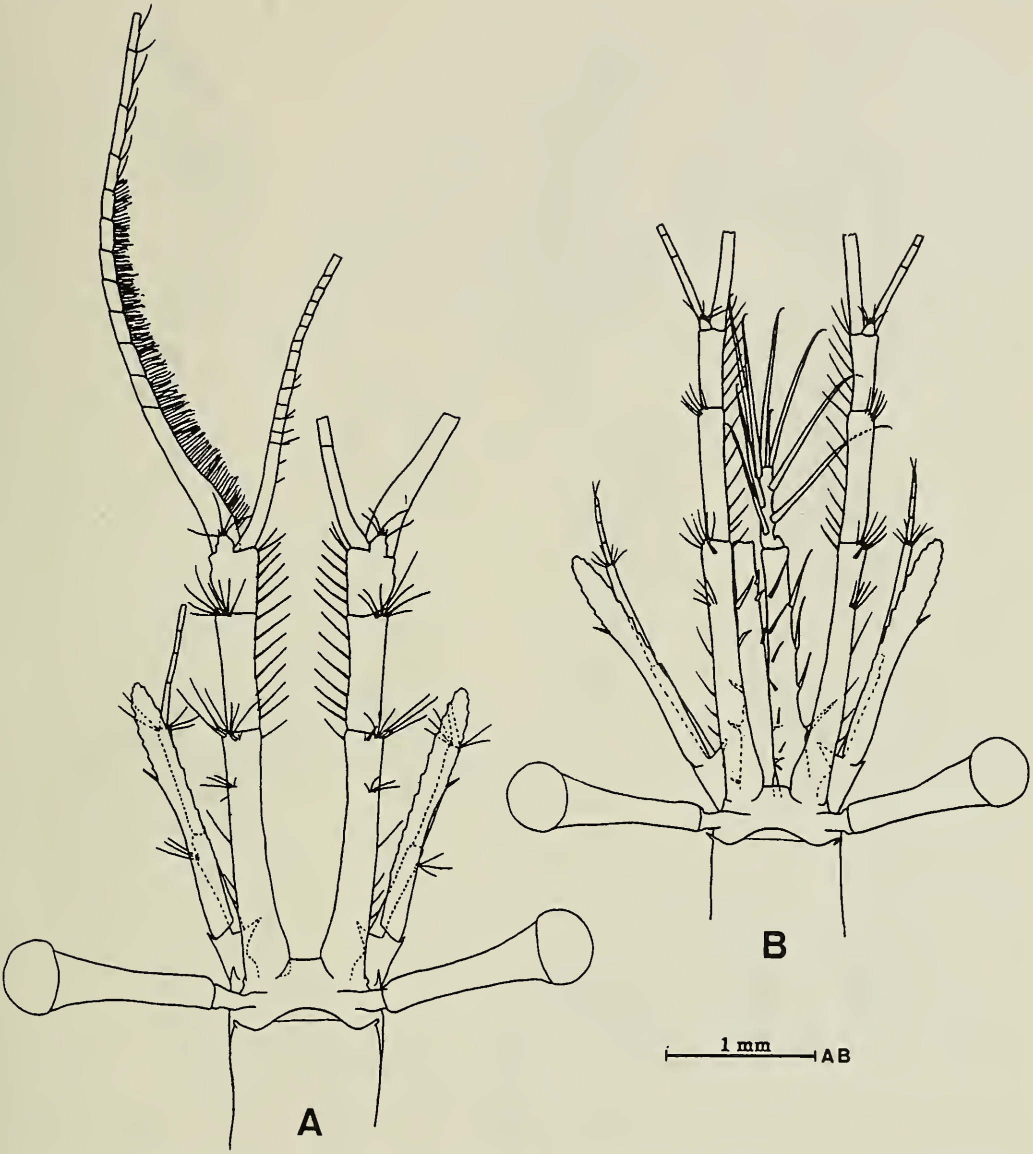

Fig. 1. *Parapetalophthalmus suluensis*, new genus, new species. A, anterior end of male (holotype); B, anterior end of female (allotype).

flagellum narrower than inner, straight, without fine setae along inner margin (Fig. 1B).

Antennal scale long, slender, extending to middle of second segment of antennular peduncle in male (Fig. 1A), extending slightly beyond anterior margin of first segment of antennular peduncle in female (Fig. 1B), about 8.5 times as long as maximum width at position of jointed spine marking end of naked part of outer margin; outer margin naked and concave in proximal ⅔, setose in distal ⅓; inner margin nearly straight, setose except proximal third naked (Fig. 2A). Antennal peduncle slightly shorter than scale; first segment very short, produced medially into triangular lobe; second segment with group of setae at distal sixth;

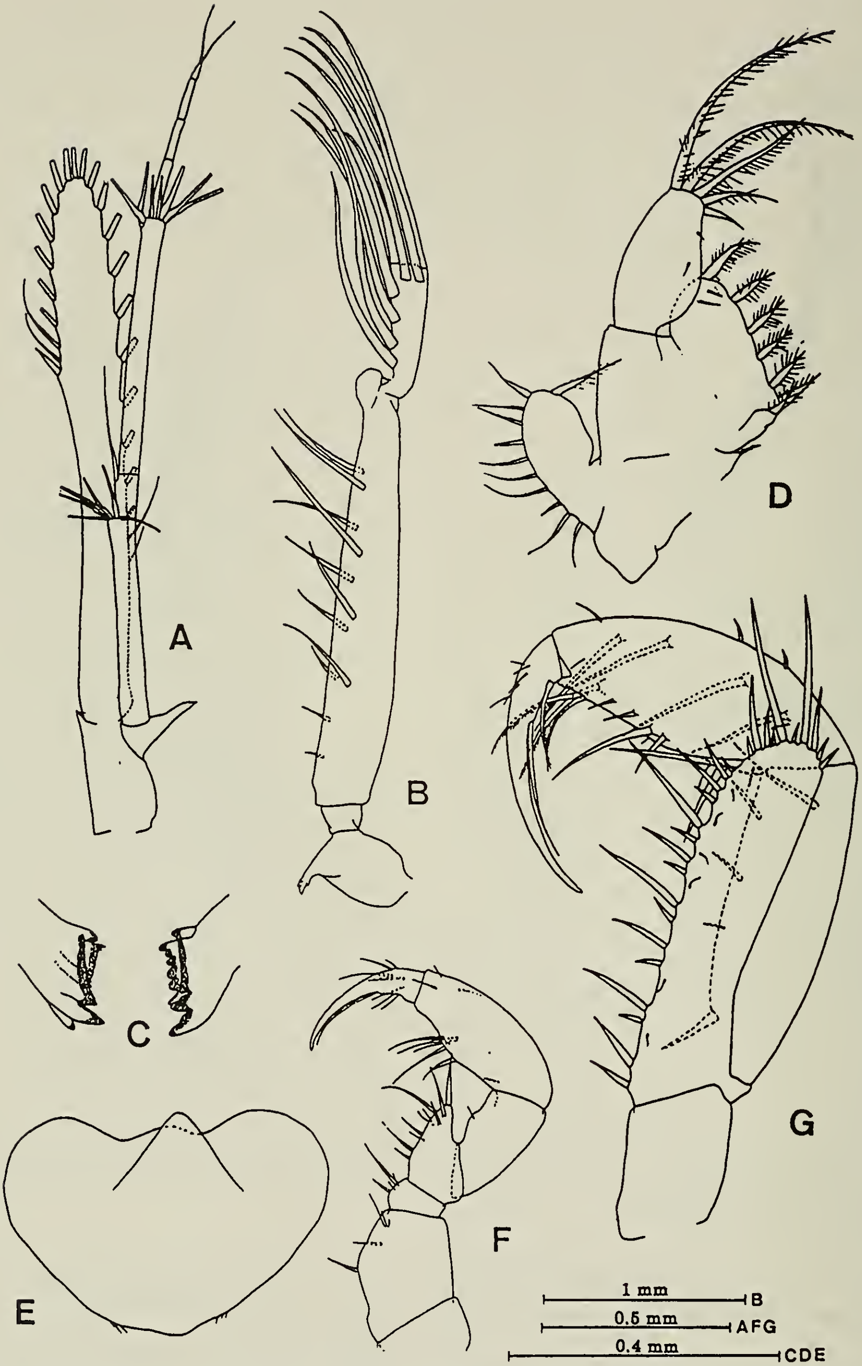

Fig. 2. *Parapetalophthalmus suluensis*, new genus, new species; A: allotype; B–G: holotype. A, antennal scale; B, mandible and mandibular palp; C, mandibles; D, maxillule; E, labrum; F, endopod of first thoracopod; G, endopod of second thoracopod.

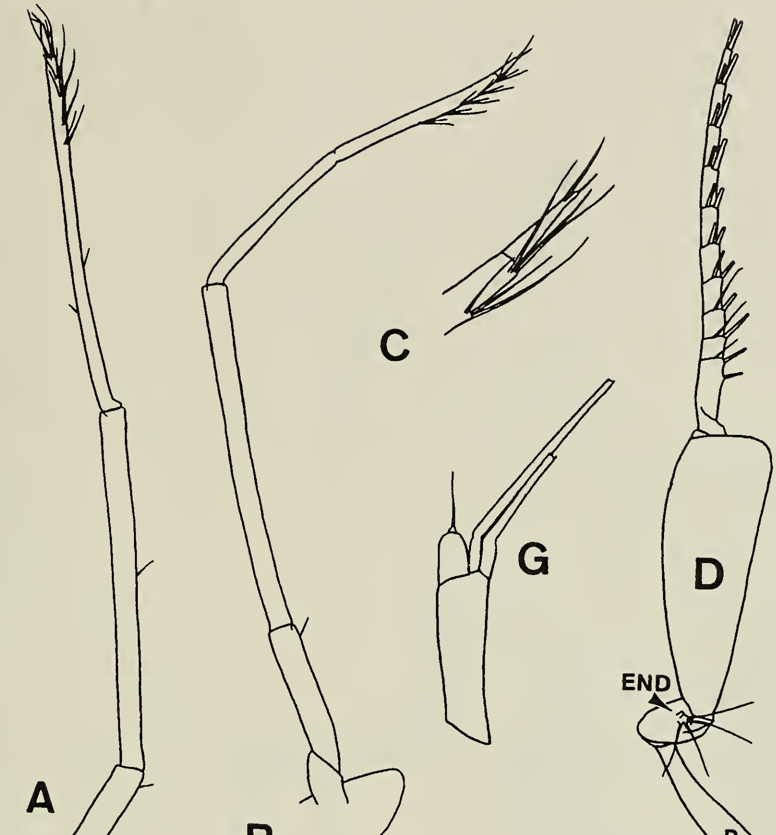

Fig. 3. *Parapetalophthalmus suluensis*, new genus, new species; A–F: holotype; G: allotype. A, endopod of third thoracopod; B, endopod of fifth thoracopod; C, distal part of endopod of fifth thoracopod; D, eighth thoracopod and penis; E, proximal part of fifth thoracopod; F, proximal part of sixth thoracopod; G, endopod of seventh thoracopod. (END: endopod; EXP: exopod; P: penis).

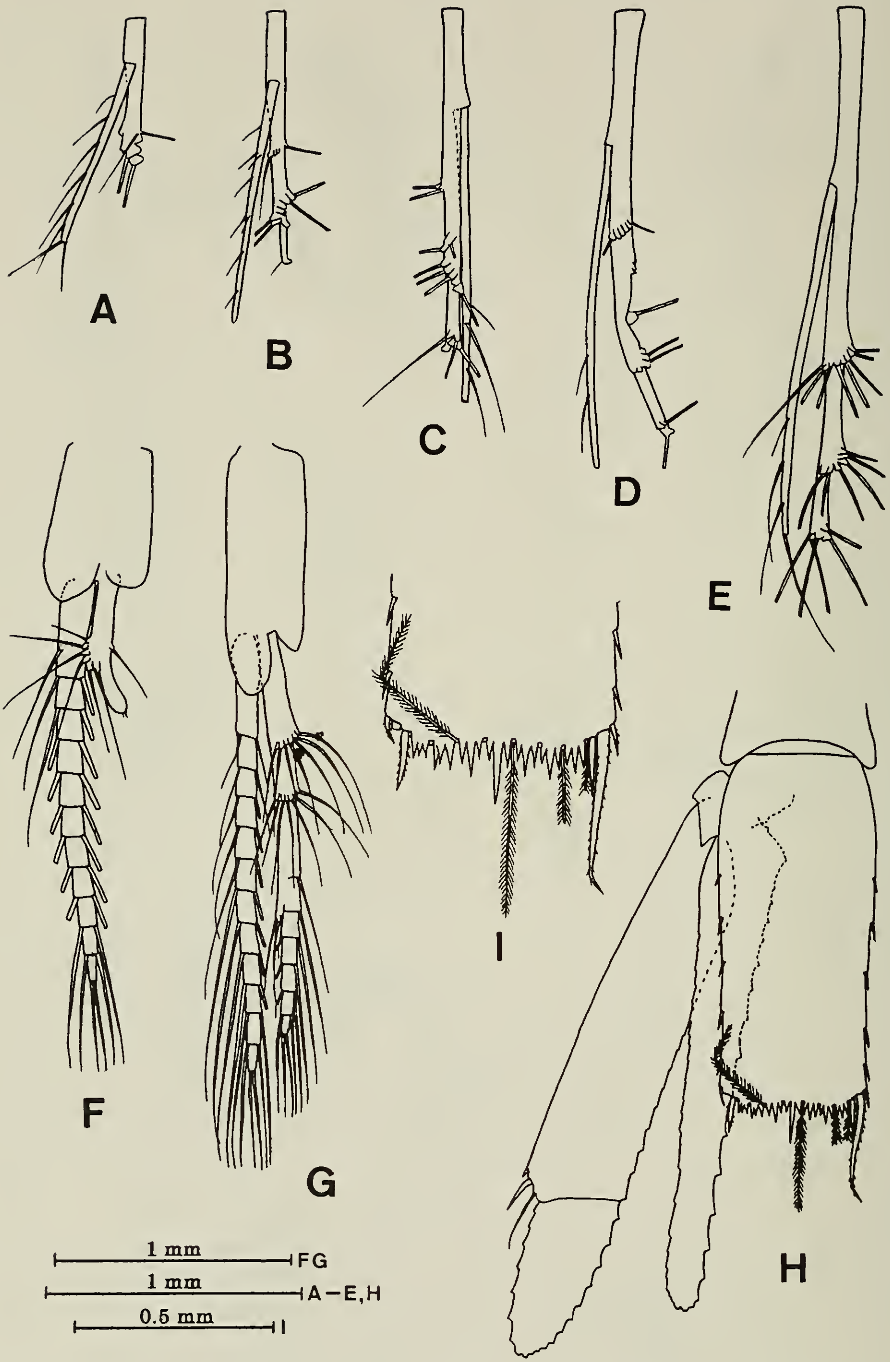

Fig. 4. *Parapetalophthalmus suluensis*, new genus, new species; A–E: allotype; F–I: holotype. A, first pleopod; B, second pleopod; C, third pleopod; D, fourth pleopod; E, fifth pleopod; F, first pleopod; G, fifth pleopod; H, uropod and telson; I, distal part of telson.

third segment equal to second in length, with group of setae at distal end. Female with flagellum 4-segmented, terminating in 2 short setae; male with flagellum about 18-segmented (Fig. 2A).

Mandible of right side with lacinia mobilis (Fig. 2C). Palp large, slender, extending anteriorly beyond anterior margin of second segment of antennular peduncle in male and slightly beyond middle of second segment in female (Fig. 1B); first segment short; second segment cylindrical, nearly 7 times longer than broad, with 4 spine-like setae along outer margin and 7 along inner margin; third segment ⅓ length of second, with flexure between second and third segments, armed with 9 strong setae, 3 on distal end, 2 on outer margin and 4 on inner margin, one of distal setae shorter than others, especially in female (Figs. 1B, 2B). Maxilla and labrum as in Fig. 2D, E, respectively.

Endopod of first thoracopod short and robust, with epipod; inner lobe on ischium developed, extending anteriorly to middle of merus, armed with several spine-like setae; carpopropodus longer than preceding 2 segments combined, inner margin slightly convex, with group of setae on middle; claw fused with dactylus, long, inwardly curved (Fig. 2F); exopod wanting. Endopod of second thoracopod robust; lobe on ischium very large, quadrangular, overreaching distal margin of merus, 4 times as long as broad, with about 27 long and short spine-like setae on inner and apical margins; carpopropodus elliptical, shorter than preceding segment; claw fused with dactylus, robust, inwardly curved (Fig. 2G); exopod wanting.

Endopods of third to fifth thoracopods extremely slender; carpopropodus as long as merus, undivided, with 5 groups of setae arranged at regular intervals on distal fourth of inner margin, each group composed of 2 or 3 setae; dactylus short, terminating in 2 short setae, without claw (Fig. 3A–C, E). Endopods of sixth to eighth thoracopods reduced to 1- or 2-segmented, small rudiments with several setae (Fig. 3D, F, G). Penis elongate, gradually thicker distally, ending in hemispherical apex, without setae (Fig. 3D). Flagelliform part of thoracic exopods 9-segmented in third and fourth pairs and 10-segmented in fifth to eighth; basal plate narrow, with outer distal corner rounded (Fig. 3D).

Abdominal somites increasing in length posteriorly, their length ratios are 1:1:1.4:1.5:1.6:2.5; last abdominal somite more than 3 times as long as maximum breadth at posterior end; anterior 5 somites with pair of small blunt projections on posterior end of lateral margin.

Pleopods of male biramous, well developed; first pleopod with unsegmented endopod and 11-segmented exopod (Fig. 4F); second to fifth pleopods similar to each other, without modified setae; exopod 12-segmented; endopod 6- or 7-segmented, slightly shorter than exopod; first segment long, with 2 groups of setae arranged transversely, without definite pseudobranchial lobe (Fig. 4G). Pleopods of female biramous, increasing in length posteriorly; exopod very slender, not segmented or segmented indistinctly, with 2 to 6 setae on outer margin and 1 or 2 setae on apex; endopod fused with sympod, shorter than exopod in first to third pleopods, subequal in fourth and slightly longer in fifth (Fig. 4A–E).

Exopod of uropod 2-segmented. Proximal segment more than 4 times as long as broad, with both margins parallel; outer margin very slightly convex, naked except for distal end armed with 1 seta and 2 spines, proximal spine very small; inner margin very slightly concave, setose. Distal segment twice as long as broad at base, 0.28 of proximal segment in length, whole margin setose (Fig. 4H). Endopod of uropod unsegmented, extending to middle of distal segment of exopod, gradually narrowing distally (Fig. 4H).

Telson rectangular, more than twice as long as broad, 0.7 of last abdominal somite in length. Lateral margins parallel, with 5 small, slender, equal-sized spines on each side. Distal margin armed with 9 grouped spines, each group consisting of 3 spines with middle one usually longest; spines of outermost groups longer, barbed, jointed at base, 8 plumose setae present between 9 spine groups (Fig. 4H, I).

Etymology.—The name *suluensis* is derived from the locality where the specimens were collected; it is an adjective agreeing in gender with the generic name.

Remarks.—As previously discussed in the remarks section of the genus, the new species is easily distinguished from two species of the most closely related genus *Pseudopetalophthalmus*, *P. japonicus* Bravo & Murano, 1997, and *P. australis* (Panampunnayil, 1982).

Parapetalophthalmus suluensis was collected in the depth of 285–306 m which was deeper than habitats of two species of *Pseudopetalophthalmus*, 74–130 m deep in *P. japonius* and subsurface in *P. australis.*

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Diastylis tongoyensis, a new diastylid (Crustacea: Cumacea) from the northern central coast of Chile, with an amendment to the description of *Diastylis crenellata* Watling & McCann, 1997

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Abstract.—A new species, *Diastylis tongoyensis*, is described based on specimens from north central Chile. *Diastylis tongoyensis* is distinguished from other members of the genus by the unique combination of an opercular maxilliped 3, a short telson, and an unornamented carapace. Pereopods 3 & 4 of *D. crenellata* Watling & McCann, 1997 are also illustrated. Both belong to a group of 9 species in the genus *Diastylis* having an opercular maxilliped 3, reduced exopods on pereopods 3 & 4 of the female and a telson shorter than the uropod peduncles.

Only two species belonging to *Diastylis* Say, 1818 are currently known from Chile, *Diastylis argentata* Calman, 1912 and *D. gayi* Nicolet, 1849. *Diastylis argentata* is described from off southern Chile, and *D. gayi* is described from Isla Grande de Chiloé, also in southern Chile. Both sites are within the Magellanic biogeographic province, and *D. gayi* has not been reported subsequent to its description by Nicolet (1849). *Diastylis tongoyensis* is the first species from the Diastylidae described from the Peru-Chilean province (Fig. 1), which encompasses the west coast of South America from about 40°S to 5°S.

Methods

Samples were collected with a small benthic dredge equipped with a net bag having a mesh opening of 425 μm, dragged by a small boat for 15–30 minutes in 3–30 meters of water. Because of the need to use the specimens for genetic analysis, samples were preserved directly in 95% EtOH. Drawings were prepared using a *camera lucida* on a Wild compound microscope. Body length was measured from the tip of the pseudorostral lobes to the posterior border of the last somite.

Family Diastylidae Bate, 1856
Diastylis Say, 1818
Diastylis tongoyensis, new species
Figs. 2–11

Type material.—Holotype (USNM 260767), ovigerous female; paratypes (USNM 260768), 1 adult ♂, 8 subadult ♂, 9 subadult ♀♀, 15 manca 1; paratypes (Museo Nacional de Historia Natural de Chile, Santiago CUM-no. 11153), 1 ovigerous ♀, 7 subadult ♀♀, 8 subadult ♂, 4 manca 1; Bahia Tongoy, Chile, 30°16.67′S, 71°30.25′W.

Other material.—Bahia Tongoy, Chile, 30°16.67′S, 71°30.25′W, 4 ovigerous ♀♀, 30 subadult ♀♀, 2 adult ♂, 31 subadult ♂, 132 manca 1, 381 individuals not sexed. Bahia Guanaquero, Chile, 30°11.66′S, 71°25.30′W, 6 subadult ♀♀, 14 subadult ♂, 80 manca 1.

Diagnosis.—Within the genus, distinguished by the combination of unornamented carapace, telson considerably shorter than uropod peduncles, opercular maxilliped 3, pereonite 1 visible only dorsally,

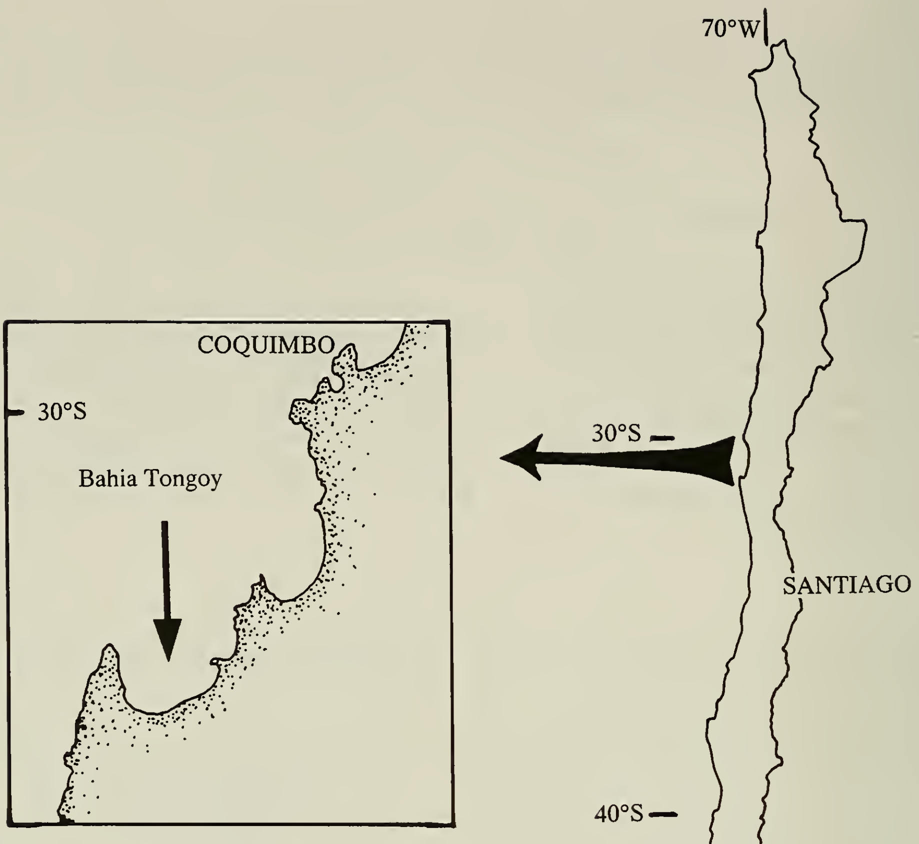

Fig. 1. Map of Chile, with enlargement of Bahia Tongoy area.

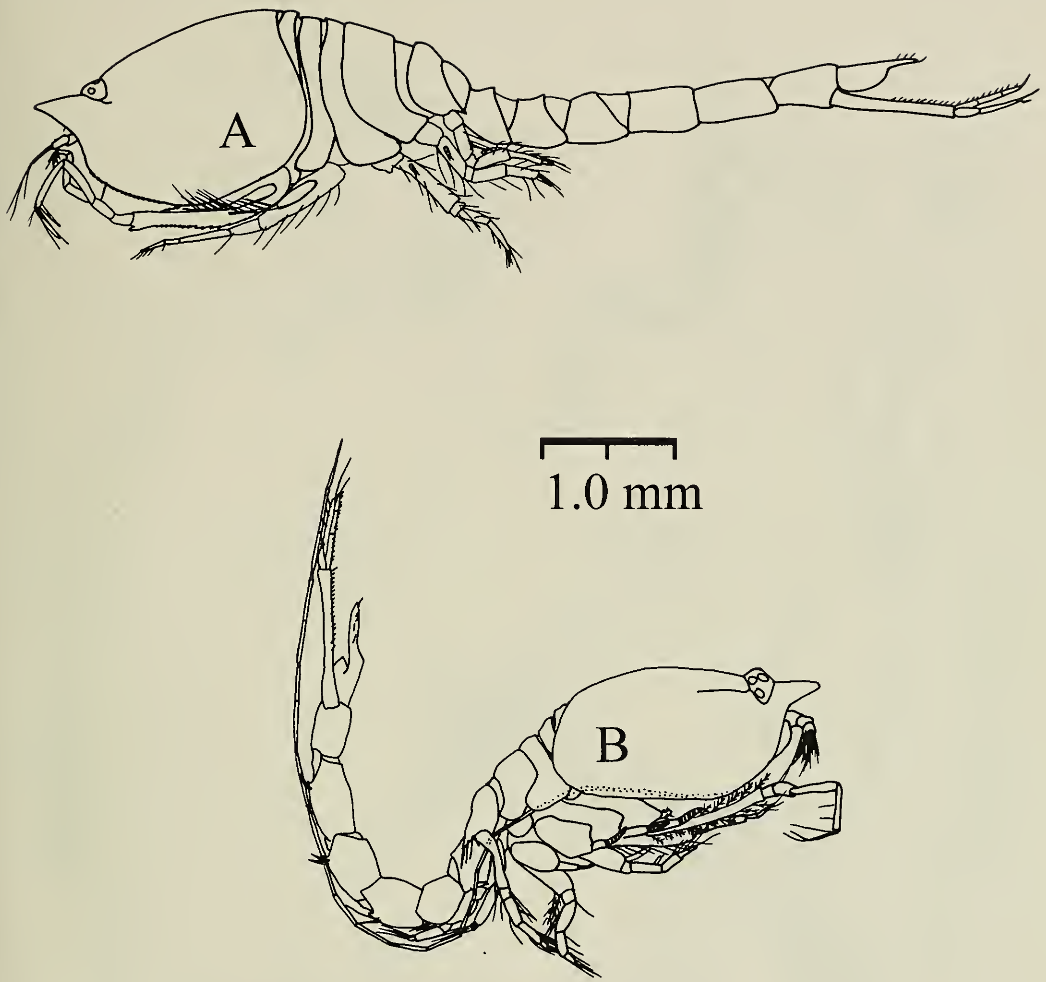

Fig. 2. *Diastylis tongoyensis*, new species. A, adult ♀; B, adult ♂.

and rudimentary exopods on pereopods 3 & 4 in female.

Description.—Ovigerous female, 6.0 mm. Pseudorostral lobes 0.2 carapace length, eyelobe 0.1 carapace length, with 3 lenses; antennal notch oblique; anteroventral corner slightly produced; ventral margin lined with small teeth, otherwise carapace smooth. Branchial siphon not extending beyond pseudorostral lobes. Pereonite 1 nearly obscured by carapace, slightly exposed dorsally. Pereonite 5 produced posteriorly as small acute lappet (Fig. 2A).

Antennule elongate and stout, extending beyond pseudorostral lobes; peduncle articles 1 and 2 stout, article 3 slender; article 1 with 2 plumose setae distally; article 2 with 2 pedunculate setae distally; accessory flagellum of 2 articles, extending beyond article 1 of main flagellum; main flagellum of 4 articles, bearing 2 stout annulate setae (Fig. 3D).

Antenna rudimentary; article 1 stout, 1 plumose seta distally; article 2 reduced, 1 simple seta distally (Fig. 3E).

Mandible navicular with row of 11 lifting setae. Right lacinia mobilis very stout with two cusps, left lacinia mobilis slender with single cusp (Fig. 4A).

Maxillule with 2 endites; outer endite with

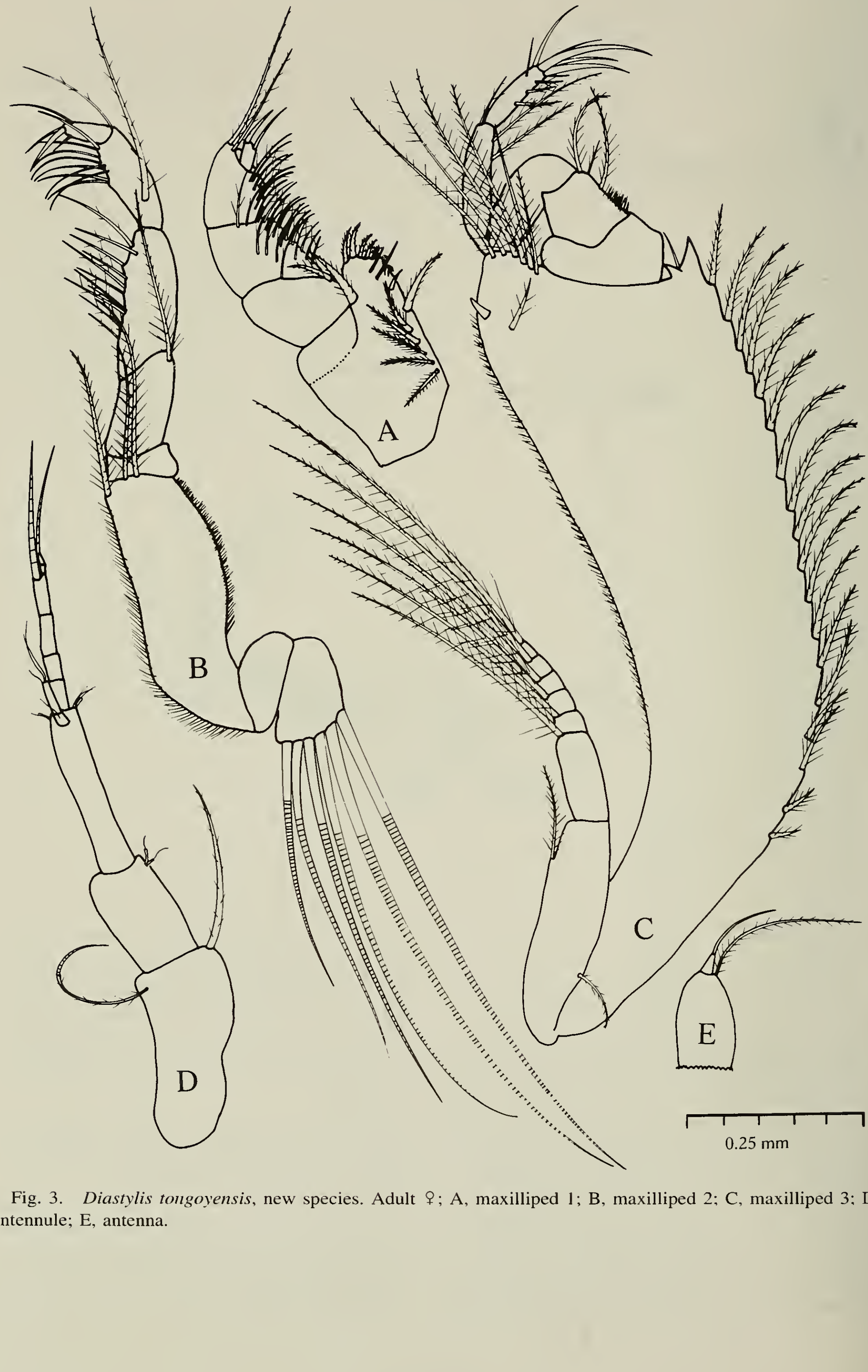

Fig. 3. *Diastylis tongoyensis*, new species. Adult ♀; A, maxilliped 1; B, maxilliped 2; C, maxilliped 3; D, antennule; E, antenna.

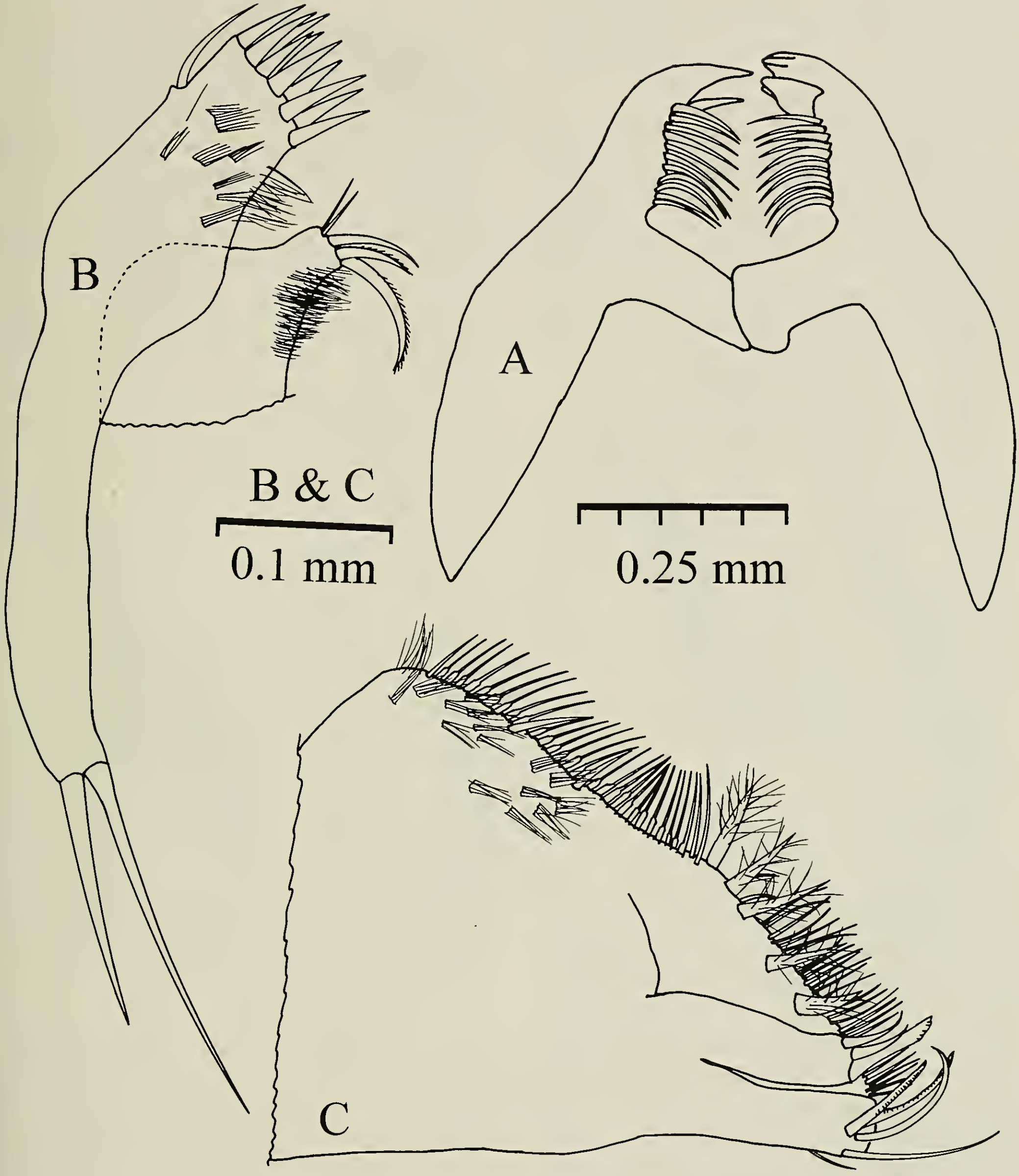

Fig. 4. *Diastylis tongoyensis*, new species. Adult ♀; A, mandibles; B, maxillule; C, maxilla.

double row of stout simple setae distally, 1 slender simple seta on lateral margin, anterior face with several groups of very fine simple setae; inner endite with 5 setae terminally, 2 stout microserrate setae, 1 stout simple seta, 2 slender simple setae, anterior face with many fine simple setae; palp with 2 long stout simple setae distally (Fig. 4B).

Maxilla with 3 endites; broad endite distal half of medial margin with double row of fine simple setae, 5 large stout papose setae, proximal half of medial margin with row of 29 simple setae, 2 stout simple setae set below row, many groups of fine simple setae on anterior-medial face; inner narrow endite with 3 setae terminally, 2 stout simple setae, 1 broad blade-like seta; outer narrow endite with 4 long setae terminally, 2 microserrate and 2 simple, lateral margin with 1 simple seta (Fig. 4C).

Maxilliped 1 basis produced distally as blunt lobe, 2 hooks medially, medial margin beset with stout plumose setae; ischium partially fused; merus with 2 stout plumose setae; carpus and propodus subequal, both with field of slender plumose setae on medial face, propodus also bearing 2 long plumose setae distally; dactyl reduced, bearing 2 short simple setae distally (Fig. 3A).

Maxilliped 2 endite with 5 long stout annulate setae; basis margins lined with fine hairs, distal medial corner with 3 long plumose setae; ischium compressed, bearing no setae; merus, carpus, propodus subequal in length, merus distal lateral corner bears single long plumose seta; carpus medial margin bearing row of slender sparsely plumose setae; propodus with 1 long plumose seta proximally, row of slender simple setae on distal half of medial margin; dactyl with 3 simple setae, 1 stout and 2 slender (Fig. 3B).

Maxilliped 3 basis expanded, twice as long as all other articles together, medial margin with row of stout plumose setae, lateral margin beset with fine hair setae, distal lateral corner with group of long plumose setae, slightly proximally 2 stout setae, 1 simple and 1 plumose, distal medial corner produced as 2 teeth with short slender simple seta between; ischium broad, incised distally, with no setae; merus medial distal margin with 2 long plumose setae and 1 short slender plumose seta, medial proximal margin beset with fine hairs; carpus reflexed, without setae; propodus bearing 2 long plumose setae on medial distal margin; dactyl medial margin with 3 short plumose setae, tip with simple setae, 2 stout and 4 slender; exopod basal article with 1 proximal and 1 distal plumose seta, flagellum bearing many long plumose setae, basis and flagellum together half endopod basis length (Fig. 3C).

Pereopod 1 basis as long as carpus, propodus, dactyl together, anterior and posterior margins with many long plumose setae, distal margin with row of long plumose setae on medial margin, lateral margin produced as 2 large teeth, basis body with stout triangular scales that appear as teeth on margins; ischium with tooth on distal corner, otherwise unarmed; merus longer than ischium, unarmed; carpus, propodus, dactyl subequal in length, carpus with few delicate setae, propodus distal corner with single long plumose seta; dactyl with 3 plumose setae distally; plumose setae on propodus and dactyl having closely set short setules, not similar to plumose setae on basis; exopod shorter than endopod basis, basal article with 5 short plumose setae, flagellum with many long plumose setae (Fig. 5A).

Pereopod 2 basis slightly expanded, as long as next 4 articles together, anterior and posterior margins with many long plumose setae; ischium short, posterior margin with 1 long plumose seta; merus 4 times ischium length, distal corner with 1 plumose seta; carpus longer than propodus and dactyl together, unarmed; propodus half as long as dactyl, 1 simple seta distally; dactyl with several simple setae; exopod longer than endopod basis, exopod basal article shorter than flagellum with 3 slender plumose setae posteriorly, flagellum with many long plumose setae (Fig. 6B).

Pereopod 3 basis as long as remaining articles combined, with 2 pedunculate setae at distal corner, armed with several long plumose setae and 2 smaller annulated setae; ischium margin with several plumose setae and several annulate setae; merus as long as carpus and propodus together, distal corner with single annulate seta, lateral face with 1 annulate seta; carpus margin lined with long annulate setae, carpus as long as dactyl and propodus together; propodus unarmed; dactyl 0.5 width of propodus, single very stout simple seta distally; exopod reduced, 2 small articles, distal article bearing single annulate seta and several fine setae (Fig. 7B).

Pereopod 4 basis as long as merus and

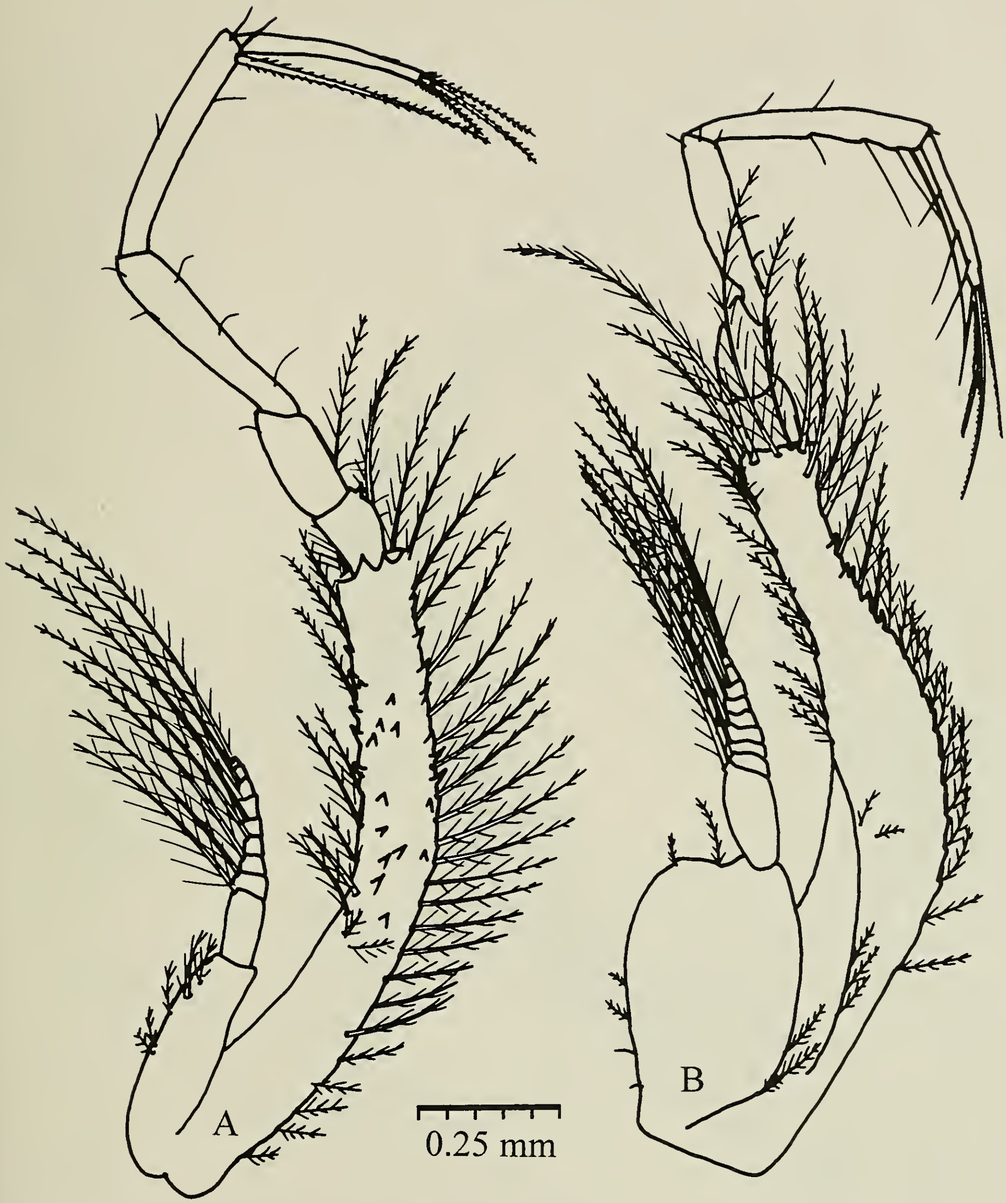

Fig. 5. *Diastylis tongoyensis*, new species. A, adult ♀ pereopod 1; B, adult ♂ pereopod 1.

carpus together, posterior margin with several long stout plumose setae, 1 pedunculate seta and 3 slender annulate setae on outside; ischium with 5 long annulate setae; merus half basis length, posterior margin with 4 long annulate setae; carpus with row of long stout annulate setae distally, few slender annulate setae not on margin; propodus with 1 extremely stout annulate seta distally; dactyl reduced, 0.5 width of propodus, bearing single short stout seta distally; exopod reduced, 2 articles, distal article with 1 plumose seta (Fig. 6A).

Pereopod 5 basis as long as merus and

Fig. 6. *Diastylis tongoyensis*, new species. Adult ♀; A, pereopod 4; B, pereopod 2.

Fig. 7. *Diastylis tongoyensis*, new species. A, adult ♂ pereopod 4; B, adult ♀ pereopod 3.

carpus together, distal corner with 1 plumose seta, proximally 2 plumose setae, distally 1 stout annulate seta; ischium distal corner with single annulate seta, row of 3 annulate setae laterally; merus ⅔ basis length, margins with few slender annulate setae; carpus with 2 long annulate setae distally, 5 short annulate setae on outside; propodus with single extremely stout annulate seta distally; dactyl reduced, 0.5 width of propodus, with 1 short stout simple seta distally (Fig. 8D).

Telson length 0.7 length of uropodal peduncles, pre-anal and post-anal sections subequal in length, post-anal portion very slender with 3 pairs of lateral setae, 1 pair of short stout simple setae terminally (Fig. 9A).

Uropod peduncles longer than rami, peduncle medial margins armed with 9 or 10 stout setae. Uropod endopod of 3 articles; article 1 medial margin with 4 stout setae, lateral margin with 2 pedunculate setae, lateral distal corner with single seta; article 2 medial margin with 3 setae, lateral distal corner with single seta; article 3 medial margin with 2 setae, lateral margin with single pedunculate seta, 1 large stout seta and 1 small slender seta on distal margin. Uropod exopod of 2 articles; article 1 one-fourth length article 2, armed with 1 short seta; article 2 lateral margin lined with simple setae, medial distal corner with single seta, distal margin with 2 long stout setae. All setae on medial margins, both peduncle and endopod, and large seta on the endopod distal margin, short, stout setae with single setule sub-terminally (Fig. 9A).

Adult male, 5.8 mm. Carapace pseudorostral lobes 0.2 total carapace length, not upturned; antennal notch completely oblique; anteroventral corner slightly serrate, otherwise smooth. Carapace generally smooth. Eye large, 0.7 length of pseudorostral lobes, with at least 3 lenses. Branchial siphon not extending beyond pseudorostral lobes. Pereonite 1 almost completely covered by carapace, exposed dorsally. Pereonite 5 produced acutely posteriorly, much longer than in female, with 4 long terminal setae on lappet. Pleonites 1–5 with 2 setae on each posterior-ventral corner (Fig. 2B).

Antennules much longer than pseudorostral lobes, peduncle articles very stout; article 1 equal to articles 2 and 3 together, margins beset with fine hairs, 2 simple short setae distally; articles 2 and 3 subequal, article 2 unarmed; article 3 entire distal margin bearing very slender setae, equal in length to peduncle of main flagellum; accessory flagellum of 3 articles, proximal article bears single pedunculate seta proximally; main flagellum of 5 articles, distal article bears 2 simple setae, as long as setae on article 3 (Fig. 10A).

Antennal peduncle of 5 articles; first 4 articles equal in length to article 5, articles 1 and 2 subequal; article 1 with 1 plumose seta; article 2 with 2 plumose setae; articles 3 and 4 subequal, together equal to article 2, both unarmed; article 5 stout, with 19 rows of fine setae on anterior margin; flagellum extends at least to end of uropod rami, comprising at least 20 articles, each article bearing several rows of fine setae, articles increasing in length and decreasing in width distally (Fig. 8A).

Maxilliped 3 basis expanded, medial margin with many short plumose setae; ischium expanded, incised distally, unarmed; merus medial margin with 2 short plumose setae; carpus reflexed, unarmed; propodus medial margin with 2 long simple setae, distally 2 short simple setae; dactyl margins with several simple setae, 2 long simple setae distally. Exopod 0.7 endopod basis; exopod basal article expanded, unarmed; flagellum bearing long plumose setae (Fig. 11B).

Pereopod 1 basis equal to all other articles together, with plumose setae on anterior, posterior, and distal margins, increasing in length distally, medial margin with several teeth; ischium shorter than merus, unarmed; merus with 2 small setae distally; carpus with 2 small simple setae on margin; propodus longer than carpus, with 3 slender

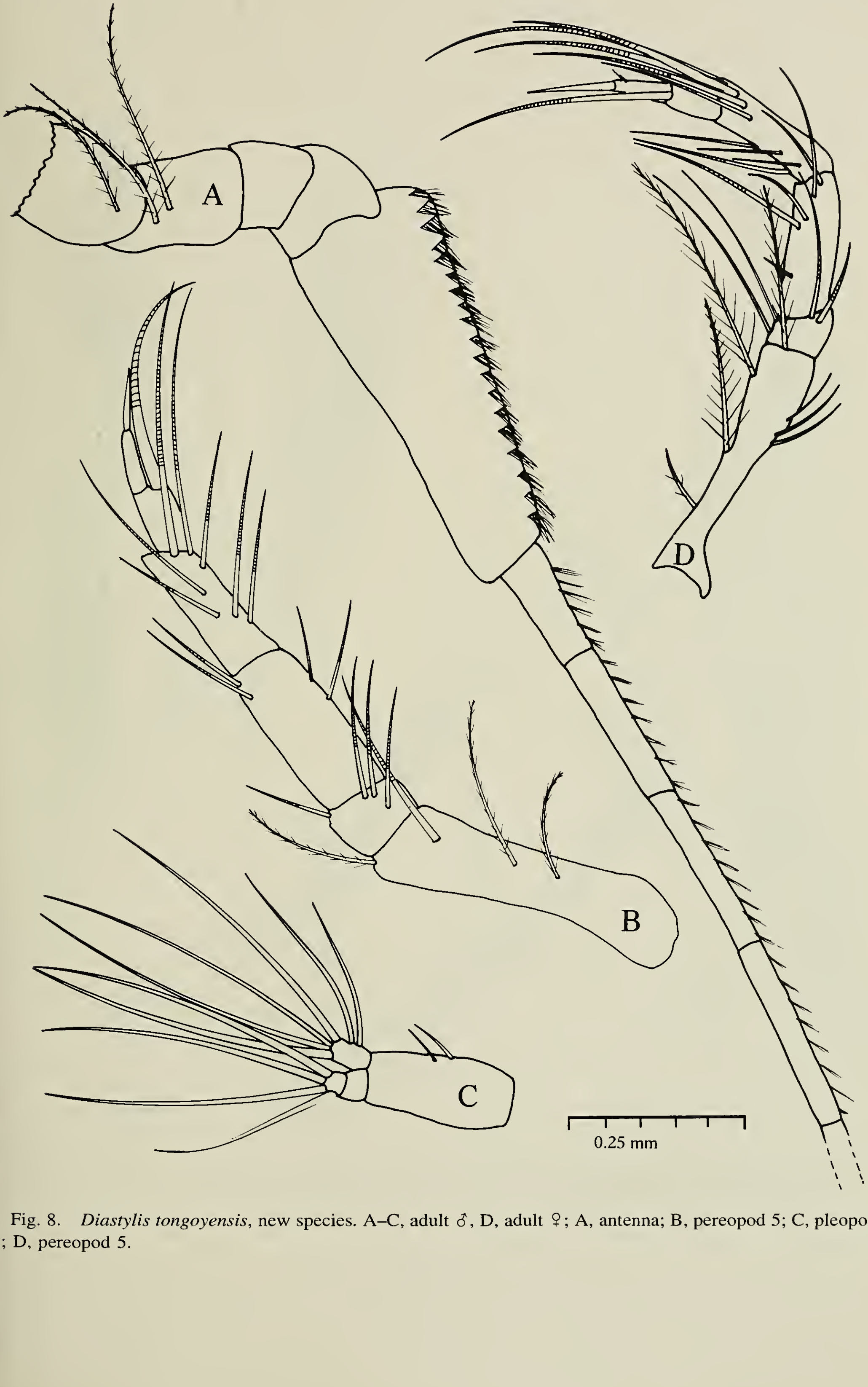

Fig. 8. *Diastylis tongoyensis*, new species. A–C, adult ♂, D, adult ♀; A, antenna; B, pereopod 5; C, pleopod 2; D, pereopod 5.

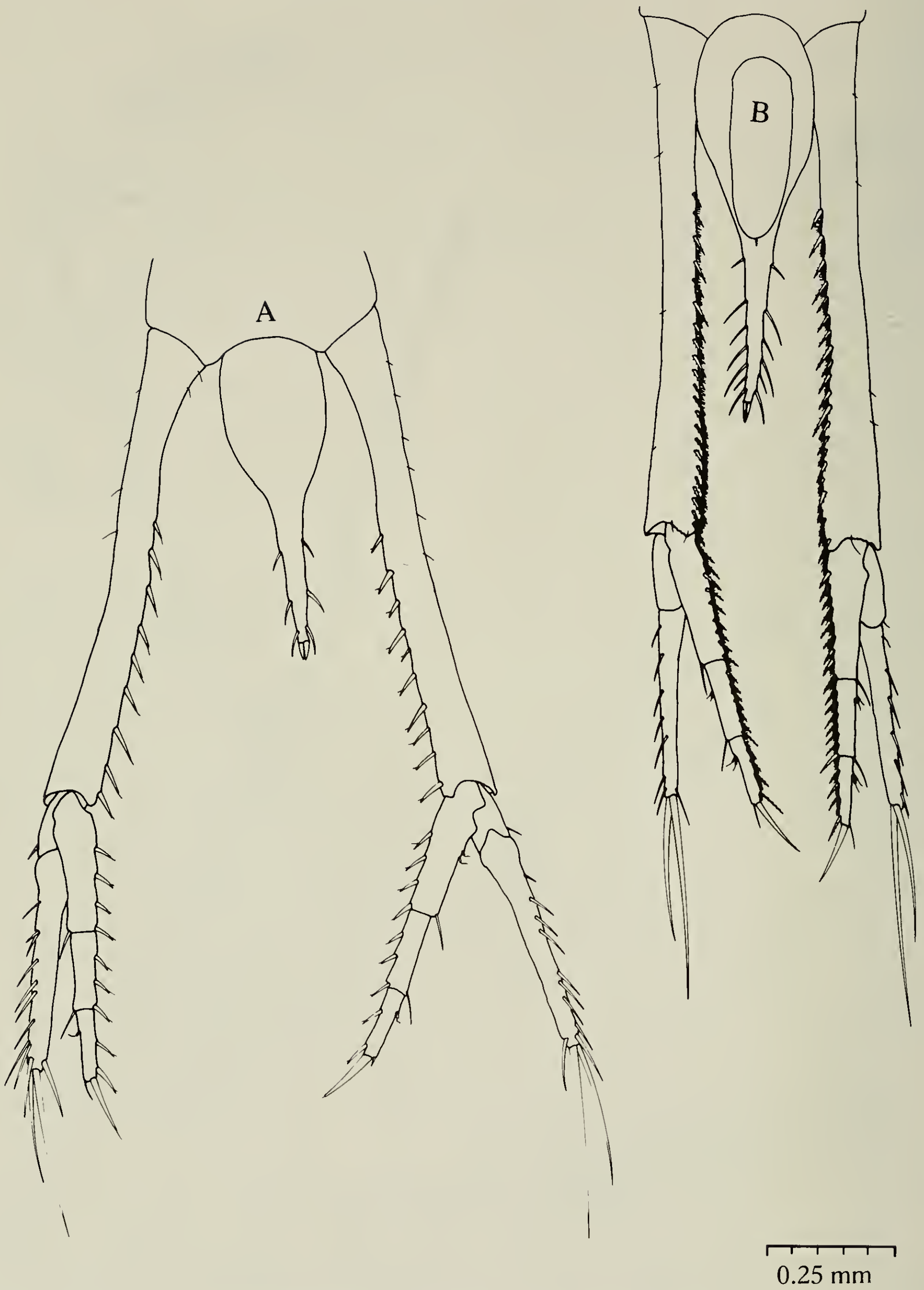

Fig. 9. *Diastylis tongoyensis*, new species. A, adult ♀ telson and uropods; B, adult ♂ telson and uropods.

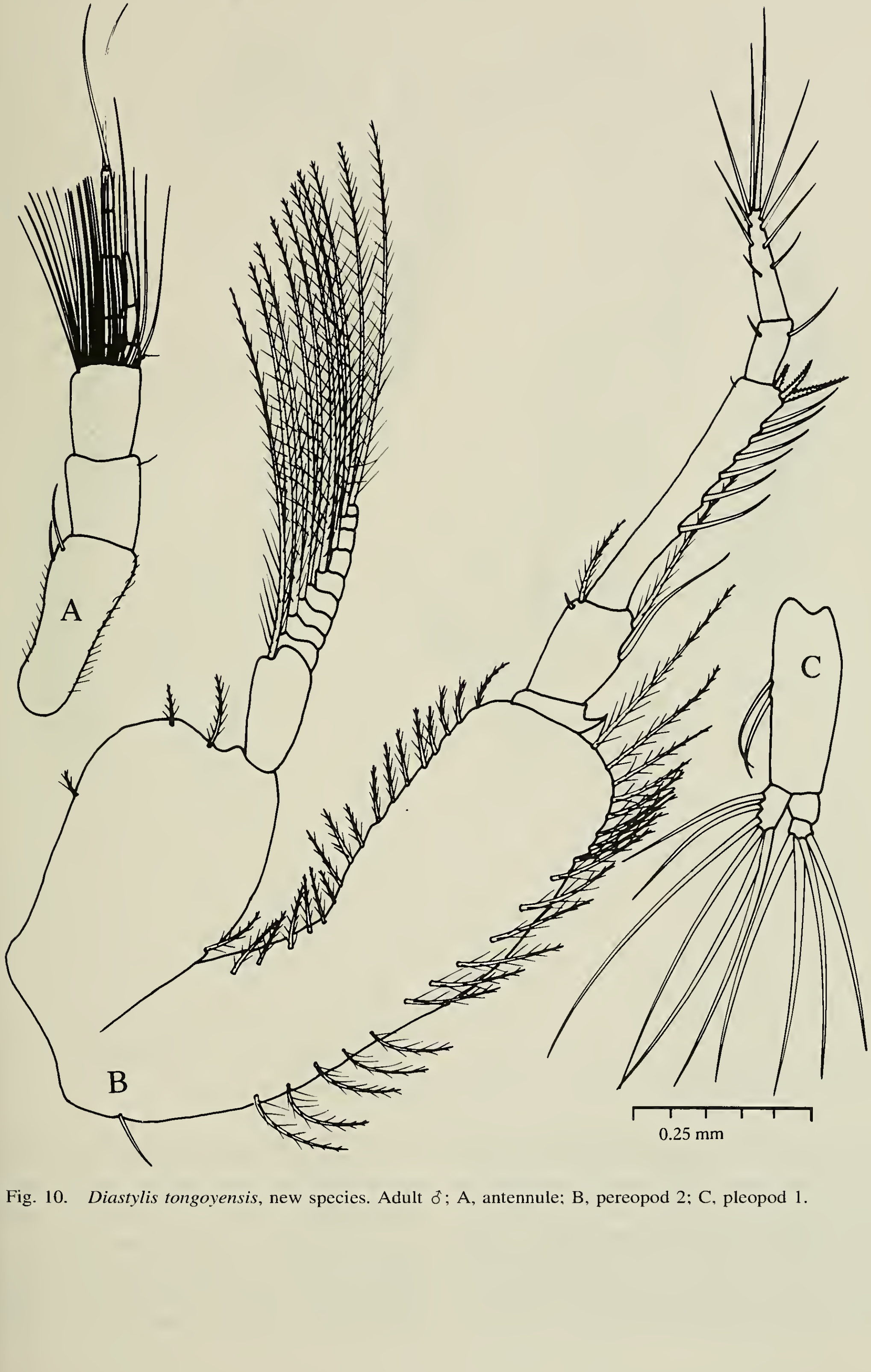

Fig. 10. *Diastylis tongoyensis*, new species. Adult ♂; A, antennule; B, pereopod 2; C, pleopod 1.

Fig. 11. *Diastylis tongoyensis*, new species. Adult ♂; A, pereopod 3; B, maxilliped 3.

simple setae on margin; dactyl subequal to carpus, posterior margin with 3 simple setae, distal margin with 4 long serrate setae; exopod three-fourths length endopod basis; exopod basal article expanded, with few short plumose setae, flagellum bears many long plumose setae (Fig. 5B).

Pereopod 2 basis expanded, length equal to all other articles together, margins beset with plumose setae, increasing in length distally; ischium shorter than wide, produced as large marginal tooth, otherwise unarmed; merus one-third length of carpus, distal corners with plumose setae, single

Fig. 12. *Diastylis crenellata* Watling & McCann 1997. Adult ♀; A, pereopod 3; B, pereopod 4.

long simple seta and single small simple seta on margins; carpus margin with row of stout simple setae, distal corner with group of 3 stout serrate setae; propodus half dactyl length, with 2 simple setae; dactyl lateral and distal margins with several long simple setae, increasing in length distally; exopod as long as endopod basis, ischium, merus together, basal article expanded, armed with few short plumose setae, flagellum longer than basal article, bearing many long plumose setae (Fig. 10B).

Pereopod 3 basis as long as remaining articles together, expanded, bearing few plumose setae; ischium short, distal margin with row of annulate setae; merus margin with 3 long annulate setae, lateral face of article with several small simple setae; carpus as long as propodus and dactyl together, posterior margin with row of short annulate setae and anterior margin with row of stout long annulate setae; propodus with single extremely stout annulate seta distally; dactyl with single short stout simple seta distally; exopod as long as first 4 articles of endopod together, basal article expanded with 2 short plumose setae and 1 stout simple seta distally, flagellum bearing many long plumose setae (Fig. 11A).

Pereopod 4 basis as long as ischium, merus, carpus together, expanded, few short simple setae on margin, distally 2 long plumose setae and 1 long simple seta; ischium with row of long simple setae distally; merus as long as carpus and propodus together, anterior margin with 4 long simple setae; carpus anterior margin with 2 long annulate setae, posterior margin with single short simple seta, distal margin with row of long stout annulate setae; propodus as long as dactyl, bearing 1 extremely stout, long annulate seta distally; dactyl 0.5 width of propodus, bearing short stout simple seta distally; exopod as long as endopod basis and ischium together, basal article expanded and unarmed, flagellum bearing many long plumose setae (Fig. 7A).

Pereopod 5 basis narrow proximally, as long as ischium and merus together, posterior margin with 3 long plumose setae, anterior margin with 3 simple setae, distal margin with 1 plumose seta; ischium posterior margin with 2 long annulate setae, distal margin with 2 annulate setae; merus as long as carpus, 4 long annulate setae distally, 1 short simple seta proximally; carpus posterior margin with 4 long annulate setae, distal margin with row of very stout, very long annulate setae; propodus as long as dactyl, bearing single stout long annulate seta distally; dactyl margin with single pedunculate seta, distally 1 short stout seta (Fig. 8B).

Pleopod 1 biramous, peduncle lateral margin with 2 simple setae; endopod bi-articulate, distal article with 4 very stout long simple setae distally; exopod uni-articulate, bearing 6 long stout simple setae (Fig. 10C).

Pleopod 2 biramous, peduncle lateral margin with 2 short simple setae; endopod bi-articulate, distal article bearing 4 long stout simple setae; exopod uni-articulate, bearing 6 long stout simple setae (Fig. 8C).

Telson length 0.75 uropod length, pre-anal portion subequal to post-anal portion. Preanal portion produced as hump dorsally, with oval ridge surrounding a dorsal depression, hump serrated distally, otherwise unarmed. Post-anal portion very slender, with 6 pair simple setae laterally, 1 pair short stout simple setae terminally (Fig. 9B).

Uropod peduncles twice as long as rami, distal ⅔ of medial margin armed with 22 short stout plumose setae with short setules. Uropod endopod 3-articulate, medial margin armed with 20 short stout plumose setae with short setules; articles 1 and 2 each with 1 slender seta at lateral distal corner; articles 2 and 3 each with 1 pair pedunculate setae on lateral proximal margin; article 3 with single stout seta and single slender seta terminally. Uropod exopod bi-articulate, article 2 with 5 slender setae laterally, 2 very long setae terminally (Fig. 9B).

Etymology.—The species is named for the type locality, Bahia Tongoy, Chile.

Diastylis crenellata Watling & McCann, 1997
Fig. 12

Material examined.—San Diego, California, 32°38.75′N, 117°20.06′W, 2 ovigerous ♀♀.

Description (*amended*).—As in Watling & McCann 1997, with the addition that pereopods 3 & 4 in the female bear rudimentary exopods (Fig. 12A, B).

Table 1.—A comparison of characters in *D. rathkii* and *L. longimana,* "typical" members of their genera, with those of *D. tongoyensis,* which represents a transitional group of species.

	Diastylis rathkii (Krøyer, 1841)	*Diastylis tongoyensis*	*Leptostylis longimana* (Sars, 1865)
Length of telson relative to telsonic somite	2 times that of telsonic somite	1.5 times telsonic somite	Shorter than telsonic somite
Length of telson relative to uropod peduncle	Equal to length of uropod peduncle	⅔ length of uropod peduncle	⅓ length of uropod peduncle
Number of pairs of lateral setae on telson	10 in adult ♀, 16 in adult ♂	3 in adult ♀, 6 in adult ♂	1 in adult ♀, 1 in adult ♂
Antenna 1 in adult male relative to female	Slightly laterally expanded, ring of setae terminally	Laterally expanded, ring of setae terminally	Greatly laterally expanded, multiple rings of setae terminally
Antenna 2 flagellum in adult male	Extends beyond telson	Extends beyond telson	Does not extend beyond thorax
Exopods on pereopods 3 & 4 in female	None	Rudimentary	Rudimentary

Discussion

As Day (1980) pointed out, the genera *Diastylis*, *Leptostylis*, and *Makrokylindrus* are problematical because their definitions overlap to such an extent that it is impossible to separate them cleanly. Characters used to diagnose the genera *Leptostylis* and *Diastylis* include the number of lateral setae on the telson, relative proportions of the pre- and post-anal portions of the telson, and antennule morphology of the adult male. Species assigned to *Leptostylis* and *Diastylis* overlap in the telson to uropod peduncle ratio, length of telson relative to telsonic somite, lateral spination of the telson, exopod state on pereopod 3 and 4 of the female, and morphology of the adult male antennule. *Diastylis tongoyensis* is one of the species that fits within the current diagnosis of *Diastylis*, yet also exhibits characters similar to *Leptostylis*. Table 1 compares *D. tongoyensis* to "typical" species of *Diastylis* and *Leptostylis*, viz., *D. rathkii* (Krøyer, 1841) and *L. longimana* (Sars, 1865). For all the characters listed, *D. tongoyensis* is transitional between *D. rathkii* and *L. longimana*.

Within the genus *Diastylis*, there is a group of species, in concert with *D. tongoyensis*, that share the characters opercular maxilliped 3, short telson, and rudimentary exopods on pereopods 3 & 4 in the female. The species included in this group are *D. abbotti* Gladfelter, 1975, *D. alaskensis* Calman, 1912, *D. calderoni* Donath-Hernandez, 1988, *D. crenellata* Watling & McCann, 1997, *D. insularum* Calman, 1908, *D. paratricinta* Kang & Lee, 1996, *D. pellucida* Hart, 1930, *D. planifrons* Calman, 1912, *D. sympterygiae* Bacescu & Lima de Quieroz, 1985. With the exception of *D. sympterygiae*, which is from the Southeast Atlantic, all are found in the North Pacific, East Pacific, or Antarctic. This species group seems to represent a transitional state between what is represented by the "typical" members of the genus *Diastylis* and those of *Leptostylis*.

A significant portion of the problem with separating these two genera is the lack of designated types. The designated type of *Diastylis* is *D. arenarius* Say, 1818; however, the original material is lost and the description is so vague that it could describe any adult male telson-bearing cumacean (Day 1980). In the case of *Leptostylis*, the genus was created for four species but no type was designated (Sars 1869, Day 1980). A proposal for designating *D. rathkii* as the type for *Diastylis* has been submitted to the ICZN.

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Redescription of the poorly known porcelain crab, *Lissoporcellana nakasonei* (Miyake, 1978) (Crustacea: Decapoda: Anomura: Porcellanidae)

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Abstract.—*Lissoporcellana nakasonei* (Miyake, 1978a) is redescribed based on the holotype specimen, which Miyake (1957) established as *Porcellana maculata*, and on material recently obtained. Miyake's *P. maculata* is a junior primary homonym of *P. maculata* H. Milne Edwards, 1837 (=*Neopetrolisthes maculatus*) and was replaced with *P. nakasonei* by Miyake (1978a). Reexamination of Miyake's specimen has revealed that *P. nakasonei* belongs in *Lissoporcellana* and resembles *L. miyakei* Haig, 1981 more closely than previously realized. *Lissoporcellana nakasonei* is distinguishable from *L. miyakei* primarily by the subparallel branchial margins of the carapace.

Lissoporcellana nakasonei (Miyake, 1978a) was originally described as *Porcellana maculata* by Miyake (1957), based on three male specimens collected from Tanabe Bay, Wakayama Prefecture (Kii Peninsula of Honshu mainland, Japan). In a species list of decapod crustaceans around the Amakusa Marine Biological Laboratory on the western coast of Kyushu, Japan, a new name, *Porcellana nakasonei*, was proposed by Miyake (1978a) for his *P. maculata* without comment, but probably because he noticed that the latter name was a junior primary homonym of *Porcellana maculata* H. Milne Edwards, 1837 [=*Neopetrolisthes maculatus* (H. Milne Edwards)]. Miyake's taxon can be readily distinguished from H. Milne Edwards' by the structure of the carapace. Haig (1978), unaware of Miyake's replacement of the name, assigned his *Porcellana maculata* to her new genus *Lissoporcellana* in a revision of the genus *Porcellana* Lamarck, 1801, and also pointed out that Miyake's species required a new name because of the homonymy; however, she did not examine material of Miyake's taxon.

Examination of the holotype of Miyake's species and comparison with material recently obtained from Kushimoto near the type locality, have confirmed that *Porcellana nakasonei* belongs in the genus *Lissoporcellana.* This species is here redescribed in detail, and is compared with the closely similar congener, *L. miyakei* Haig, 1981.

The carapace length (CL), an indication of specimen size, was measured from the anteromedian notch of rostrum to the posteromedian end of carapace. Measurements of chelipeds were made as follows: length of carpus, along dorsomedian longitudinal axis, and breadth on dorsal transverse midline (excluding the extensor teeth); length of chela, along extensor margin, and height along dorsodistal transverse line of palm; and length of dactyl, along flexor margin. Measurements of ambulatory legs were made as follows: length of merus, carpus, and propodus, along extensor margin; and height of propodus along lateral transverse midline. The holotype remains deposited in the Seto Marine Biological Laborotory, Kyoto University (SMBL) and additional specimens examined are deposited in the Natural History Museum and Institute, Chiba (CBM).

Lissoporcellana nakasonei
(Miyake, 1978a)
Figs. 1–3

Porcellana maculata Miyake, 1957:75, figs. 1–3 (type locality: Shiso-jima, Tanabe Bay, Wakayama Pref.).—Miyake et al., 1962:125 (list). Not *Porcellana maculata* H. Milne Edwards, 1837 [=*Neopetrolisthes maculatus* (H. Milne Edwards)].

Porcellana nakasonei Miyake, 1978a:28 (list); 1978b:173 (key, English part), 149 (key, Japanese part).

Lissoporcellana maculata.—Haig, 1978: 712.

Lissoporcellana nakasonei.—Miyake, 1982:204 (list), 240 (key).

Material examined.—Holotype, male (CL 3.8 mm), Shiso-jima (Tanabe Bay, Shirahama, Wakayama Pref.), commensal with *Dendronephthya gloriosa*, lobster gill net, 1 May 1954, coll. T. Yamamoto, SMBL 164.—1 male (CL 3.4 mm), Takatomi, Kushimoto, Wakayama Pref., associated with *Dendronephthya nipponica*, lobster gill net, 31 Mar 1995, coll. M. Osawa, CBM-ZC 3687.—1 female (CL 3.2 mm), 1 ovig. female (CL 3.7 mm), data as in CBM-ZC 3687, but attached to different host colony, CBM-ZC 3688.

Description.—Carapace (Fig. 1A, B) weakly or moderately convex dorsally, approximately 1.2 times as long as broad, broadest on median branchial margin. Branchial margins very weakly convex, subparallel, without distinct longitudinal ridge; anterior margin minutely denticulate, 1 or 2 spines at anterior corner larger than others; median margin with well developed spine; posterior margin and adjacent region with long oblique rugae. Rostrum (Fig. 1D–F) broad, horizontal, produced well beyond eyes, trilobate anteriorly; median lobe approximately 3.0 times as broad as laterals, with median longitudinal, shallow groove extending near protogastric region, divided into 2 sublobes by V- or U-shaped anterior notch bearing 1 or 2 small spines or minute denticles; lateral lobes curved inwards on lateral distal margin, sharply pointed anteriorly; dorsal surface with numerous, very short, faint, transverse striae. Orbits (Fig. 1K, L) relatively shallow; supra-orbital margin strongly oblique, slightly convex, unarmed; outer orbital angle produced into acute, small or minute spine. Protogastric ridge almost very weakly demarcated. Gastric region covered with short, faint, transverse striae. Hepatic regions less striate than in gastric and branchial regions, bearing minute setae; lateral margin with strong acute spine. Cervical grooves weakly demarcated. Anterior branchial regions with short, faint, transverse striae less numerous than in gastric region. Inner posterior branchial and cardiac regions punctate or weakly striate, several striae with short setae.

Pterygostomian flaps (Fig. 1B, C) with strong longitudinal ridges, relatively weakly narrow posteriorly; anterior angle acutely pointed; anterodorsal margin with small spine near posterior end.

Third thoracic sternite (Fig. 1G, H) rather weakly depressed, trilobate anteriorly; median lobe much broader than laterals, with broadly truncate anterior margin; lateral lobes narrow, not exceeding median, with rounded apex. Fourth thoracic sternite with series of short, faint striae bearing several short or long setae along strongly concave, anterior margin.

Telson (Fig. 1I) composed of 7 plates; proximolateral plates much smaller than others; distal plates relatively broad.

Ocular peduncles (Fig. 1K) large, short, with several short and long striae on dorsal surface; dorsal extension onto cornea broadly triangular, with rounded apex.

Basal segment of antennular peduncles (Fig. 1J) transversely rugose on anterior region of ventral surface. Anterior margin minutely denticulate or tuberculate except for

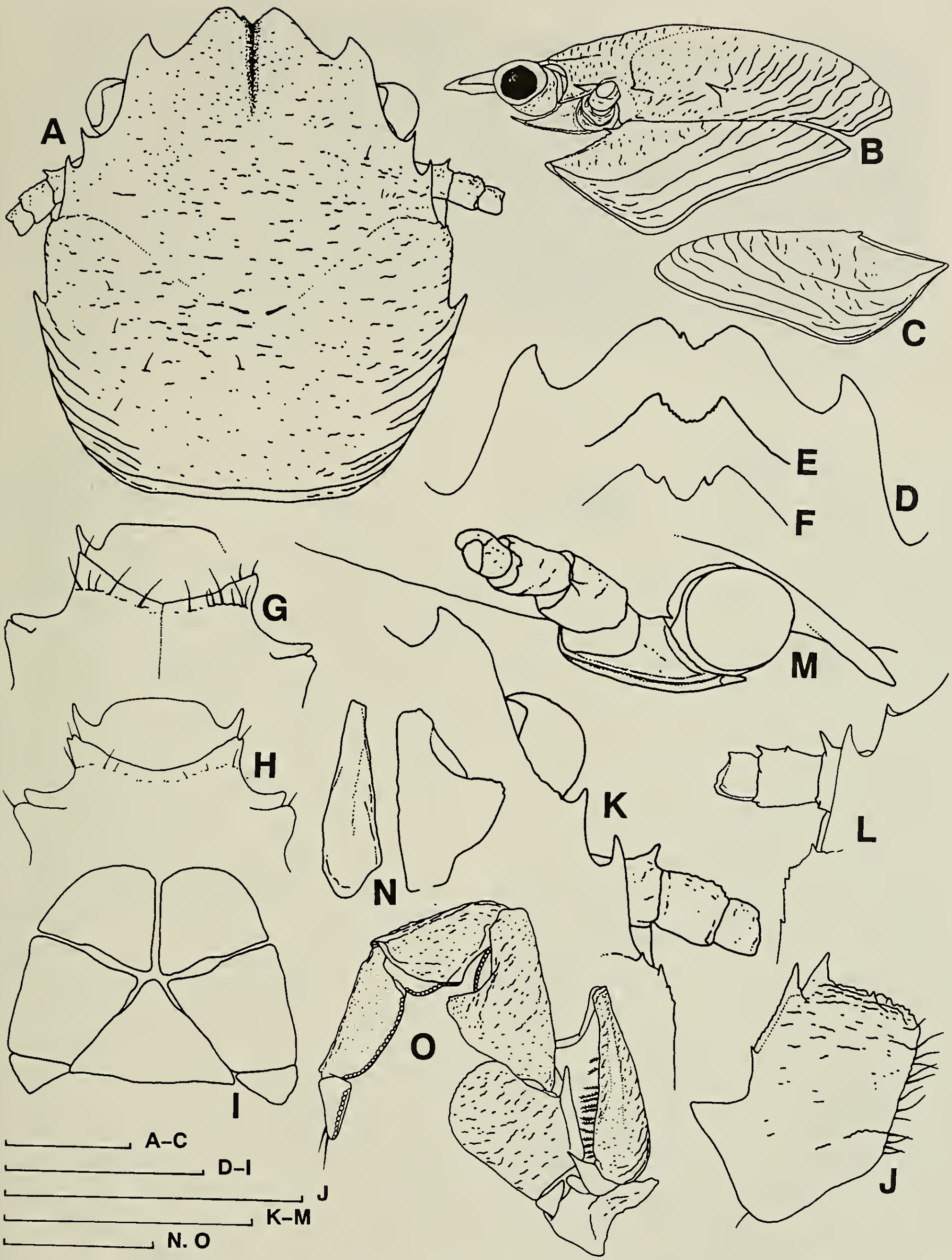

Fig. 1. *Lissoporcellana nakasonei* (Miyake, 1978a). A, C, D, G, I, K, M, N, holotype, male (CL 3.8 mm, SMBL 164); B, E, H, J, L, O, male (CL 3.4 mm, CBM-ZC 3687); F, ovig. female (CL 3.7 mm, CBM-ZC 3688). A, carapace, dorsal; B, carapace and left pterygostomian flap, lateral; C, right pterygostomian flap, lateral; D, rostrum, dorsal; E, F, same, median lobe, dorsal; G, H, anterior thoracic sternites, ventral; I, telson, exposed; J, left basal segment of antennular peduncle, ventral; K, right anterior lateral part of carapace, eye, and antennal peduncle, dorsal; L, left anterior lateral part of carapace and antennal peduncle, dorsal; M, right eye and antennal peduncle, lateral; N, right third maxilliped, merus and exopod, ventral; O, left third maxilliped, ventral. Scales equal 1.0 mm.

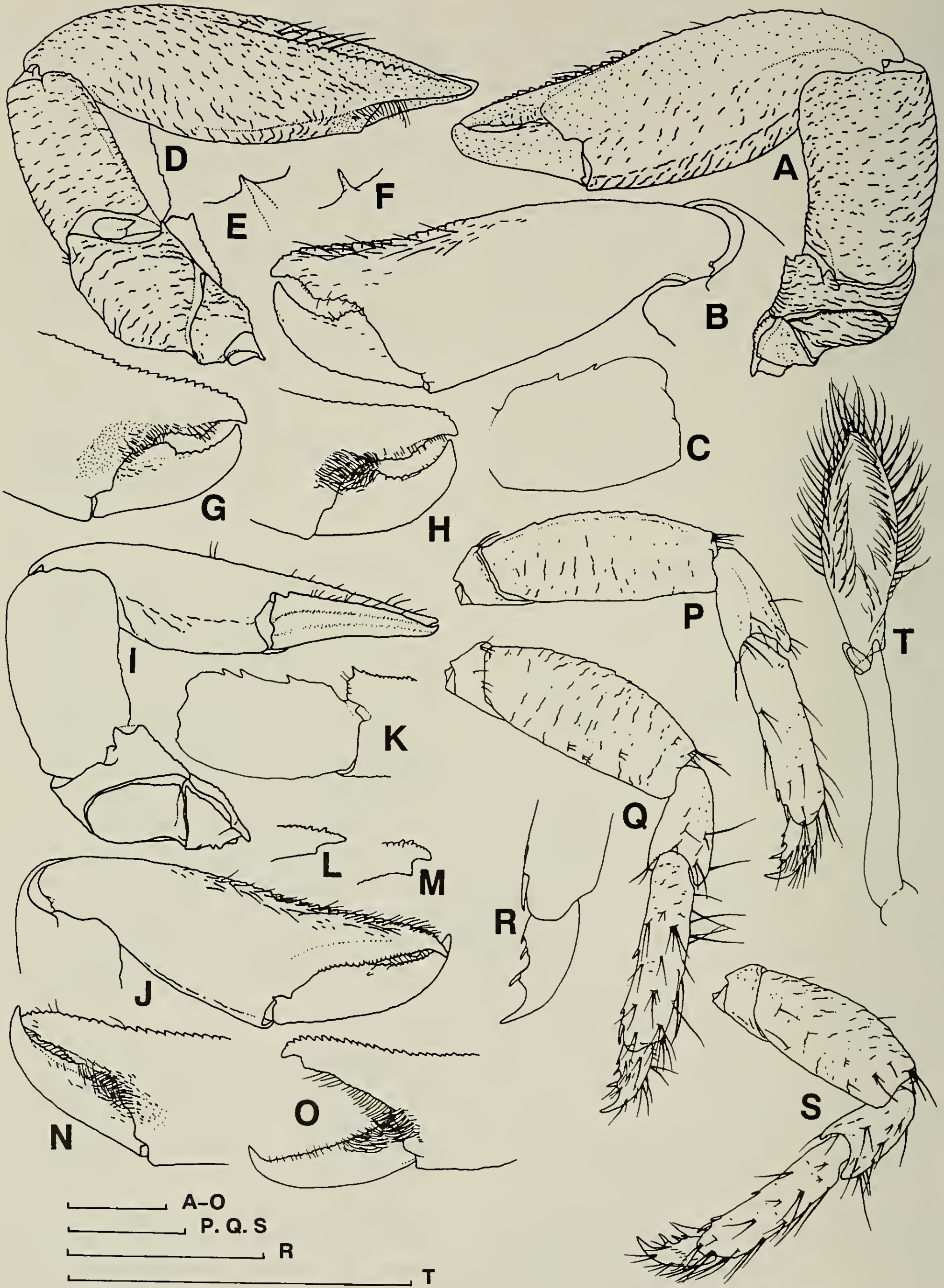

Fig. 2. *Lissoporcellana nakasonei* (Miyake, 1978a). A, B, D, E, G, I, J, L, N, P–S, holotype, male (CL 3.8 mm, SMBL 164); C, F, H, K, O, T, male (CL 3.4 mm, CBM-ZC 3687); M, ovig. female (CL 3.7 mm, CBM-ZC 3688). A, larger cheliped, right, dorsal; B, same, chela, dorsoextensor; C, same, carpus, dorsal; D, same, ventral; E, F, same, merus, distoflexor corner, ventral; G, H, same, chelae, distal part, ventral; I, smaller cheliped, left dorsal; J, same, chela, dorsoextensor; K, same, merus and carpus, dorsal; L, M, same, immovable

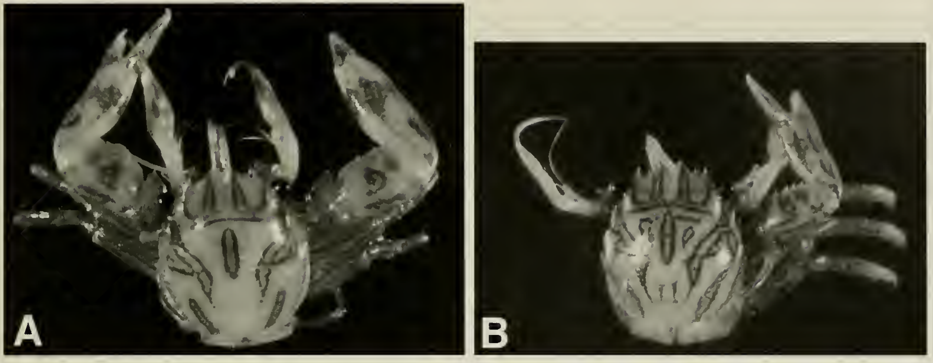

Fig. 3. *Lissoporcellana nakasonei* (Miyake, 1978a). Entire animal, dorsal. A, male (CL 3.4 mm), CBM-ZC 3687; B, female (CL 3.2 mm), CBM-ZC 3688.

2 strong acute spines at mesial corner. Lateral margin fringed with short setae.

Antennal peduncles (Fig. 1K–M) relatively short; first segment immovable, following 3 segments movable. First segment largest, strongly produced forward in lateral view, broadly in contact with anterior margin of carapace, acutely pointed anteriorly; with longitudinal rugose ridge along ventral margin. Second segment with slender spine near anterior distal corner. Third segment rather weakly elongate; anterior margin with minute protuberances, distal corner usually with small spine (unarmed or with weakly developed spine in each side of holotype). Fourth segment small, rounded. Dorsal and ventral surfaces of second to fourth segments slightly rugose.

Third maxillipeds (Fig. 1N, O) with ischium broad, ovate, transversely rugose on ventral surface; with longitudinal ridge along extensor margin; distoextensor corner with slender projection. Merus with laminate, subrectangular lobe bearing rounded projection on ventroflexor margin; moderately rugose on ventral surface. Carpus with broad triangular projection on median region of flexor margin and longitudinal rows of short rugae along extensor margin on ventral surface. Propodus relatively slender, nearly smooth except for short rugae along extensor margin. Dactyl small, subtriangular; ventral surface smooth. Merus to dactyl with long setae on flexor margin (not illustrated). Exopod laminate, relatively robust; proximal region strongly inflated; distal region slender, with flagellum.

Chelipeds (Fig. 2A–O) subcylindrical, unequal (right larger than left in three of four specimens examined), not showing sexual dimorphism. Larger cheliped (Fig. 2A–H) with short merus; dorsal surface transversely rugose, with distinct transverse ridge submedially; dorsoflexor margin crenulated, distally with rounded or subrectangular lobe bearing small spine; dorsodistal margin unarmed; ventral surface transversely rugose, flexor corner with moderately or well developed, acute spine. Carpus 1.7–1.8 times as long as broad, broadened distally; dorsal surface with numerous, faint, short transverse rugae; dorsoextensor margin with strong oblique rugae, unarmed entirely; dorsoflexor margin weakly concave, slightly crenulated, lacking or with up to 3 acutely pointed, small teeth; dorsodistal

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←

finger, distal end, extensor; N, O, same, chela, distal part, ventral; P, right first ambulatory leg, lateral; Q, right second ambulatory leg, lateral; R, same, dactyl and distal part of propodus, lateral; S, right third ambulatory leg, lateral; T, male pleopod on second abdominal somite, inner. Scales equal 1.0 mm.

margin with broad rounded lobe on flexor part; ventral surface weakly rugose transversely, flexor margin slightly crenulate. Chela relatively narrow, elongate, approximately 2.1 times as long as carpus, 2.9 times as long as high, lying on extensor side; dactyl opening at more or less sharply oblique angle; extensor margin thin, weakly concave on distal ⅓, unarmed except for serrated or denticulate distal part of palm and fixed finger, with short or minute setae on median part of palm to fixed finger. Palm with dorsal surface convex, covered with faint, short oblique rugae or small pits, no distinct median longitudinal ridge; dorsoflexor margin with longitudinal rugose ridge; ventral surface obliquely rugose. Fixed finger with slightly curved distal claw; dorsal surface with very short rugae, small pits, and several minute setae; dorsoflexor proximal part with broad, weakly developed rounded projection extending onto dactyl; cutting edge minutely tuberculate, median part with broad, low, rounded or subtriangular tooth; ventral surface with very short rugae and small pits, proximal flexor part with fringe of short setae extending to cutting edge. Dactyl approximately 0.4 of chela length, as long as fixed finger, with strongly curved distal claw, dorsal and ventral surfaces with very short rugae and small pits; cutting edge minutely tuberculate, with broad, rounded tooth and more or less developed fringe of short setae on ventral proximal part.

Smaller cheliped (Fig. 2I–O) almost identical to larger, except for: carpus lacking or with up to 4 acutely pointed, small teeth on dorsoflexor margin; chela narrower, approximately 3.5 times as long as high, with dactyl usually opening at near vertical angle; fingers crossed distally, with more sharply pointed claw; fixed finger with dorsal surface provided with broad subtriangular or narrowly pointed projection extending onto dactyl on proximal flexor part, cutting edge lacking distinct tooth, distal end weakly bifurcate; and dactyl approximately 0.5 of chela length, slightly longer than fixed finger.

Ambulatory legs (Fig. 2P–S) relatively slender, with scattered, short and relatively long setae (propodus and dactyl more setose than in other segments). Merus elongate, first and second legs subequal and longer than third, lateral surface with short transverse rugae, extensor margin unarmed but slightly serrated, distoflexor part with rounded lobe minutely granulated or serrated marginally. Carpus with 1 or 2 weakly marked, longitudinal rows of short rugae on lateral surface; disto-extensor corner unarmed. Propodus 1.6–1.7 times as long as carpus, 4.0–4.1 times as long as high; lateral surface with several short, oblique rugae; flexor margin with 4 movable spines, distal pair much larger than median and subdistal spines. Dactyl terminating in narrow, moderately or strongly curved claw; flexor margin with 3 corneous spines progressively smaller proximally, proximal 2 spines movable, distal spine fixed, distinctly larger than others, with enlarged, produced base adjacent to terminal claw.

Fifth pereopod small, slender, chelate; propodus with approximately 10 hooked setae.

Males with pair of developed pleopods on second abdominal somite (Fig. 2T); protopod naked; endopod spoon-shaped, ovate with narrowly rounded distal apex, bearing numerous marginal setae except for proximal part; exopod small, ovate, naked; no traces of pleopods on third to fifth abdominal somites. Females with paired pleopods on third to fifth abdominal somites; third pair small, fourth and fifth pairs well developed.

Color (Fig. 3A, B).—Background color of carapace, abdomen, and pereopods white. Carapace with reddish line along protogastric ridge and lateral lobes of rostrum, and reddish ovate ring markings on following regions: 2 in frontal, 1 in gastric, and 3 in branchial regions, each sometimes with smaller markings. Chelipeds with several scattered, reddish ovate markings on dorsal surface. Ambulatory legs with 2 or 3 reddish, longitudinal stripes on lateral surface.

Habitat.—The specimens recently obtained were found on colonies of a reddish alcyonacean octocoral, *Dendronephthya nipponica* Utinomi, caught with gill nets used in spiny lobster fishing. The nets are generally set in depths of approximately 20 m on rocky shore.

Distribution.—This species has been recorded only from Japan, southwestern coast of Kii Peninsula of Honshu mainland (Miyake 1957, present study) and Amakusa in the middle western coast of Kyushu (Miyake et al. 1962).

Remarks.—The present species is assignable to *Lissoporcellana* based on the following: rather smooth (weakly striate) carapace with a broad, horizontal trilobate rostrum (median lobe with an anterior notch) and indistinctly marked regions; first segment of antennal peduncle strongly produced forward in lateral view, and broadly in contact with anterior margin of carapace; unequal, subcylindrical chelipeds with fingers opening at a rather sharply oblique angle; and asymmetry of chelipeds in size and armature of carpus and chela, and degree of bending of fingers (indistinctly bent), not due to sexual dimorphism.

Reexamination of the holotype specimen has revealed that a number of features had not been previously reported: the fingers of both chelae possess a weakly developed fringe of short setae on the ventral proximal base and cutting edges; the fixed finger of the smaller chela is weakly bifurcate at the distal end; and the propodi of all three ambulatory legs are provided with a median small spine on the flexor margin and their dactyls have a fixed spine with an enlarged, produced base adjacent to the terminal claw.

Although Haig (1981) discussed morphological differences between *L. nakasonei* and its closely similar congener, *L. miyakei* Haig, 1981, all differences such as presence of setae on the gape of the fingers and distal bifurcation on the fixed finger of the smaller cheliped, and armature of dactyls of ambulatory legs, were found to be incorrect during the present study. *Lissoporcellana nakasonei*, however, can be distinguished from *L. miyakei* by another character on the carapace. The branchial margins are subparallel in *L. nakasonei*, whereas they are strongly convex in *L. miyakei*.

Haig (1978) mentioned that Monod's (1973) "*Porcellana* sp." was perhaps identical with *Lissoporcellana nakasonei* (as *L. maculata*). However, Monod's figures (figs. 44–51) show a female specimen that differs from *L. nakasonei* in having strongly convex branchial margins of the carapace with two spines on the median part. As the armature of the anterior margin of the rostrum and the branchial margins of the carapace of his specimen does not appear to fit any known species of *Lissoporcellana*, it may well belong to another, perhaps undescribed species.

Lissoporcellana now contains nine Indo-West Pacific species (Haig 1981, Yang & Sun 1992). Most of the species are known to be associated with sponges, hydrozoans, or anthozoans such as scleractinians, antipatharians, alcyonaceans, and gorgonaceans (Haig 1981). *Lissoporcellana nitida* (Haswell, 1882) and *L. furcillata* (Haig, 1965), in particular, are quite distinct in that the dactyls of the ambulatory legs have deeply bifurcated tips forming two strong fixed claws (see Haig 1965). Although this structure resembles those of species of the commensal genera such as *Polyonyx* Stimpson, 1858, *Aliaporcellana* Nakasone & Miyake, 1969, and *Eulenaios* Ng & Nakasone, 1993 (see Ng & Nakasone 1993, Ng & Sasekumar 1993, Ng & Goh 1996), *Lissoporcellana* seems to be more allied to *Pisidia* Leach, 1820, in the general appearance, including the trilobate or tridentate horizontal rostrum (some species of the latter genus have a weakly or moderately deflexed rostrum) and the bending of the fingers of the smaller cheliped. The similarity of structure on the ambulatory dactyls may be the result of habitat or degree of dependence on the host.

Acknowledgments

I wish to thank Dr. S. Kubota of the Seto Marine Biological Laboratory, Kyoto University, for arranging the loan of the holotype specimen of Miyake's species. I am also indebted to Dr. P. K. L. Ng of the National University of Singapore, Dr. R. K. Kropp of Battelle Ocean Sciences, Dr. A. W. Harvey of the American Museum of Natural History, and Dr. R. Lemaitre of the National Museum of Natural History, Smithsonian Institution, for their critical review of the manuscript and helpful comments.

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A new genus and species of ghost shrimp (Crustacea: Decapoda: Callianassidae) from the Atlantic Ocean

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Abstract.—*Necallianassa berylae*, new genus and species, are named from material taken at several locations off the coasts of Georgia and South Carolina in depths ranging from 35 to 75 m. Two eastern Atlantic species, *Callianassa acanthura* Caroli, 1946, and *C. truncata* Giard & Bonnier, 1890, are transferred to *Necallianassa.* Members of this new genus can be distinguished from other members of the Callianassinae by the presence of a lateral spine on the uropodal endopod and one or two lateral spines on the telson.

An undescribed species of callianassid was found by one of us (R.W.H.) in collections made during ecological and baseline studies conducted off the coasts of Georgia and South Carolina. Nearly all of the specimens are broken, and many are fragmentary with legs detached or missing. The holotype and a series of paratypes have been deposited in the National Museum of Natural History, Washington (USNM). Additional paratypes have been deposited in the Museum of the Gulf Coast Research Laboratory, Ocean Springs (GCRL).

The specimens from Georgia were collected by M. B. Gray, Sapelo Island Research Foundation (SRF). The specimens from South Carolina were collected by Texas Instruments South Atlantic Benchmark Program for the Minerals Management Service, U.S. Department of the Interior (TI/MMS).

Abbreviations used in the accounts below include: A1, antennule; A2, antenna; cl, postorbital carapace length; ft, feet; leg., collector or collected by; m, meters; Man, mandible; Max1–2, first and second maxillae; mm, millimeters; Mxp1–3, first to third maxillipeds; P1–5, first to fifth pereopods (P1 is the cheliped, P5 the fourth walking leg); Plp1–5, first to fifth pleopods; tl, total length.

Callianassidae Dana, 1852
Callianassinae Dana, 1852
Necallianassa, new genus

Type species.—*Necallianassa berylae*, new species, by present designation.

Included species.—The type species, from the western Atlantic, and two other species from the eastern Atlantic: *Necallianassa truncata* (Giard & Bonnier, 1890), new combination; and *Necallianassa acanthura* (Caroli, 1946), new combination.

Diagnosis.—Size very small to medium, total lengths of adults 15 mm or less to about 50 mm. Carapace with dorsal oval and rostral projection or spine, lacking cardiac prominence and rostral carina. Rostral spine, when present, extending to or beyond cornea. Cornea subterminal, dorsal, small, disc-shaped. A1 peduncle similar to A2 peduncle in size and length. Mxp3 suboperculiform, length of ischium and merus similar to or less than twice width, without exopod; merus not projecting beyond articulation with carpus; distal 3 segments elongate, much slenderer than basal 2 segments; dactylus slenderer than propodus. Chelipeds unequal, both P1 with meral hook. Second abdominal somite ⅓ longer than sixth somite. Male Plp1 uniramous, 2-segmented; male Plp2 absent. Female Plp 1 uniramous, Plp2 biramous. Endopods of Plp3–5 with stubby, projecting appendices internae. Telson subrectangular, with median posterior projection and 1 or 2 much larger lateral spines. Uropodal endopod with one strong lateral spine.

Remarks.—Members of *Necallianassa* can be distinguished from members of all other genera in the Callianassidae by the presence of one or two lateral spines on the telson and a strong outer spine on the uropodal endopod.

Etymology.—From the Latin, the prefix "ne-", not, and the generic name *Callianassa.* Gender feminine.

Necallianassa berylae, new species

Figs. 1–3*a*, *b*

Material.—South Carolina: 32°00′57″N, 79°31′03″W, depth 43 m, sand, leg. TI/MMS, *G. W. Pierce* sta 9737, sample 0177-2 (3E), box core, Aug 1977: 1 ♂, cl 4.1 mm (holotype, USNM 260881), 1 ♀, cl 3.5 mm (paratype, USNM 260882).—32°00′57″N, 79°31′03″W, depth 43 m, sand, leg. TI/MMS, *G. W. Pierce* sta 9737, sample 0177-5 (3E), box core, 18 Feb 1977: 1 ♂, cl 4.5 mm, 1 damaged ovigerous ♀, cl 3.4 (paratypes, GCRL).—32°00′57″N, 79°31′03″W, depth 43 m, sand, leg. TI/MMS, *G. W. Pierce* sta 9737, sample 0177-6 (3E), box core, 18 Feb 1977: 1 ♀, cl 3.4 mm, 1 fragment (paratypes, USNM 260-883).—32°01′04″N, 79°31′05″W, depth 35 m, sand, leg. TI/MMS, *G. W. Pierce II* sta 9737, sample 0787-4 (3E), box core, 22 Feb 1977: 2 ♀♀ (1 broken), cl ca. 3.5 mm and ca. 4.0 mm (paratypes, USNM 260-884).—32°01′04″N, 79°31′05″W, depth 35 m, sand, leg. TI/MMS, *G. W. Pierce II* sta 9737, sample 0787-5 (3E), box core, 25 Aug 1977: 1 ♂, cl 2.5 mm (tl ca. 10.0 mm), 1 ♀, cl ca. 4.5 mm (tl ca. 15 mm) (paratypes, USNM 260885).

Georgia: 31°33′38″N, 79°39′01″W, depth 245 ft (75 m), SRF sta 306, bucket dredge, leg. M. Gray, 6 Aug 1963: 3 ♂♂, cl ca. 1.8 mm, 2.4 mm, and 2.5 mm (paratypes, USNM 260886).—31°33′36″N, 79°40′21″W, depth 213 ft (65 m), SRF sta 307, bucket dredge, leg. M. Gray, 6 Aug 1963: 1 damaged ♀, cl ca. 3.5 mm (paratype, USNM 260887).—31°33′30″N, 79°41′38″W, depth 175 ft (53 m), SRF sta 308, bucket dredge, leg. M. Gray, 6 August 1963: 1 ♂, cl 3.2 mm (tl ca. 12 mm) (paratype, USNM 260888).

Description.—Carapace with rostrum acute, sharp, extending approximately ¾ length of visible length of eyestalks; orbital or frontal projections absent. Dorsal oval and cervical groove distinctly defined; suture lines arising in mid-region of branchiostegites, joining dorsally in anterior region of posterior third of carapace; margins of branchiostegites and posterior margin of dorsal carapace fringed with setae, surface of branchiostegites sparsely setose.

Eyestalks (Fig. 1*a,b*) dorsoventrally flattened, extending nearly to distal margin of first segment of antennular peduncle, over 2 times longer than wide, proximal lateral margins broadly convex to level of cornea then tapering distally to blunt point; cornea relatively well developed, darkly pigmented.

Length of A1 peduncle segment 3 about 2 times that of segment 2. Flagella nearly equal in length; dorsal flagellum with 26–28 setose articles, greatest diameter subdistally between articles 17–19, 8 articles preceding terminal article bearing aesthetascs; ventral flagellum with 20–21 setose articles gradually decreasing in diameter distally.

A2 peduncle over-reaching A1 peduncle, extending distally to about article 5 of ventral antennular flagellum; flagellum with 95–98 articles, extending posteriorly past first abdominal somite.

Abdomen with first somite strongly con-

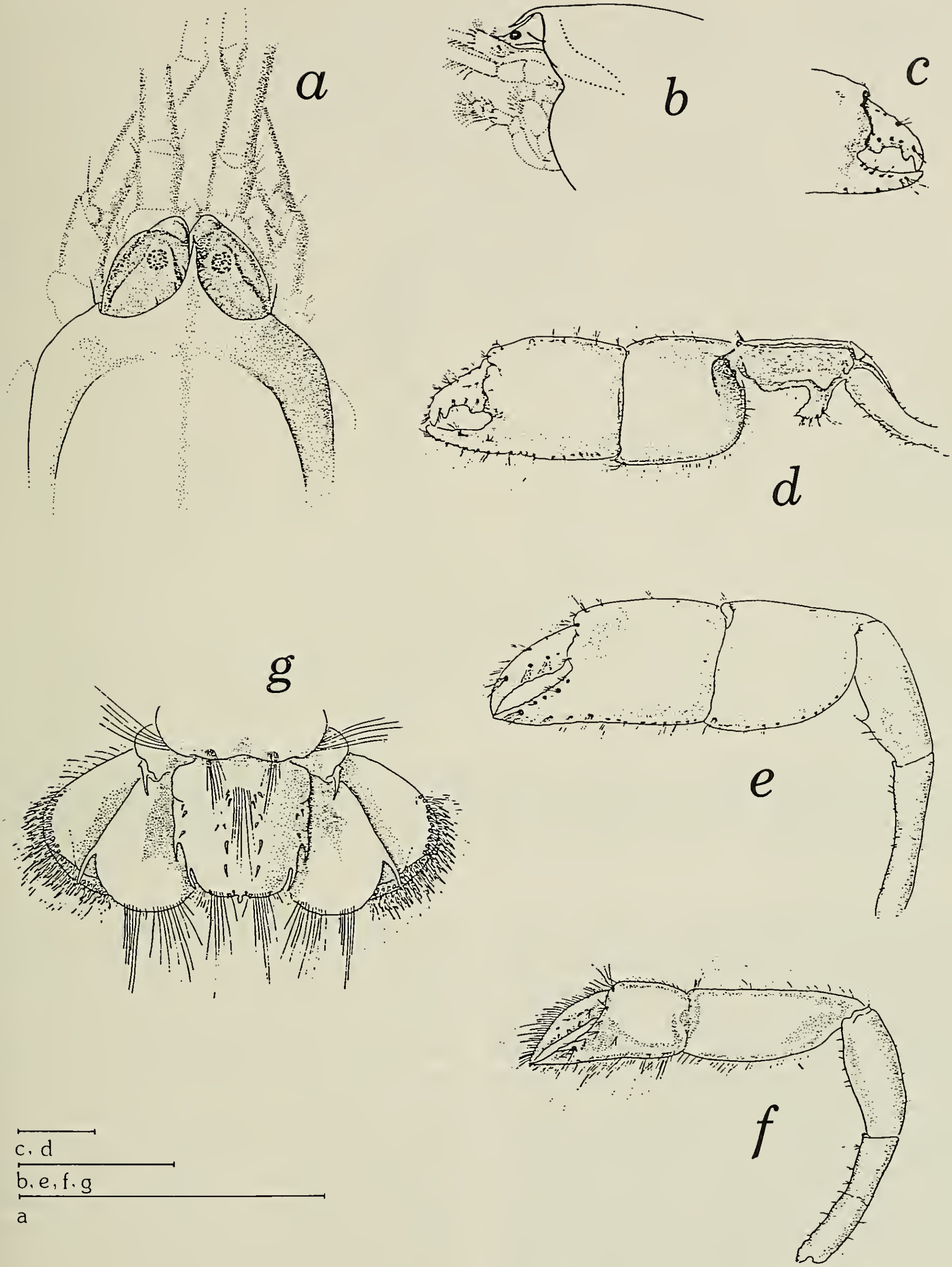

Fig. 1. *Necallianassa berylae*, n. gen., n. sp. *a*, Front, dorsal view; *b*, Front, lateral view; *c*, Fingers of major chela of male; *d*, Major cheliped of male; *e*, Minor P1 of male (same shape as major P1 of female); *f*, Minor P1 of female; *g*, Tailfan. *a–e*, *g*, male holotype (USNM 260881), cl 4.1 mm; *f*, female paratype (USNM 260884), cl ca. 3.5 mm. Scales = 2 mm.

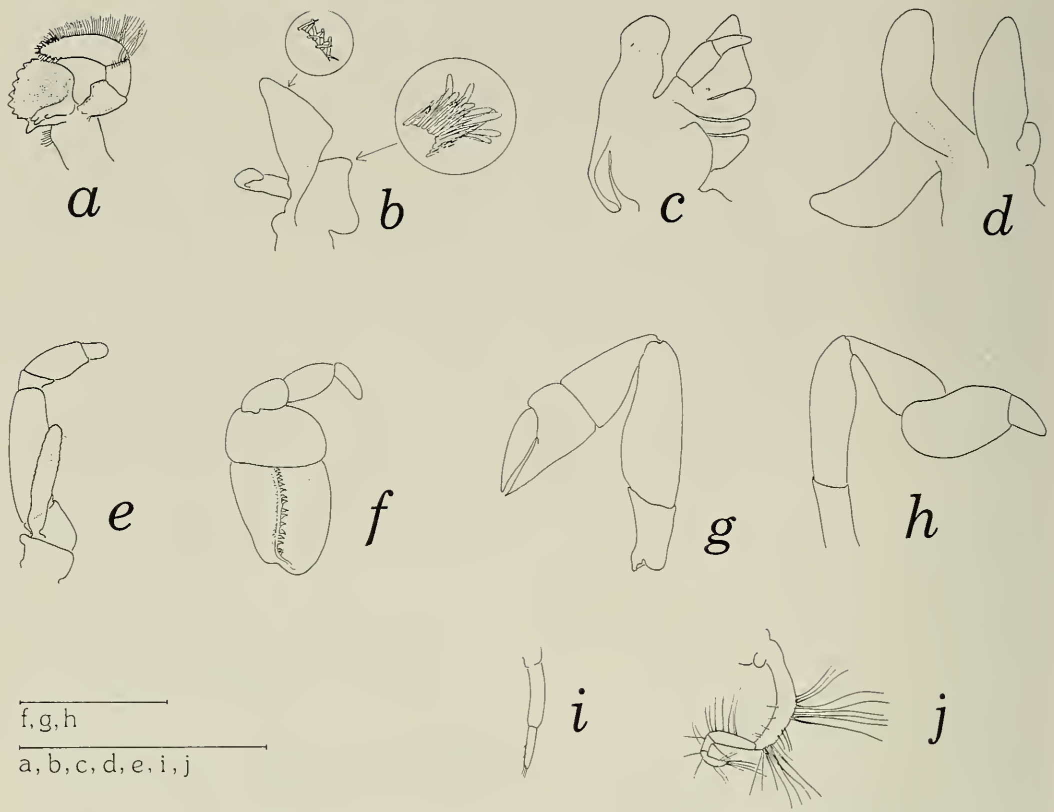

Fig. 2. *Necallianassa berylae*, n. gen., n. sp. *a*, Man; *b*, Max1 (inserts show specialized setae on margin); *c*, Max2; *d*, Mxp1; *e*, Mxp2; *f*, Mxp3; *g*, P2; *h*, P5; *i*, Male Plp1; *j*, Female plp1. *a–e*, *j*, female paratype (USNM 260884), cl ca. 3.5 mm; *f–h*, female paratype (USNM 260882), *i*, male holotype (USNM 260881), cl 4.1 mm. Scales = 1 mm.

stricted anteriorly (appearing subtriangular dorsally), pair of small setal tufts near posterodorsal margin. Second somite subquadrate, narrowest anteriorly, 1.3 times longer than first, circular patch of small setae near ventral margin of posterolateral border, a few setae along dorsal and ventral posterior margins. Third somite about as long as first, setation similar to that of second except circular patch of setae more centrally located on ventral margin. Fourth and fifth somites similar to third, but slightly shorter. Sixth somite broadest anteriorly, approximately same length as first, more setose than somites 1–5; small suture on posterior ⅓ of each lateral margin; mid-dorsal suture or groove opening on posterior margin, extending anterodorsally approximately ⅐ length of somite before closing to form indistinct, mid-dorsal line disappearing on anterior ¼ of somite.

Mouthparts (Fig. 2*a–f*) with Man, Max1, and Max2 as figured (Fig. 2*a–c*). Max1 with distinctive "golden", club-shaped setae on distolateral margin (Fig. 2*b*, enlargements).

Mxp1 (Fig. 2*d*) as figured. Mxp2 (Fig. 2*e*) with greatly reduced, vestigial, podobranch; endopod with article 2 distinctly longer than combined length of articles 3–5; exopod extending approximately ¾ length of endopodal article 2. Mxp3 (Fig. 2*f*) lacking exopod, endopod with ischium and merus stout, carpus, propodus, and dactylus relatively much narrower and attenuated; mesial surface of ischium with row of 14–

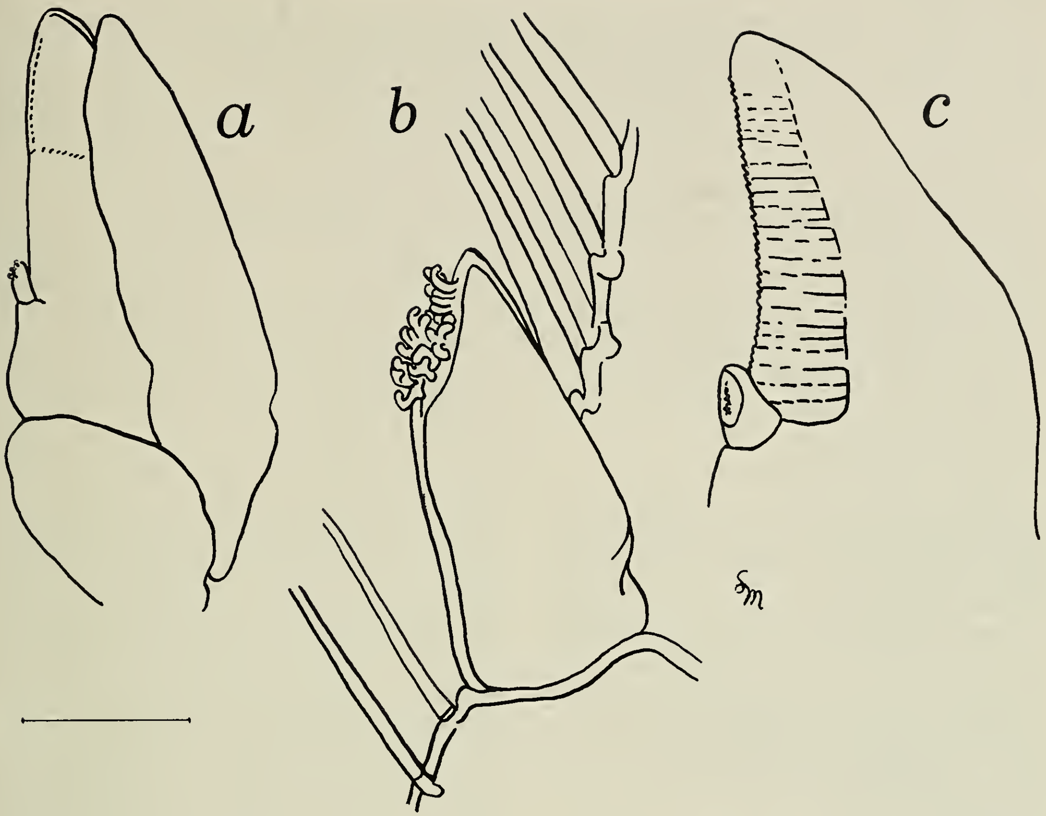

Fig. 3. *Necallianassa berylae*, n. gen, n. sp., *a*, Endopod of Plp3; *b*, Appendix interna, enlarged; *c*, Endopod of Plp3. *a*, *b*, male holotype of *N. berylae* (USNM 260881), cl 4.1 mm; *c*, *Necallianassa acanthura* (Caroli, 1946), new combination, holotype, National Natuurhistorisch Museum, Leiden. Scale = 0.5 mm (*a*, *c*), 0.05 mm (*b*).

16 small teeth along distoproximal axis; merus distinctly wider than long, approximately ⅔ length of ischium, as broad or broader than distal end of ischium; carpus, propodus, and dactylus, and dactylus less than combined length of ischium and merus.

Chelipeds (P1) distinctly unequal (Fig. 1*d*, *f*). Major cheliped with distinct gap between fixed and movable fingers; ischium relatively narrow with weakly crenulate ventral margin; merus bearing strongly developed hook-like process on proximal ventral margin, approximately twice as long as deep (excluding hook-like process); carpus subquadrate, nearly as deep as long, approximately as long as merus; propodus (excluding fixed finger) approximately ⅘ as deep as long, fixed finger lacking teeth; dactylus (movable finger) armed with distinct subdistal tooth and larger oblique proximal tooth, length slightly more than ½ length of propodal palm. Minor cheliped smaller and more weakly developed than major chela; merus unarmed, twice as long as deep; carpus attenuated, twice as long as deep; propodus with palm as long as deep, fixed finger lacking teeth, longer than palm; dactylus longer than palm of propodus, lacking teeth.

P2 as illustrated (Fig. 2*g*), chelae equal. Carpus ⅗ length of merus; fingers longer than palm.

P3 with merus longer than carpus; carpus ⅘ length of merus; propodus and carpus approximately equal in length.

Male Plp1 (Fig. 2*i*) composed of 2 articles; terminal article simple, straight, and distinctly shorter than proximal article. First pleopod of female (Fig. 2*j*) uniramous, 4-segmented.

Uropods (Fig. 1*g*) with spine-like process on distal margin of peduncle; exopod broad, rounded with indistinct suture, upper and lower plates poorly developed, distal margins densely setose with numerous small submarginal spines; endopod broadly rounded with prominent spine-like process on distolateral margin, two clusters of long setae on distal margin.

Telson (Fig. 1*g*) not extending beyond uropods; approximately as wide as long with 2 distinct pairs of posteriorly directed spine-like processes on lateral margins; spination and setation as figured.

Female similar to male except in development of the first pair of chelipeds and in that Plp1 is uniramous, Plp2 biramous. Major P1 in female resembling minor P1 of male, with meral hook. Minor P1 in female lacking meral hook.

Etymology.—Named in honor of Beryl Marie Story in recognition of her exceptional talents and many past contributions to the senior author's research.

Remarks.—*Necallianassa berylae* can be distinguished from its two eastern Atlantic congeners, *N. acanthura* and *N. truncata*, as follows: its size is much smaller, tl about 15 mm versus about 50 mm; the rostral projection, extending beyond the cornea, is much longer and sharper (compare Fig. 1*a* with Figs. 2 and 3 in de Saint Laurent & Bozic 1976); the ischium-merus of the Mxp3 is slenderer (compare Fig. 2*f* with Figs. 10 and 11 in de Saint Laurent & Bozic 1976); and there is a strong subdistal tooth on the dactylus of the major chela (compare Fig. 1*c*, *d* with Figs. 18*a* and 19 in de Saint Laurent and Bozic 1976). *Necallianassa truncata* resembles *N. berylae* in having two lateral spines on the telson, but they and the outer spine on the uropodal endopod are much smaller than the spines of the telson and uropod of *N. berylae*. *Necallianassa acanthura*, like *N. berylae*, has two large lateral spines on the telson and a large outer spine on the uropodal endopod.

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A new genus of ghost shrimp from Japan (Crustacea: Decapoda: Callianassidae)

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Abstract.—A new genus, *Nihonotrypaea,* is recognized for three species from Japan formerly assigned to *Callianassa* sensu lato: *N. japonica* (Ortmann, 1891), the type species; *N. harmandi* (Bouvier, 1901); and *N. petalura* (Stimpson, 1860).

One of us (A.T.) has carried out studies on the biology and development of the shallow water species, *Callianassa japonica* Ortmann, 1891, in an estuarine system on western Kyushu Island, Japan since 1989 (Tamaki et al. 1996, Tamaki et al. 1997). These studies revealed consistent differences in biology, development, habitat, and morphology in populations from different areas within the estuary, which extends from Ariake Sound through Tachibana Bay to the East China Sea (Tamaki et al. 1997: fig. 1). One of us (R.B.M.) examined samples from different localities within the study area and found that not only were there two species involved, but also that morphological characters warranted their separation into a new genus of Callianassinae. That two similar species occurred in Japan had been recognized by De Man (1928), who identified them as *C. japonica* and *C. harmandi* Bouvier, 1901, and clearly figured their diagnostic features; De Man's material all came from Bingo, Japan. De Man's findings generally have been ignored by subsequent students of the group. Sakai (1969) synonymized *C. harmandi* with *C. japonica* and recognized *C. petalura* Stimpson, 1860 as a distinct species.

As numerous studies on the biology of these species are in preparation by Tamaki and his colleagues and students, we decided to prepare this preliminary account to correct the specific names and make the generic name available. A more detailed account of the new genus and all three species assigned to it is in preparation by us.

Family Callianassidae Dana, 1854
Subfamily Callianassinae Dana, 1854
Nihonotrypaea, new genus

Diagnosis.—Carapace lacking rostral spine, minute median spinule present or absent. Cornea dorsal, subterminal, disc-shaped (Fig. 1*a*, *b*). Antennular and antennal peduncles similar. Third maxilliped (Fig. 1*c*, *d*) lacking exopod, ischium-merus suboperculiform, merus projecting beyond articulation with carpus; latter, propodus and dactylus slender. Chelipeds unequal, both with meral hook. First pleopod slender, uniramous in both sexes (Fig. 1*e*, *f*). Second pleopod absent in male, slender, biramous in female (Fig. 1*g*). Third to fifth pleopods with stubby, projecting appendices internae (Fig. 1*h*) in both sexes.

Type species.—*Callianassa japonica* Ortmann, 1891, by present designation.

Included species.—*Nihonotrypaea japonica* (Ortmann, 1891), new combination; *N. petalura* (Stimpson, 1860), new combination; and *N. harmandi* (Bouvier, 1901), new combination.

Etymology.—The generic name is formed by combining the Japanese name

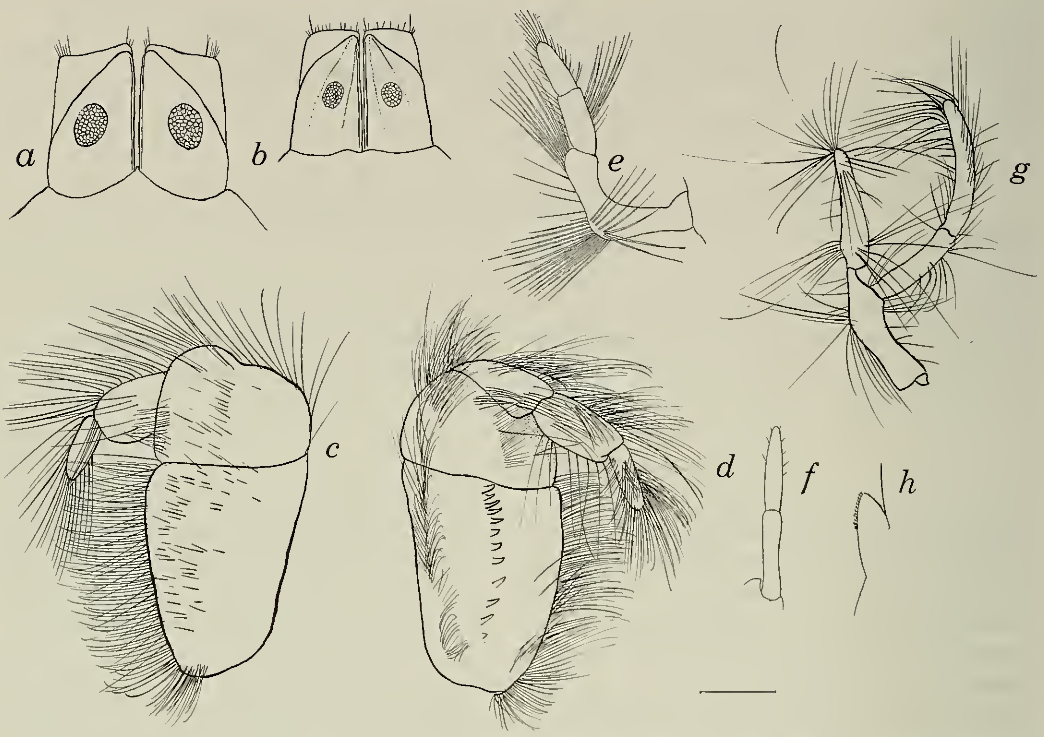

Fig. 1. *Nihonotrypaea harmandi* (Bouvier, 1901). *a*, Front and eyes; *c*, Third maxilliped, outer surface; *d*, Third maxilliped, inner surface; *e*, First pleopod of female; *f*, First pleopod of male; *g*, Second pleopod of female; *h*, Appendix interna of third pleopod of male (*a*, *e*, *f*, *h*, from De Man 1928: pl. 5, fig. 10, as *Callianassa* (*Trypaea*) *japonica*). *b*, *N. japonica* (Ortmann, 1891), from De Man 1928:pl. 3, fig. 6, as *Callianassa* (*Trypaea*) *harmandi*); *c*, *d*, *g*, female from Tomioka (National Museum of Natural History, Smithsonian Institution, Washington, D.C.). Scale = 1 mm, *c*, *d*; 0.5 mm, *g*.

for Japan, Nihon, with the generic name *Trypaea.* The gender is feminine.

Remarks.—With the addition of *Nihonotrypaea*, nine genera are now recognized in the callianassid subfamily Callianassinae. *Nihonotrypaea* can be distinguished from those with projecting appendices internae on pleopods 3–5 as follows: from *Biffarius* Manning & Felder, 1991 in that the size of adults is larger, the antennal and antennular peduncles are similar in size and shape, and the third maxilliped is much narrower; from *Calliapagurops* de Saint Laurent, 1973 by its subterminal corneas; from *Notiax* Manning & Felder, 1991 in lacking a strong median spine on the carapace and in having the merus of the third maxilliped projecting beyond its articulation with the carpus; from *Poti* Rodrigues & Manning, 1992, by the presence of a complete *linea thalassinica* on the carapace; from *Trypaea* Dana, 1852 in having a much smaller and shorter antennular peduncle.

In the three other genera in the subfamily (*Callianassa* Leach, 1814; *Gilvossius* Manning & Felder, 1992; and *Neotrypaea* Manning & Felder, 1991), the appendices internae of pleopods 3–5 are embedded in the margin of the endopod. That feature alone distinguishes members of these three genera from *Nihonotrypaea*, in which the appendices internae are projecting from the margin of the endopod.

One of the three species assigned to *Nihonotrypaea*, *N. petalura*, lives among boulders in the intertidal zone of ocean-front beaches. The two other species, *N. japonica* and *N. harmandi*, live on protected flats in estuaries. The range of *N. petalura* is identical to that of *N. harmandi*.

Although De Man (1928) was correct in recognizing *C. japonica* and *C. harmandi* as distinct species, he assigned the wrong name to each of them, for he did not have access to their types and the original accounts were quite short. The two species can be distinguished by the size of their cornea alone, as shown by De Man (1928). In *N. harmandi* (Fig. 1*a*) the cornea is relatively large, at least half the width of the stalk, whereas in *N. japonica* (Fig. 1*b*) the cornea is much smaller, one-third to one-fifth the width of the stalk. In *N. harmandi*, the front often is ornamented with a minute spinule, which is lacking in *N. japonica*.

All members of the genus are relatively small, total lengths up to about 65 mm.

The two species also differ in aspects of biology, habitat, and their parasites (Manning & Tamaki, in preparation).

The original citations of the two species are:

Callianassa subterranea var. *japonica* Ortmann, 1891:56, pl. 1, fig. 10a [=*Callianassa* (*Trypaea*) *harmandi* sensu De Man, 1928:13, pl. 3, fig. 6].

Callianassa Harmandi Bouvier, 1901:333 [=*Callianassa* (*Trypaea*) *japonica* sensu De Man, 1928:13, pl. 5, fig. 10].

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Lamoha hystrix, a new species of deep-water porter crab (Crustacea: Decapoda: Brachyura: Homolidae) from the central Pacific

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Abstract.—A new species of deep-water porter crab, *Lamoha hystrix* (Homolidae), is described from Canton Island (Phoenix Island group) in the central Pacific. *Lamoha hystrix* appears to be most closely allied to *L. longipes* (Alcock & Anderson, 1899), *L. murotoensis* (Sakai, 1979) and *L. inflata* (Guinot & Richer de Forges, 1981) from the Indian Ocean, Japanese and central Pacific waters respectively, but can easily be distinguished from them by its proportionately longer ambulatory legs and the presence of spines on the dorsal margin of the merus of the fifth ambulatory leg.

Recently, a series of homolid specimens collected from various parts of the Pacific and deposited in the Bernice P. Bishop Museum (BPBM), Honolulu, were examined. Among this material was an interesting specimen of the genus *Lamoha* Ng, 1998, from Canton Island, Phoenix Island group, which could not be referred to any known species. The genus is a replacement name proposed by Ng (1998) for *Hypsophrys* Wood-Mason & Alcock, 1891, who showed that the latter name was preoccupied by *Hypsophrys* Agassiz, 1859, a genus of freshwater fish. In the family revision by Guinot & Richer de Forges (1995), eight species of *Lamoha* (as *Hypsophrys*) were recognized from the Indo-Pacific and Atlantic Oceans.

Lamoha hystrix, new species, is here described. The terminology used follows Guinot & Richer de Forges (1995). The abbreviations P1–5 refer to the pereiopods (P1, cheliped, and P2–5, first to fourth ambulatory legs); M, Pr, and D are for merus, propodus, and dactylus respectively.

Taxonomic Account

Genus *Lamoha* Ng, 1998

Hypsophrys Wood-Mason & Alcock, 1891: 269 (preoccupied by *Hypsophrys* Agassiz, 1859:408) (see Ng 1998 for a discussion on the correct authorship for *Hypsophrys* Wood-Mason & Alcock, 1891).

Lamoha Ng, 1988:121.

Type species.—*Hypsophrys superciliosa* Wood-Mason & Alcock, 1891, by original designation.

Lamoha hystrix, new species
Figs. 1–3

Material examined.—Holotype, ovigerous female, carapace width 38.7 mm, carapace length (tip of rostrum to posterior carapace margin) 48.9 mm, BPBM 511810, Canton (Kanton) Island, ca. 2°50′S 171°40′W, Phoenix Island Group, east of Kiribati, southwest of Hawaii, ca. 305–366, coll. T. Morin, Jun 1979.

Diagnosis.—Carapace longitudinally rect-

Fig. 1. *Lamoha hystrix*, new species. Holotype female, carapace width 38.7 mm, carapace length 48.9 mm, BPBM 511810. A, overall dorsal view; B, frontal view, C, left cheliped.

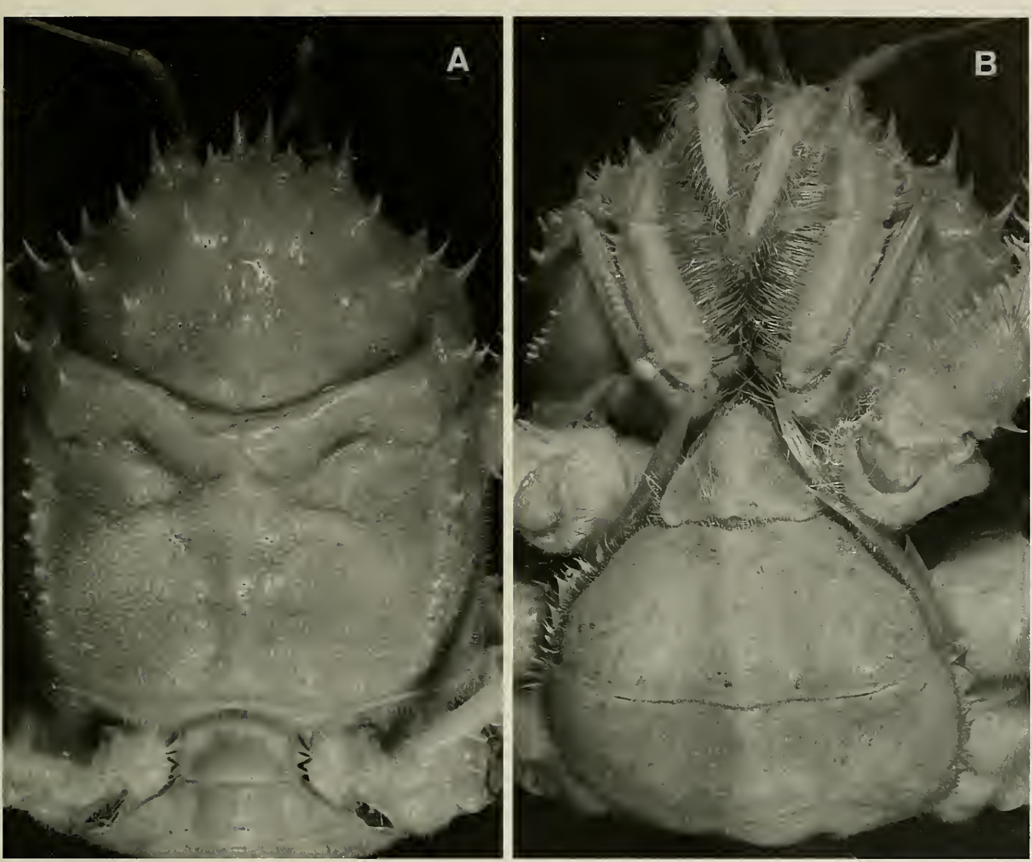

Fig. 2. *Lamoha hystrix*, new species. Holotype female, carapace width 38.7 mm, carapace length 48.9 mm, BPBM 511810. A, carapace, dorsal view; B, abdomen.

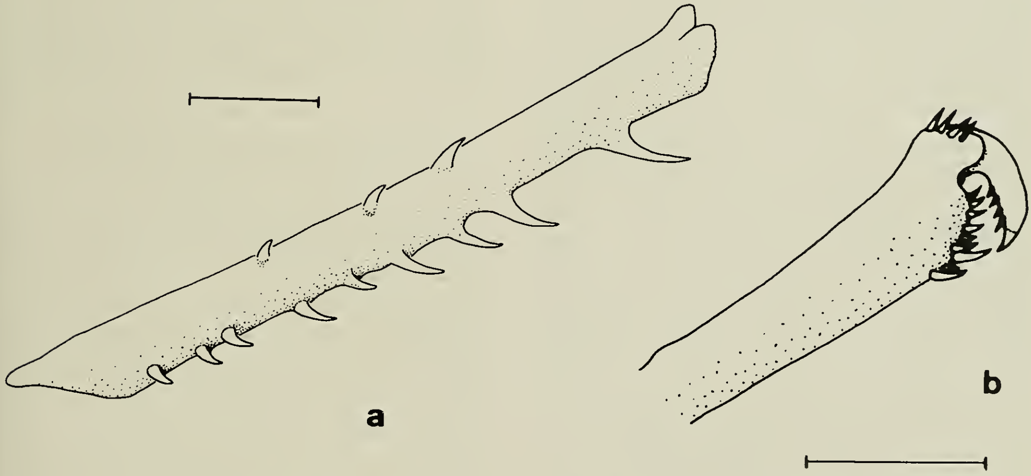

Fig. 3. *Lamoha hystrix*, new species. Holotype female, carapace width 38.7 mm, carapace length 48.9 mm, BPBM 511810. a, right merus of fifth ambulatory leg; b, subchelate structure on right fifth ambulatory leg. Scales = 5.0 mm.

angular (length to width ratio 1.26); rostrum bifurcated, with relatively elongate base; posterolateral margin with row of granules; protogastric region with 4 spines; mesogastric region with 1 spine; metagastric region granulated; subhepatic region with 2 lateral spines and 5 other spines on surface; P2–4 elongate, M2–4 relatively wide, with 14–18, 19–20, 18 dorsal spines respectively; P5 with 3 dorsal spines and 8–9 ventral spines; Pr4 with 6–7 spines; subchelate margin of propodus of P5 with 9–10 spines.

Description of holotype female.—Carapace longitudinally rectangular, regions well defined (Figs. 1A, 2A). Entire carapace and pereiopod surfaces with short, stiff, simple setae. Rostrum well developed, base relatively elongate, distal part bifurcated with 2 sharp spines. Pseudorostral spines as long as rostral spines, sharp. Supraorbital spines very long (Figs. 1A, 2A). Anterolateral margin with 2 lateral and 2 subdorsal spines. Posterolateral margin gently convex, lined with a row of small sharp and rounded granules along "linea homolica" (Fig. 2A). Protogastric region with 3 large and 1 small (inner posterior) spines. Mesogastric region with 1 short, sharp spine. Metagastric region granulated but without spines. Branchial regions covered with fine granules. Subhepatic region with 2 lateral spines, 1 small submarginal spine, 1 subdorsal spine and 3 subventral spines (Figs. 1B, 2A). Posterior part of pterygostomial region covered with granules and spinules. Gastro-cervical groove deep, contiguous medially. Branchio-cardiac groove deep (Fig. 2A). Basal antennal article with 1 inner spine. Antennular peduncle with 1 sharp spine. Posterior carapace margin sinuous, median part concave. Main proepistomal spine long, sharp; lateral spines distinctly shorter (Fig. 1B). Merus of third maxilliped with group of 2–3 spines medially, rest of margin with scattered spines and spinules; ischium with outer margin anterior ⅓ of outer margin spinate, with distinct granulated longitudinal median ridge; exopod slender, reaching to mid-point of outer margin of merus, proximal half with granule-lined longitudinal median ridge.

P1 (chelipeds) subequal, elongate, slender (Fig. 1A). Carpus with 3–4 sharp, curved spines on inner distal margin; outer surfaces of chelae with several rows of spinules, spines and granules, those along outer surface flatter or blunter, without any trace of pigmented spot (Fig. 1C). Fingers elongate, distal part curving inwards, dactylus with strong longitudinal ridge and sulcus, distal one-third of dactylus and cutting margins pigmented dark brown in preservative, cutting edges smooth, blade-like (Fig. 1C). P2 and 3 longest (Fig. 1A). Rest of armature on pereiopods as follows: M5 with 3 dorsal and single row of 8–9 ventral spines (Fig. 3a); M4 with 18 dorsal and 2 rows of ventral spines (posterior row with 17–18 spines, anterior row with 21 spines); M3 with 19–20 dorsal spines and 2 rows of ventral spines (posterior row with 19–23 spines, anterior row with 28 spines); M2 with 14–18 dorsal spines and 2 rows of ventral spines (posterior row with 16–21 spines, anterior row with 19–26 spines); M1 with 14 dorsal spines (with 1 distally positioned) and 2 rows of ventral spines (posterior row with 12–13 spines, anterior row with 15–17 spines); Pr4 with 6–7 spines of which 2 are distally positioned, movable and bracketing base of dactylus; D3 and D4 with 19 spines on ventral margin; D2 with 16–18 spines on ventral margin. Dorsal armature of all pereiopods with median spines largest; spines on ventral armature of pereiopods progressively larger towards distal end, with numerous granules of varying sizes at proximal surface which makes counting of exact number of spines difficult; rows of spines on ventral margins not linear but uneven, especially along proximal part; all spines curving outwards. Dactylus and distal part of propodus of P5 forming subchelate structure; anterior tip of propodus with 4–5 movable spines; subchelate margin of propodus with 9–10 spines; ventral margin of dactylus with 4 movable spines (Fig. 3b). Basis-ischium of

P1 with 1 sharp dorsal spine and several smaller spines and granules; those of P2–4 with 2 dorsal spines bracketing merus; that of P5 with 1 median dorsal spine. Coxa of P1 with 1 sharp on inner dorsal angle and 1 large granule on outer dorsal angle; those of P2–4 with 2 sharp spines on dorsal margin bracketing basis-ischium; that on P5 without spines or spinules.

Abdomen covering entire thoracic sternum; telson triangular, with distal part of lateral margins concave (Fig. 2B).

Remarks.—Lamoha hystrix, new species, appears to be closest to *L. longipes* (Alcock & Anderson, 1899) (Indian Ocean), *L. murotoensis* (Sakai, 1979) (Japan, Taiwan, and Madagascar and Seychelles with doubt) and *L. inflata* (Guinot & Richer de Forges, 1981) (Loyalty Islands, Samoa and Tuamotu). This group of species is essentially defined by the form of the frontal and supraorbital margins, the proepistome possessing a distinct vertical spine and the propodus of Pr5 being very short with the propodal finger of the subchelate process very low (Guinot & Richer de Forges, 1995: 444). In addition, all four species have similar fourth ambulatory meri which are armed with spines along the ventral margin. None of these species, however, have the dorsal margin of the merus armed with spines as in *L. hystrix*. The spines on the dorsal margin of the fourth leg in *L. hystrix* are relatively small but very distinct (Fig. 3a).

The carapace features of *L. hystrix* appear to be closest to *L. longipes* with regards to the posterolateral margin lined with small granules. In addition to the earlier mentioned presence of spines on the dorsal margin of the fourth ambulatory leg, *L. hystrix*, can easily be separated from *L. longipes* by the its proportionately longer ambulatory meri (M4 length to maximum width ratio 8.1 in *L. hystrix*, 7.5–7.6 in *L. longipes*), larger number of spines on the ambulatory meri (e.g., M4 with 18 in *L. hystrix*, 13–14 dorsal spines in *L. longipes*), presence of spines on the ventral margin of Pr4 (absent in *L. longipes*) (cf. Alcock 1901: pl. 6 fig. 25), and the larger number of teeth on the subchelate margin of the propodus of P5 (9–10 spines in *L. hystrix*, 6 in *L. longipes*) (cf. Williams 1974:489, fig. 8). The outer surface of the female chela also lacks a dark spot.

A note on *L. longipes* is relevant here. The carapace proportions for the various reported specimens of *L. longipes* seem different, although this may be a result of difference in sizes. The specimen (apparently a male 39.4 by 30.6 mm, carapace length to width) figured by Alcock (1901: pl. 6 fig. 25) has a carapace length to width ratio of 1.29. Alcock (1901:69) also mentions a large ovigerous female measuring 38.0 by 30.0 mm (ratio 1.27). The female specimen of *L. longipes* from the Seychelles examined and figured by Guinot & Richer de Forges (1995:447, fig. 56a, b), however, measures 33.2 by 29.0 mm, and has a length to width ratio of 1.14, that is, the carapace is more squarish. The spines on the protogastric and mesogastric regions of this specimen also appear to be lower and more scattered, with the rostral base very short, compared to the material described and illustrated by Alcock & Anderson (1899:6), Alcock (1899:15, pl. 1 fig. 1; 1901:69, pl. 6 fig. 25) and Doflein (1904: pl. 11 fig. 1, 2; pl. 50 fig. 4; pl. 51 fig. 1; pl. 52 figs. 1–5). Whether this material is really *L. longipes* cannot be ascertained as only one specimen from the Seychelles was obtained. In any case, Guinot & Richer de Forges (1995:447) had referred the specimen to the species with reservations. The carapace proportions of *L. hystrix*, new species (length to width ratio 1.26) are comparable with those of *L. longipes* sensu stricto.

The positions and strengths of the spines on the gastric region of *L. hystrix*, new species, are very similar to that on *L. murotoensis*, but *L. murotoensis* is easily separated by the strong longitudinal ridge on its posterolateral margin. *Lamoha inflata* is a very distinctive species with the gastric carapace regions unarmed.

In addition to *L. murotoensis* and *L. inflata*, three other species are known from the Pacific, i.e., *L. williamsi* (Takeda, 1980) (Kyushu-Palau Ridge), *L. personata* (Guinot & Richer de Forges, 1981) (Polynesia, Vanuatu, Samoa, Kiribati, Australia), and *L. futuna* (Guinot & Richer de Forges, 1995) (Wallis and Futuna Islands) (Guinot & Richer de Forges 1995). These species, however, differ markedly from *L. hystrix* in a multitude of pereiopod and carapace features (Guinot & Richer de Forges 1995).

According to the collection data on the specimen of *Lamoha hystrix*, new species, it was caught in a trap baited with mullet set in the afternoon and left for 24 hours between 305 to 366 metres. The colour in life was recorded as "rose-pink". The ecology and habits of the species is not known, but is probably similar to that of other Pacific *Lamoha* species (Guinot et al. 1995).

Etymology.—The species is named after the porcupine (*Hystrix*) because of its spiny carapace and legs. The name is used as a noun in apposition.

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A new freshwater crab of the genus *Neostrengeria* Pretzmann, 1965, from Colombia (Crustacea: Decapoda: Brachyura: Pseudothelphusidae), with a key to the species of the genus

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Abstract.—A new species of freshwater crab of the pseudothelphusid genus *Neostrengeria* Pretzmann, 1965, *N. perijaensis*, is described and illustrated. This discovery means the genus now contains a total of 17 species and 2 subspecies, all endemic to the Eastern Andes of Colombia. The general characteristics of the genus are given, and a key for the identification of the species based primarily on the morphology of the male first gonopod, is presented.

The genus *Neostrengeria* Pretzmann, 1965, of the family Pseudothelphusidae, comprises a group of freshwater crabs that live in mountain springs and streams on the slopes and high plains of the Eastern Andes of Colombia (about 3° to 9°40′N, 73° to 74°50′W), at altitudes ranging from 400 to 3000 m above sea level. The systematics of this genus were clarified by Rodríguez (1982), and more recently were reviewed by Campos (1992, 1994). The geographical distribution of the genus was discussed by Campos & Rodríguez (1985) and Campos (1992, 1994). The new species described herein, *N. perijaensis*, was collected from humid habitats south of the Serranía of Perijá, at altitudes ranging between 1200 and 1800 m above sea level. With this discovery, the genus now contains 17 species and two subspecies.

The general carapace morphology of most species of *Neostrengeria* is very similar. They are distinguished primarily by the relative length of the exognath of the third maxilliped, which is 0.5 to 0.7 times as long as the ischium; the orifice of the efferent branchial channel, which is open; and by the male first gonopod which has a distinct lateral lobe usually divided in two halves, forming an accessory lobe. The shape of the apex of the first gonopod varies according to species, and is either oval, oblong, or expanded. A key to the species and subspecies of the genus is presented, based almost exclusively on the morphology of the first gonopod. The terminology used for the morphology of the first gonopod follows Smalley (1964) and Rodríguez (1982).

The material is deposited in Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santa Fé de Bogotá (ICN-MHN); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Instituto Venezolano de Investigaciones Científicas (IVIC). The abbreviations cb and cl indicate carapace breadth and length, respectively. Color nomenclature used follows Smithe (1975). Coordinates of collecting sites were taken using a Geographical Positioning System (GPS).

Family Pseudothelphusidae Rathbun, 1893
Tribe Strengerianini Rodríguez, 1982
Genus *Neostrengeria* Pretzmann, 1965
Neostrengeria perijaensis, new species
Figs. 1, 2

Holotype.—Quebrada El Zumbador, Vereda El Zumbador, Corregimiento La Vic-

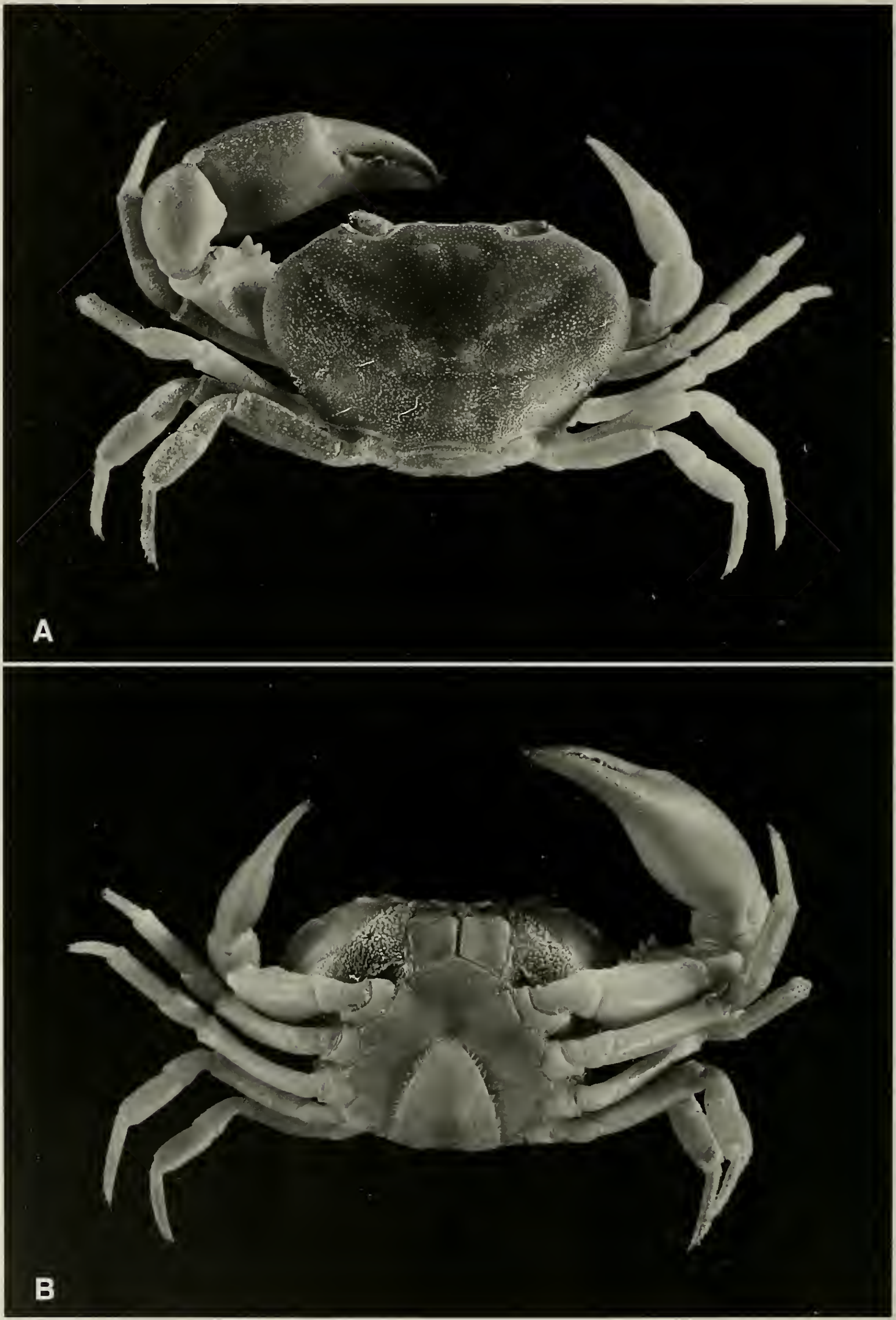

Fig. 1. *Neostrengeria perijaensis*, new species, male paratype, cb 17.5 mm, cl 11.0 mm (USNM 276145). A, dorsal view; B, ventral view.

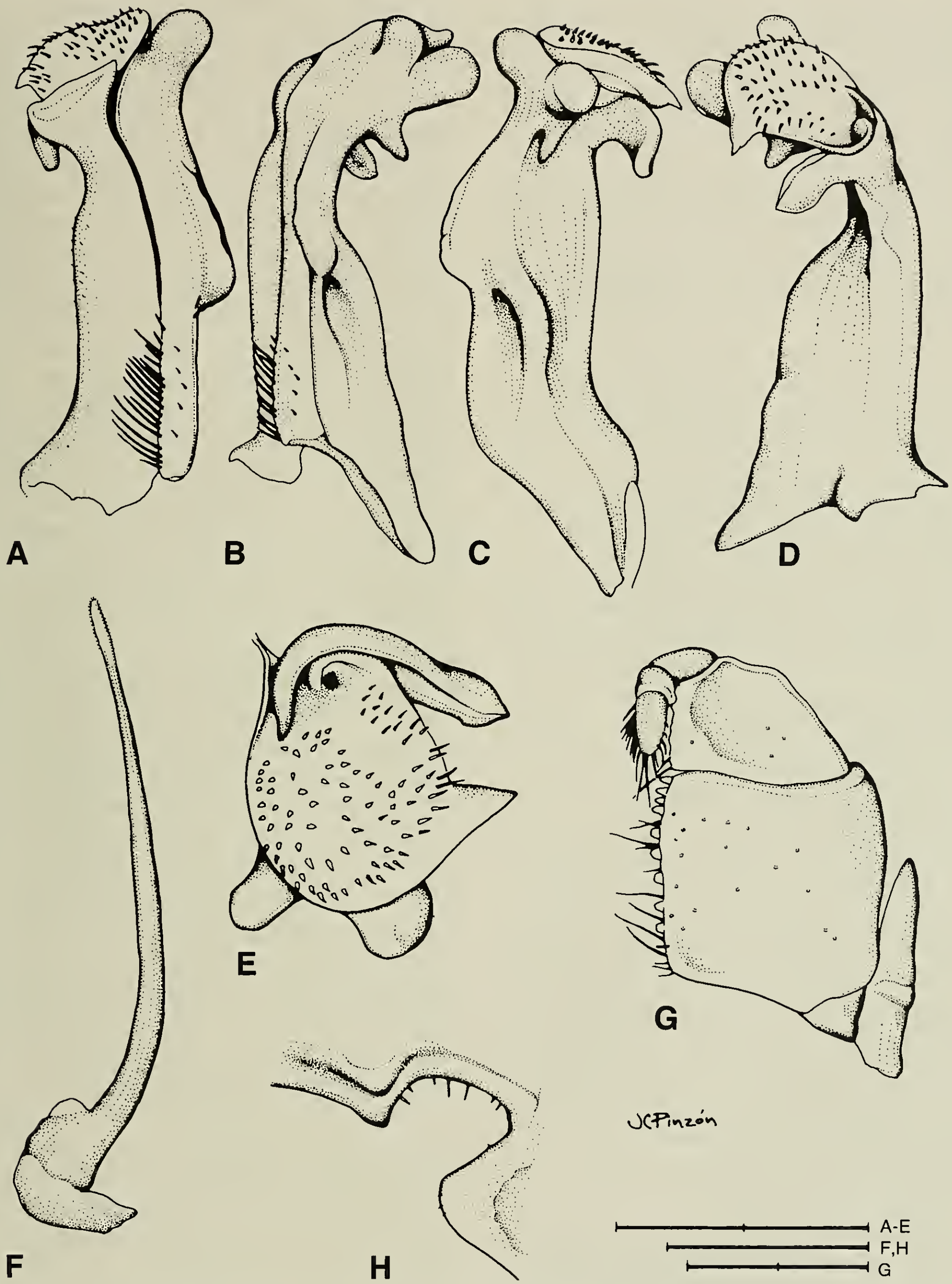

Fig. 2. *Neostrengeria perijaensis*, new species, male holotype, cb 22.0 mm, cl 13.5 mm (ICN-MHN-CR 1561). A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, left second gonopod, caudal view; G, left third maxilliped, external view; H, opening of left efferent branchial channel, external view. Scales equal 2 mm (A–E, G), and 1 mm (F, H).

toria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 9°33′10.8″N, 73°9′10.7″W, 1300 m alt., 13 Mar 1996, leg. M. R. Campos: 1 ♂, cb 22.0 mm, cl 13.5 mm, (ICN-MHN-CR 1561).

Paratypes.—Same locality data as holotype: 1 ♂, cb 17.5 mm, cl 11.0 mm, (USNM 276145), 1 ♂, cb 15.0 mm, cl 9.3 mm, 4 ♀, cb range 20.7–11.6 mm, cl range 12.9–10.0 mm (ICN-MHN-CR 1562).

Non-paratypes.—Quebrada El Zumbador, Vereda El Zumbador, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 9°33′14.2″N, 73°9′17.8″W, 1270 m alt., 15 Mar 1996, leg. M. R. Campos: 2 ♂, cb 16.5, 11.5 mm, cl 10.4, 7.2 mm, 5 ♀, cb range 19.5–14.4 mm, cl range 12.0–8.8 mm (ICN-MHN-CR 1565).—Alto de Cantarrana, Vereda El Zumbador, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 9°32′49.8″N, 73°8′46.9″W, 1800 m alt., 18 Mar 1996, leg. M. R. Campos: 1 ♂, cb 17.1 mm, cl 10.6 mm (IVIC), 11 ♂, cb range 18.4–11.1 mm, cl range 11.2–7.4 mm, 10 ♀, cb range 23.2–13.0 mm, cl range 13.8–8.5 mm (ICN-MHN-CR 1568).—Finca Peralonso, Vereda El Zumbador, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 9°32′37.8″N, 73°9′42.5″W, 1320 m alt., 19 Mar 1996, leg. M. R. Campos: 6 ♂, cb range 20.1–12.8 mm, cl range 12.2–8.1 mm, 11 ♀, cb range 21.2–13.7 mm, cl range 13.3–8.4 mm (ICN-MHN-CR 1569).

Type locality.—Quebrada El Zumbador, Vereda El Zumbador, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 9°33′10.8″N, 73°9′10.7″W, 1300 m alt.

Diagnosis.—First male gonopod straight, wide in caudal view; apex expanded cephalically into acuminate projection forming strong, wide-based spine; mesial lobe developed into distinct elongate projection.

Description of holotype.—Carapace (Fig. 1A) with cervical groove straight, shallow, ending some distance from lateral margin. Anterolateral margin with shallow depression behind external orbital angle, followed by series of papillae on anterior half; posterior half smooth. Postfrontal lobes small, rounded, delimited anteriorly by 2 depressions; median groove shallow. Surface of carapace in front of postfrontal lobes inclined anteriorly, depressed towards midline. Front rounded, lacking distinct upper border in frontal view, slightly bilobed in dorsal view; lower margin strongly sinuous in frontal view. Orbital margins each with row of small tubercles. Dorsal surface of carapace smooth, covered by small papillae; regions distinctly marked. Third maxilliped with merus having sharp angle on distal half of external margin; exognath approximately 0.58 times length of ischium (Fig. 2G). Orifice of efferent branchial channel irregularly ovate (Fig. 2H).

First pereiopods heterochelous; left cheliped larger than the right. Merus with 3 longitudinal crests as follows: upper one with rows of tubercles, internal lower one with rows of teeth, and external lower one with few tubercles. Carpus with 5 tubercles on internal crest and prominent blunt spine distally. Palms of both chelipeds smooth, swollen. Fingers of chelae not gaping when closed, tips crossing; outer and inner surfaces with rows of small tubercles.

Walking legs (pereiopods 2–5) slender (Fig. 1A). Dactyli elongated, each about 1.6 times as long as propodi, with papillae and 5 longitudinal rows of large spines diminishing in size proximally. Spines and papillae on each dactylus arranged as follows: 1 anterolateral row and 1 anteroventral row each with 5 spines and 2 intercalated papillae; 1 external row with 4 spines, 3 intercalated papillae and 1 pair of proximal papillae; and 1 posteroventral row and 1 posterolateral row each with 4 spines.

First gonopod (Fig. 2A–E) straight, wide;

mesial border straight on subdistal portion; with wide, deep notch in caudal view. Accessory lobe rounded distally, slightly shorter than lateral lobe and directed caudally; lateral lobe wide, distal end rounded, directed cephalically, with prominent spine-like process on external margin (Fig. 2A–C). Apex in distal view (Fig. 2E) expanded cephalically into acuminate projection forming strong, wide-based spine; surface covered by dark colored spines; mesial lobe developed into distinct elongated projection, surface rough; mesocaudal projection of spermatic channel terminating acutely, perpendicular to apical expansion (Fig. 2D, E). Second gonopod (Fig. 2F) with spinules distally; tip cup-shaped.

Color.—The alcohol preserved holotype is dark brown (near 223, Raw Umber), with pale brown (Verona Brown, 223 B) specks on the dorsal side of the carapace. The walking legs are brown (Mars Brown, 223 A) dorsally, and buffy-brown (Sayal Brown, 223C) ventrally. The large chela is pale brown (Verona Brown, 223C) dorsally, and buffy-brown (Sayal Brown, 223C) ventrally. The small chela is reddish-brown (Tawny, 38). The ventral surface of the carapace is buffy-brown (Sayal Brown, 223C).

Habitat.—The specimens were collected in shaded, moist banks of springs and small streams. They were found in soft mud, under rocks, or in burrows. The largest populations were found in one location at Alto de Cantarrana, Vereda El Zumbador, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Cesar Department.

Etymology.—The specific name refers to the Serranía de Perijá, where all the specimens were collected.

Remarks.—This species is most similar to *Neostrengeria lobulata* Campos, 1992. The two can be differentiated by features of the first gonopod. The first gonopod (in caudal view) of *N. lobulata* is narrow and constricted near its midsection, while the first gonopod of *N. perijaensis* is wide and straight (cf. Campos 1992). The mesial lobe of the first gonopod of *N. perijaensis* is developed into a distinct elongate projection, while this lobe is rudimentary, represented by only a subterminal swelling in *N. lobulata.* The apex of the first gonopod of *N. lobulata* is formed by a wide, irregularly shaped expansion with curved borders that is projected cephalically into an acute lobe, while in *N. perijaensis* the apex consists of an acuminate projection ending in a strong, broad-based spine.

Key to the species of the genus *Neostrengeria* based primarily on the male first gonopod

1. Laterodistal expansion of first gonopod curved, forming wide lobe (Fig. 3A) . . . . *N. botti* Rodríguez & Türkay, 1978
– Laterodistal expansion of first gonopod not curved, lacking lobe 2
2. Mesial lobe of first gonopod triangular 3
– Mesial lobe of first gonopod semicircular (Fig. 3B) . . . . *N. guenteri* Pretzmann, 1965
3. First gonopod with lateral and accessory lobes distinctly separated 4
– First gonopod with lateral and accessory lobes not separated from gonopod 12
4. Apex of first gonopod with outer surface smooth 5
– Apex of first gonopod with outer surface spinulose 17
5. Accessory lobe of first gonopod subequal in length to lateral lobe 6
– Accessory lobe of first gonopod distinctly shorter than lateral lobe 7
6. Accessory lobe of first gonopod unarmed (Fig. 3C) *N. gilberti* Campos, 1992
– Accessory lobe of first gonopod armed with spines (Fig. 3D, E) . . . . *N. aspera* Campos, 1992
7. Margins of accessory lobe of first gonopod smooth in caudal view 8
– Margins of accessory lobe of first gonopod festooned in caudal view (Fig. 3F) . . . . . . *N. monterrodendoensis* Bott, 1967
8. Longitudinal rows of spines on dactyli of walking legs each with 3 to 5 spines 9
– Longitudinal rows of spines on dactyli of walking legs each with 6 to 10 spines 10

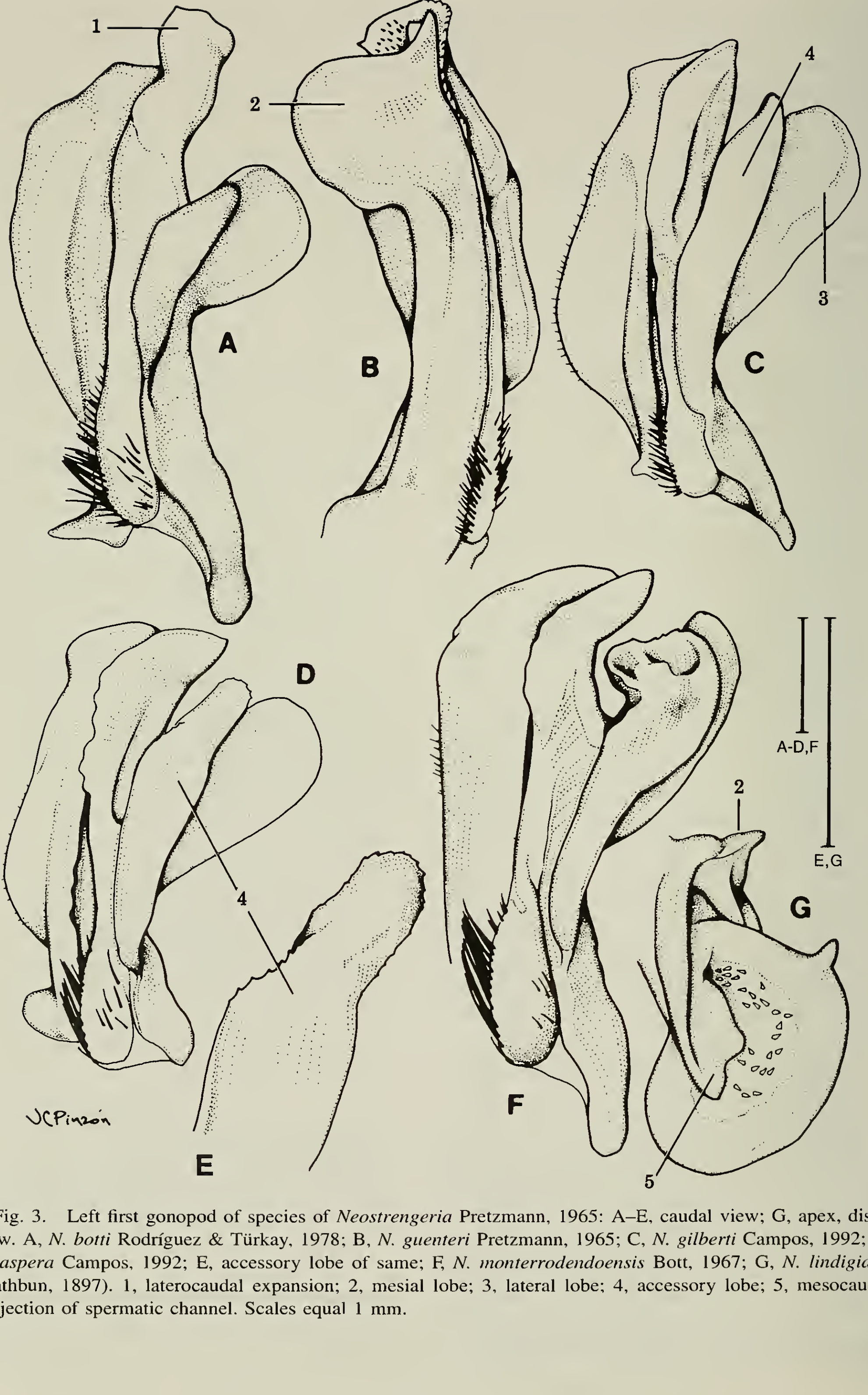

Fig. 3. Left first gonopod of species of *Neostrengeria* Pretzmann, 1965: A–E, caudal view; G, apex, distal view. A, *N. botti* Rodríguez & Türkay, 1978; B, *N. guenteri* Pretzmann, 1965; C, *N. gilberti* Campos, 1992; D, *N. aspera* Campos, 1992; E, accessory lobe of same; F, *N. monterrodendoensis* Bott, 1967; G, *N. lindigiana* (Rathbun, 1897). 1, laterocaudal expansion; 2, mesial lobe; 3, lateral lobe; 4, accessory lobe; 5, mesocaudal projection of spermatic channel. Scales equal 1 mm.

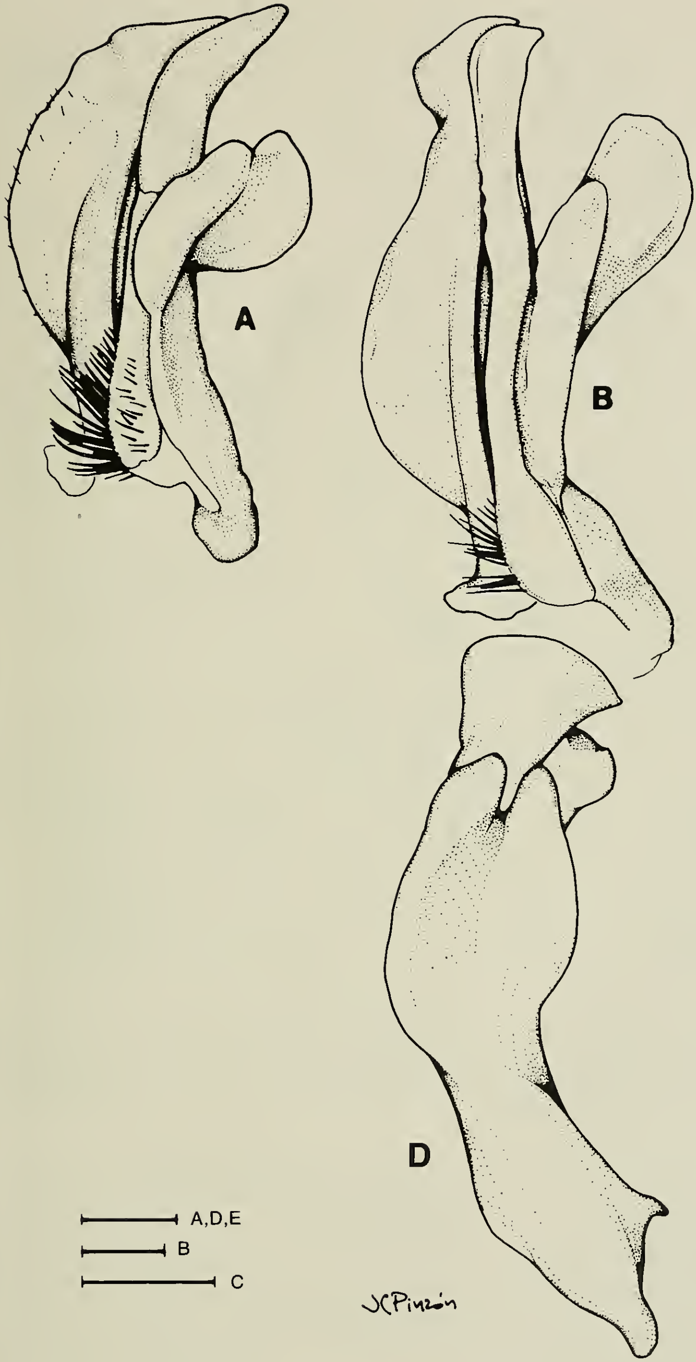

Fig. 4. Left first gonopod of species of *Neostrengeria* Pretzmann, 1965, caudal view. A, *N. charalensis* Campos & Rodríguez, 1985; B, *N. macarenae* Campos, 1992; C, *N. lobulata* Campos, 1992; D, *N. libradensis libradensis* Rodríguez, 1980; E, *N. l. appressa* Campos, 1992. Scales equal 1 mm.

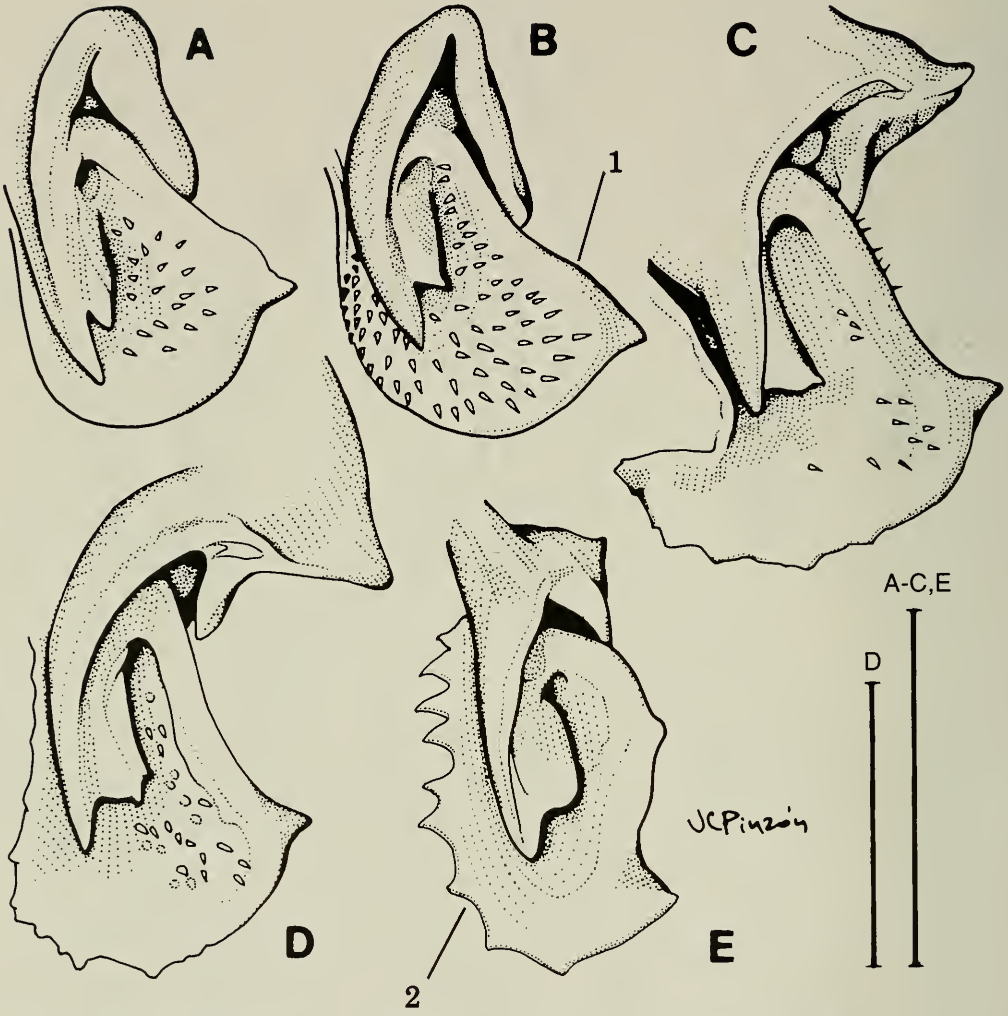

Fig. 5. Apices of left first gonopod of species of *Neostrengeria* Pretzmann, 1965, distal view. A, *N. tonensis* Campos, 1992; B, *N. tencalanensis* Campos, 1992; C, *N. boyacensis* Rodríguez, 1980; D, *N. lasallei* Rodríguez, 1980; E, *N. niceforoi* (Schmitt, 1969). 1, cephalic margin; 2, laterocaudal margin. Scales equal 1 mm.

9. Apex of first gonopod oval in distal view 11
– Apex of first gonopod semicircular in distal view, expanded cephalically (Fig. 3G) ...... *N. lindigiana* (Rathbun, 1897)
10. Walking legs unusually long, total length (measured from coxa to tip of dactyl) of each about 1.3 times carapace width .... *N. sketi* Rodríguez, 1985
– Walking legs normal in length, total length (measured from coxa to tip of dactyl) of each subequal to carapace width .... *N. macropa* (H. Milne Edwards 1853)
11. Lateral lobe of first gonopod short, distal margin semicircular in caudal view (Fig. 4A) .... *N. charalensis* Campos & Rodríguez, 1985
– Lateral lobe of first gonopod long, distal margin broadly rounded (Fig. 4B) .... *N. macarenae* Campos, 1992
12. Laterodistal margin of first gonopod widening distally, forming lobe (Fig. 4C) .... *N. lobulata* Campos, 1992
– Laterodistal margin of first gonopod not widening distally, not forming lobe .. 13
13. Mesocaudal projection of spermatic

channel of first gonopod terminating in acute bifid projection 14
- Mesocaudal projection of spermatic channel of first gonopod terminating in acute simple projection (Fig. 2E) .... *N. perijaensis*, new species

14. Lateral lobe of first gonopod directed apically 15
- Lateral lobe of first gonopod curved cephalically 16

15. Distal portion of accessory and lateral lobes of first gonopod separated by deep notch in lateral view (Fig. 4D) .. *N. libradensis libradensis* Rodríguez, 1980
- Distal portion of accessory and lateral lobes of first gonopod not separated by deep notch, nearly continuous, in lateral view (Fig. 4E) .... *N. libradensis appressa* Campos, 1992

16. Cephalic margin of apex of first gonopod constricted subdistally, terminating in spine (Fig. 5A) .... *N. tonensis* Campos, 1992
- Cephalic margin of apex of first gonopod not constricted subdistally, terminating in acuminate projection (Fig. 5B) ..... *N. tencalanensis* Campos, 1992

17. Laterocaudal side of apex of first gonopod expanded (Fig. 5C) .... *N. boyacensis* Rodríguez, 1980
- Laterocaudal side of apex of first gonopod not expanded 18

18. Outer laterocaudal surface of apex of first gonopod with small blunt spines (Fig. 5D) ... *N. lasallei* Rodríguez, 1980
- Outer laterocaudal surface of apex of first gonopod with large, sharp spines (Fig. 5E) ... *N. niceforoi* (Schmitt, 1969)

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A new species of mud shrimp, *Upogebia toralae,* from Veracruz, México (Decapoda: Thalassinidea: Upogebiidae)

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Abstract.—*Upogebia toralae,* a new species of mud shrimp from Veracruz, México is described and illustrated. The unique female holotype was collected intertidally in the Port of Veracruz which is strongly impacted by human activity. The species shares with many members of the genus from the western hemisphere a strongly developed proximal mesioventral spine on the merus of the second pereopod. The species stands alone, however, with respect to other characters. The triangular rostrum has no ventral spines, the anterior gastric region bears many anteriorly setose spines that are more or less transversely elongate and scalelike, and the palms of the chelae have a dorsal ridge that bears three erect and somewhat hooked spines on its proximal end.

Infaunal crustaceans collected from the State of Veracruz, México in the southwestern Gulf of México are known to include a wide variety of decapod crustacean species (Hernández-Aguilera et al. 1996). This species richness has been attributed to the location of Veracruz in the tropical zone, with wet weather and abundant rains, where temperature varies from 10° to about 35°C (Soto & García 1989). Nearshore habitats include a great variety of biotopes such as sandy beaches, estuaries, extensive mangrove swamps, marshes, and nearly 28 coral reefs. A mud shrimp, *Upogebia toralae,* new species, has been collected in intertidal waters of this environment in an area of the Port of Veracruz that is strongly impacted by human activity, including oil spills and industrial pollution, urban effluents, and tourism.

Upogebia toralae, new species
Fig. 1

Material examined.—México: USNM 285522, 1 ♀ (holotype), S of Puerto de Veracruz, Ver. México, 19°11′43″, 96°07′36″W, intertidal, 8 May 1997, col. R. E. Toral-Almazán and J. L. Hernández-Aguilera.

Diagnosis.—Projections to either side of rostrum each ending in a spine; single spine on postocular margin; anterior gastric region bearing many anteriorly setose spines more or less transversely elongate and scalelike. Abdominal sternites unarmed. Telson subrectangular. Merus of cheliped bearing subdistal dorsal spine and row of 5 spines on ventral margin; carpus with strong mesiodistal dorsal spine and 2 moderate spines on mesiodistal margin; palms of chelae bearing 3 erect and somewhat hooked spines on proximal end of dorsal ridge. Merus of pereopod 2 with proximal mesioventral spine and 1 subdistal dorsal spine; carpus with 1 subdistal dorsal spine and 1 distoventral spine. Merus of pereopod 3 with 1 distodorsal spine and row of 3 spines on ventral margin. Merus of pereopod 4 spineless.

Description.—Rostrum triangular, horizontal in lateral view but with slightly downturned tip exceeding eyestalks by in-

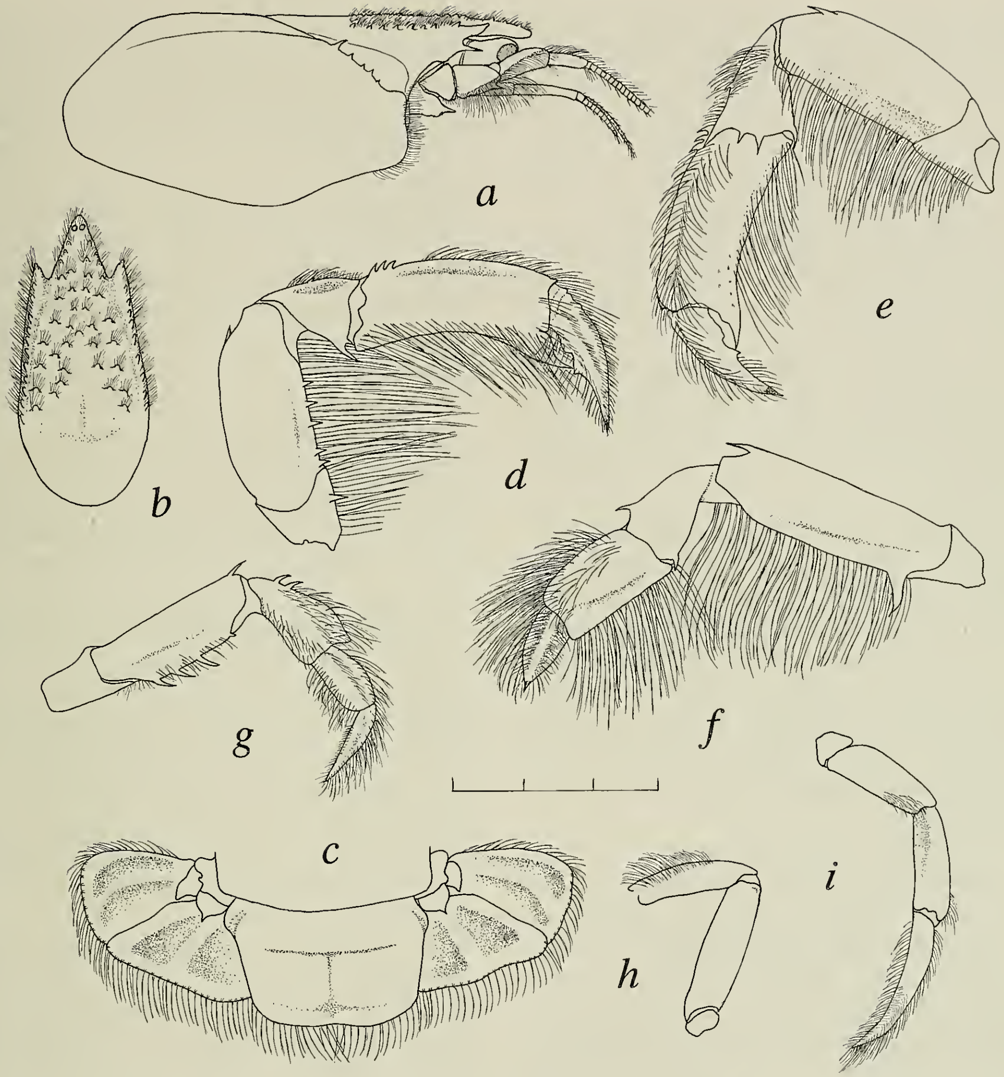

Fig. 1. *Upogebia toralae,* new species, USNM 285522, ♀ Holotype; *a,* carapace and cephalic region, lateral; *b,* anterior carapace, dorsal; *c,* telson and uropods, and part of abdominal segment 6, dorsal; *d,* cheliped, right lateral; *e,* cheliped, right mesial; *f,* pereopod 2, left; *g,* pereopod 3, right; *h,* pereopod 4, left (fragment); *i,* pereopod 5, right. Scale = 3 mm.

terval equal to length of cornea; 2 subdistal erect dorsal spines with tiny corneous tips followed on each side by smaller marginal spines, 3 on right, 4 on left; median line raised into low ridge. Pilose-armed field on anterior gastric region of carapace ornamented with rather sparse, transversely elongated, well separated scalelike spines bearing short setae anteriorly, about 10 of these spines along each lateral margin of anterior gastric region; scattered smaller scalelike spines mesial to each lateral margin, posterior region of carapace glabrous. Lateral ridge on either side of anterior gastric region extended anteriorly into process lateral to rostrum and bearing crest of 9 and 11 spines, more on left than on right. Shoulder lateral to cervical groove bearing about 4–5 spines below intersection with thalassinidean line, dorsal 2 spines prominent and acute, spines anteroventral to these much smaller or obsolescent; thalassinidean line continuing to posterior margin of carapace without interruption; postocular margin of carapace armed with acute spine at level of eyestalk.

Abdominal sternites unarmed.

Telson subrectangular, posterior margin shallowly biarcuate, smooth; transverse proximal ridge prominent, lateral ridge at each side obsolescent.

Eyestalk stout, slightly elevated distally, reaching along basal ⅔ of rostrum; lower margin slightly convex; cornea narrower than diameter of stalk and directed ventrolaterally.

Antennular peduncle reaching to about ⅔ length of terminal article of antennal peduncle, combined length of proximal 2 articles subequal to length of terminal article.

Antennal peduncle with distal article and distal half of penultimate article extending beyond tip of rostrum; article 2 bearing strong, slender, subdistal ventral spine; moderate oval scale bearing small upturned distal spine.

Maxilliped 3 bearing epipod.

Epistomal projection rather broad in lateral view, bearing prominent apical spine.

Chelipeds with ventral margin of ischium bearing 1 spine. Merus with row of 5 spines on ventral margin and a subdistal spine on dorsal margin. Carpus trigonal, with shallow longitudinal lateral groove, strong spine at anterior ventrolateral corner; dorsal crest margin bearing only 1 spine on basal ⅓ of its length, obscured by oblique tuft of setae; short spine on anterodorsal margin mesial to articulation with propodus; 2 moderate spines on anteromesial margin. Chela length about 2.7 times chela height; palm with dorsal ridge bearing 3 prominent slightly hooked spines at its proximal end, paralleled by sparsely setose mesiodorsal ridge ending in small distal spine; ciliated oblique ridge on lower lateral surface; both lateral and mesial surfaces of palm obscurely punctate. Fixed finger with extended slender tip and lobular tooth on occlusive edge. Dactyl at least twice length of fixed finger, drawn to corneous tip and bearing 2 lobular teeth on proximal half of occlusive edge, distalmost tooth opposing tip of fixed finger; dorsal and lateral longitudinal ridges heavily setose.

Pereopod 2 reaching about to distal ¼ of cheliped palm; carpus with acute subdistal dorsal spine and nearly equal subdistal ventral spine; merus with slender subdistal-spine on dorsal margin and very strong proximal mesioventral spine. Pereopod 3 with carpus bearing 2 somewhat hooked dorsal spines on proximal ⅓ of length; merus bearing distodorsal spine and 3 strong spines on ventral margin. Pereopod 4 (fragmentary) with spineless merus. Pereopod 5 of usual form, with cleaning brush on propodus.

Uropods with acute spine on protopod above base of mesial ramus; lateral ramus with mesial rib bearing smaller spine proximally; both rami slightly exceeding telson, and with distal margins bearing rather uniformly spaced row of granules.

Measurements (*in mm*).—Anterior carapace length 5.3, carapace length 7.5, length of chela including fixed finger 3.5, midlength height of chela 1.3.

Known range.—Confined to type locality.

Remarks.—*Upogebia toralae,* new species, shares with many eastern Pacific and western Atlantic members of the genus a second pereopod on which the merus bears a strong proximal mesioventral spine (see keys to species in Williams 1986, 1993). The abdominal sternites and pleura bear no ventral spinules.

The species stands alone, however, with respect to several characters. The triangular rostrum has no ventral spines. The anterior gastric region bears many anteriorly setose spines that are more or less transversely elongated and scalelike rather than being simple spines or spinelike tubercles. The palms of the chelipeds have a dorsal ridge that bears 3 erect and somewhat hooked spines on its proximal end. Moreover, the carpus has a mesiodorsal crest that bears 1 spine on the basal ⅓ of its length as well as the usual strong distal spine rather than a series of spines along all of its length. In the key to species of *Upogebia* in the Western Atlantic (Williams 1993), *U. toralae* lies closest to *U. marina* Coelho.

Etymology.—The species is named in honor of Rosa Estela Toral-Almazán, Facultad de Ciencias, UNAM, who has contributed to many collections from the Gulf of Mexico, in one of which the holotype was taken.

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Pinnotheres malaguena Garth, 1948, a new member of the genus *Fabia* Dana, 1851 (Crustacea: Brachyura: Pinnotheridae)

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Abstract.—The original description and figures of the male holotype of the pinnotherid crab *Pinnotheres malaguena* Garth are emended. The morphology of this species excludes it from *Pinnotheres* Bosc, 1802 but supports its transfer to the genus *Fabia* Dana, 1851. *Fabia malaguena* can be distinguished from other members of *Fabia* by its unique gonopod shape and its abdomen, which has somites 5 to the telson fused.

The pinnotherid crab species *Pinnotheres malaguena* Garth, 1948 was described on the basis of an adult male collected in Málaga Bay, Colombia [Málaga = 6°44′N, 72°45′W] (Garth 1948). Gore (1986) and Campos (1996), based on Garth's account, suggested that *P. malaguena* may belongs in the genus *Fabia* Dana, 1851. Our study of the male holotype, deposited in the American Museum of Natural History (AMNH), allows us to confirm this. The morphology of *P. malaguena* does not agree with *Pinnotheres* sensu stricto (see Manning 1993 for the characteristics of that genus), but it largely concurs with those of the genus *Fabia*.

In addition to transferring *P. malaguena* to *Fabia*, we emend its original description (underlined in the text) and figures, since several mistakes and omissions in the original account were detected. Other abbreviations used are WL = walking legs; MXP3 = third maxilliped.

Fabia malaguena (Garth, 1948), new combination
(Fig. 1)

Pinnotheres malagueña Garth, 1948:53–55, fig. 5.

Pinnotheres malaguena.—Silas & Alagarswami, 1967:1202, 1218.—Schmitt et al., 1973:56.—Gore, 1986:147.—Lemaitre & Alvarez León, 1992:61.—Hendrickx, 1995:142.—Campos, 1996:1161.

Distribution.—Known only from the type locality, Málaga Bay, Colombia, in 4–9 m depth (Garth 1948).

Material examined.—Male holotype (AMNH 10012).

Measurements.—Carapace length 2.6 mm, width 2.3 mm; frontorbital width 1.1 mm; length of chela 1.1 mm, of dactyl 0.5 mm; length of manus 0.6 mm (after Garth 1948).

Redescription.—Carapace (Fig. 1A) slightly longer than broad, widest at middle, suboctagonal, angles rounded, dorsal surface smooth and bare, porcelain-like, strongly convex, without indications of regions, frontal and anterolateral margins clothed with shaggy hair-like setae. Front advanced considerably beyond orbits, its edges representing a continuation of anterolateral margins interrupted only by sinuous indentation of orbits. Anterior margin subtruncate, appearing bilobed, edges concealed by fringing setae. Anterolateral margin longer than posterolateral, sloping at fairly steep angle from

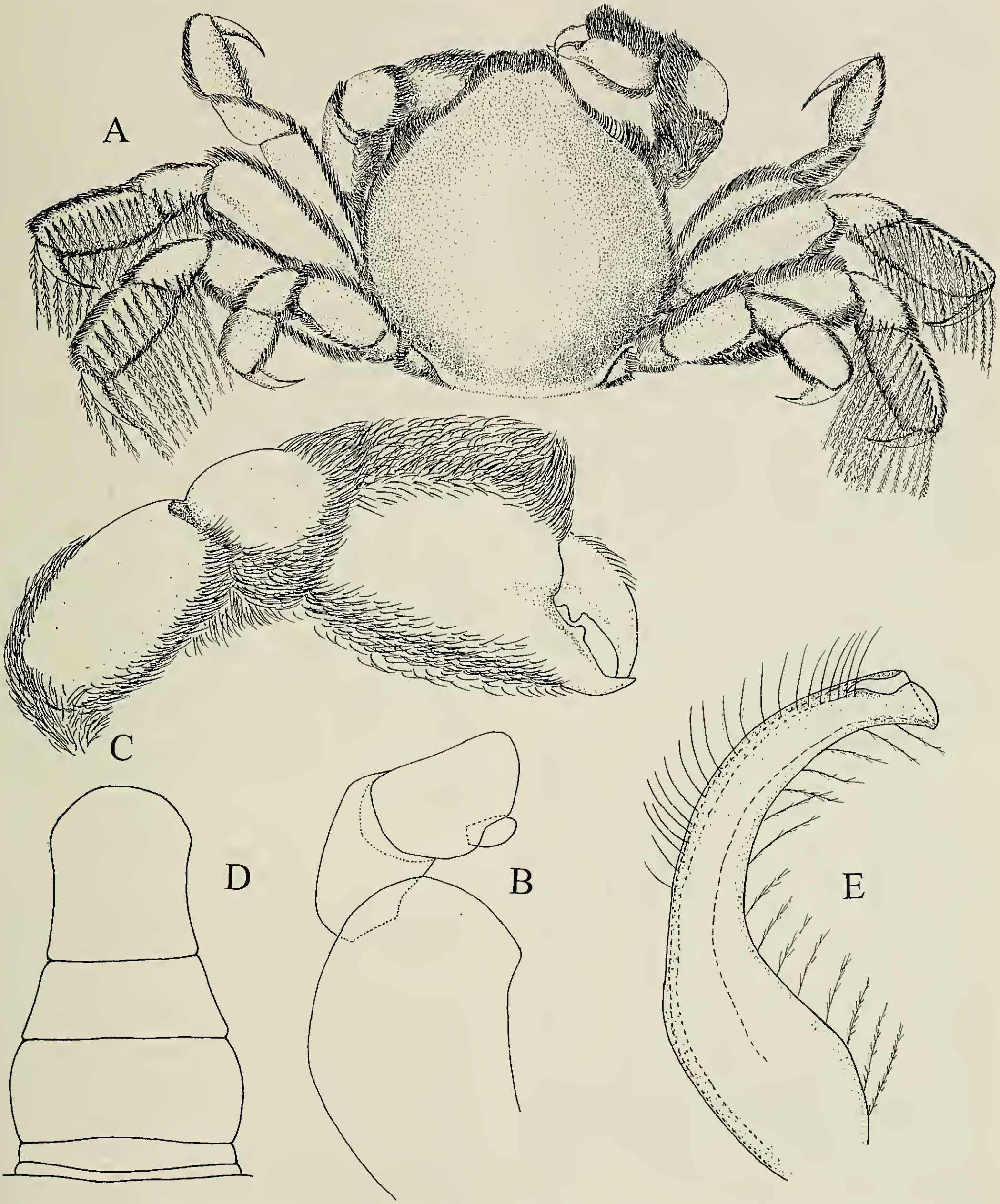

Fig. 1. *Fabia malaguena* (Garth, 1948), male holotype (AMNH 10012). Carapace length 2.6 mm, width 2.3 mm. A, Dorsal view; B, MXP3; C, Right chela, outer face; D, Abdomen; E, Gonopod. Setae omitted in Fig. 1B, D.

the orbits, their gentle arching accentuated by a thick fringe of fur-like pile, longest medially. A suggestion of short, transverse line of hairs at gastric level. Posterior margin almost straight, rimmed and bare. Orbits small and circular, eyestalks short, eyes filling sockets, corneas when retracted concealed by setae in dorsal view. Antenna short, basal article hiatus, flagellum only extending beyond margin of front.

MXP3 (Fig. 1B) nearly transverse in position, gently convex distally, carpus longer than wide, cylindrical, curving inward and broadening distally; propodus subequal to carpus in length, flattened and broadened medially, outer surface lacking neither row of setae nor transverse ridge as described and figured in original account; dactylus small, digitiform, placed in angular notch in middle third on ventral margin of propodus, and falling short of end of propodus.

Chelipeds (Fig. 1C) stout, equal, merus and carpus fringed with setae above and below, leaving a smooth, bare space between; chela with similar open area, fringing setae as dense as those of anterolateral margins of carapace, forming superior crest. Fingers slender, thin, tapering distally, sharply pointed, dactylus curving strongly downward, pollex little deflexed, both fingers with subtruncated tooth proximally placed on cutting edge, a few long setae visible in narrow gape, tips crossing until pointed in almost opposite directions.

Sternal plastron flattened at center, slightly concave towards margins, latter fringed with setae, segmentation clearly indicated. Male abdomen (Fig. 1D) widest at third somite, sides of latter broadly rounded, tapering to narrowest point at middle of fused fifth somite to telson, then broadening slightly before the semicircular tip which is edged with fine setae (omitted in Fig. 1D). Gonopod (Fig. 1E) cylindrical, sickle shaped, tapering gradually from base almost to gutter-like tip which flares slightly and divided longitudinally for short distance along its length; margins setose, long plumose setae extending to base of appendage externally.

WL (Fig. 1E) symmetrical, laterally compressed, with exception of dactyli, margins covered with fringe of furry setae; WL1 twisted, WL 2–3 with two fringes of long swimming setae, one on outer face of carpus and propodus, one on ventral margin of propodus. Meri subequal in shape and width; carpi trigonal, slender proximally, broadening distally; propodi widest at midpoint, obliquely rounded distally; dactyli long, tapering abruptly to sharp, transparent, curved nails, prehensile edge smooth. Relative length of WL 2 > 3 > 1 > 4.

Remarks.—The following features support the inclusion of the male of *Pinnotheres malaguena* in the genus *Fabia:* the carapace is convex, smooth, shiny, porcelain-like; the frontorbital and anterolateral margins with stout, hair-like setae; MXP3 with a subtrapezoidal propodus subequal to the cylindrical carpus, and digitiform dactylus inserted in the middle third on the ventral margin of the former article; WL1 are twisted and margins of the compressed WL1–4 are covered with a fringe of hair-like setae; and the abdomen with somites 1–4 free, 5 to the telson fused. Males in the genus *Pinnotheres* have the dactylus of MXP3 styliform, inserting basally on the ventral margin of the propodus and all of the abdominal somites and telson free.

Fabia malaguena can be separated from other species of the genus *Fabia* by its singular gonopod shape (Fig. 1E) and because abdominal somites 5 to the telson are fused (Fig. 1D).

Acknowledgments

We are indebted to Lara L. Tolchin, American Museum of Natural History, for the loan of the holotype of *Pinnotheres malaguena* (Garth, 1948); and to Alma Rosa de Campos for her fine artistic work. This work was partially supported by the project UABC-CONACyT 3587-N9311, and the program 0134-UABC "Systematics of the symbiotic crustaceans of the Mexican Pacific." This is contribution #447 from the Smithsonian Marine Station at Fort Pierce; support of that program for Manning's studies on pinnotherids is gratefully acknowledged.

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Cave chaetognaths in the Canary Islands (Atlantic Ocean)

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Abstract.—Morphological and biometric observations of chaetognaths found in a submarine cave on the southeast coast of Tenerife (Canary Islands) are presented. The specimens, that we have called *Spadella* aff. *ledoyeri*, differ notably from the coastal species *Spadella cephaloptera*, which is a well known inhabitant of the submerged seagrass beds of the infralittoral areas of the islands. Because the genus *Paraspadella* was previously described from an anchialine cave on the Grand Bahama Island (western Atlantic Ocean), this is the second record of an Atlantic cave chaetognath and the first for the genus *Spadella* in Atlantic Ocean caves.

The Canary Island benthic chaetognaths, unlike the pelagic species, have only rarely been studied. Among the few studies done are those of Hernández & Jiménez (1992) and Broerse (1993), which deal with biometric aspects of *Spadella cephaloptera* (Busch, 1851) in the island of Tenerife. This species has been found in beds of the submerged sea grass *Cymodocea nodosa* and on patches of the alga *Caulerpa prolifera* in shallow infralittoral areas of the islands of Tenerife (Hernández & Jiménez 1992, Broerse 1993) and Gran Canaria, especially in areas with a sandy substratum. The discovery of benthic cave chaetognaths in the Mediterranean (Casanova 1986, 1992) and in the Bahamas (Bowman & Bieri 1989) has led us to trawl for them in dark submarine caves. Specimens of these organisms were found, but they were different from descriptions of the benthic species *S. cephaloptera*, which is well known in the islands.

Materials and Methods

The material collected comes from a dark, submarine cave, situated on the southeast coast of the island of Tenerife (Canary Islands) (Fig. 1), between the towns of Santa Cruz and Candelaria. Two trawls were carried out, using a 200 μm, manual plankton net, 12 m from the entrance and a few cm above the bottom. A total of 42 chaetognath specimens belonging to the genus *Spadella* was obtained.

The specimens were measured to give data on total length, caudal length, ovarian length, and the number of grasping spines and teeth. For comparison, we used specimens of *Spadella cephaloptera*, which were caught on the same dates as the cave species. These were caught in trawls over beds of sea grass and algae off the islands of Tenerife and Gran Canaria.

Cave Characteristics

The cave is a volcanic pipe at the bottom of a submarine canyon. It has a broad entrance and a sandy floor. The cave narrows close to the entrance and then widens out again after about one m. The back of the cave is marked by a natural blockage of sand. The cave is 16 m below ground level, with a slope of 1.3 m and is 15 m deep. Geological interest in the cave stems from the fact that it forms part of the lava fields that flowed from the back of La Esperanza (Tenerife) to the coast and into the sea.

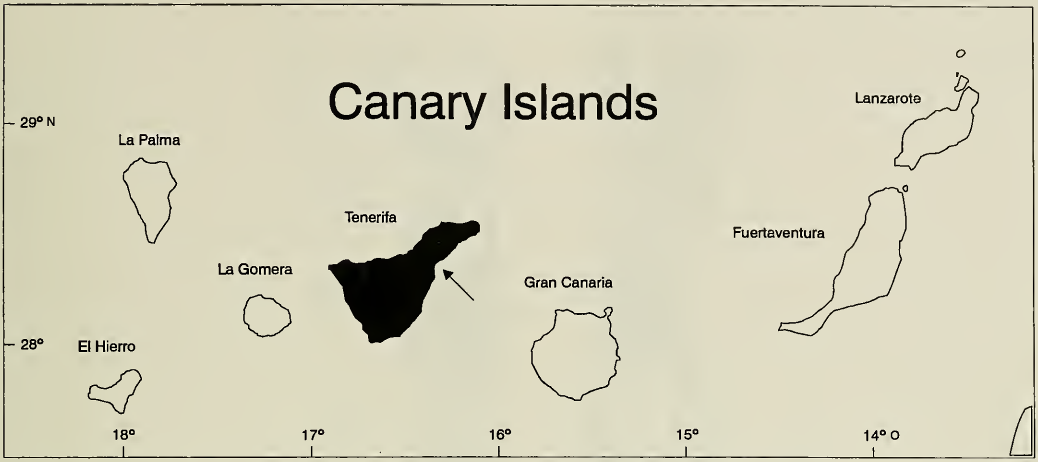

Fig. 1. Location of the sample station in the southeast of Tenerife (Canary Islands).

Apart from the chaetognaths, other fauna found in the cave included shrimps (spawning females of *Plesionika narval*), tubicular Polychaeta, sponges, formations of *Nadracis asperula* (corals), prawns (*Lysmata grabhami*) and echiurids (*Bonellia viridis*).

Results and Discussion

The chaetognaths studied showed the following taxonomic characteristics (Figs. 2, 3): General aspect of the body: white, long, thinner than in *Spadella cephaloptera*, which is thicker and yellowish brown. Head square, not oval as in *S. cephaloptera* (Fig. 2). Short lateral fins (only 50% of the caudal region), wider than in *S. cephaloptera*, which start just before the tail. Ocular pigment present. The ciliata corona is completely circular and different from that of *S. cephaloptera* studied in Tenerife and Gran Canaria, where it is more flattened and bilobed (Fig. 3). Caudal fin completely triangular; in *S. cephaloptera*, it is spatula shaped. Triangular seminal vesicles, separated from the lateral and caudal fins. In *S. cephaloptera*, the seminal vesicles touch both fins. Caudal region strong and broad. Cephalic tentacles and intestinal diverticulae were not observed. Ovaries with large, rounded ovules. Ten or eleven reddish-light brown grasping spines. Only 3–4 anterior teeth observed. The maximum size for stage III sexual maturity is 4.5 mm (4.3 mm, mean) (Table 1). Biometric data is also provided for each sexual stage of the specimens of this study (Table 1). These data have been compared with the specimens corresponding to the Tenerife (Hernández & Jiménez 1992) and Gran Canaria specimens (Table 2).

The specimens collected in the cave belong to the genus *Spadella*, but do not present the typical characteristics of *Spadella cephaloptera*. The specimens studied are closer to *Spadella ledoyeri*, a cave dwelling chaetognath of the Mediterranean (Casanova 1986). Among the morphological differences between our specimens and those of *S. cephaloptera*, we observed: the shape of the ciliata corona, shape and position of seminal vesicles, shape, position and extension of the lateral fins, shape and general aspect of the body, shape and size of the collarette and the aspect of the eye pigment. Although the shape of the ciliata corona can vary (Ghirardelli 1968), the characteristics are valid and have a high taxonomic value.

Concerning Atlantic cave-dwelling chaetognaths, the only other species on record is *Paraspadella anops*, described from a single specimen from Sagittarius Cave near Gran Bahama Island (Bowman & Bieri

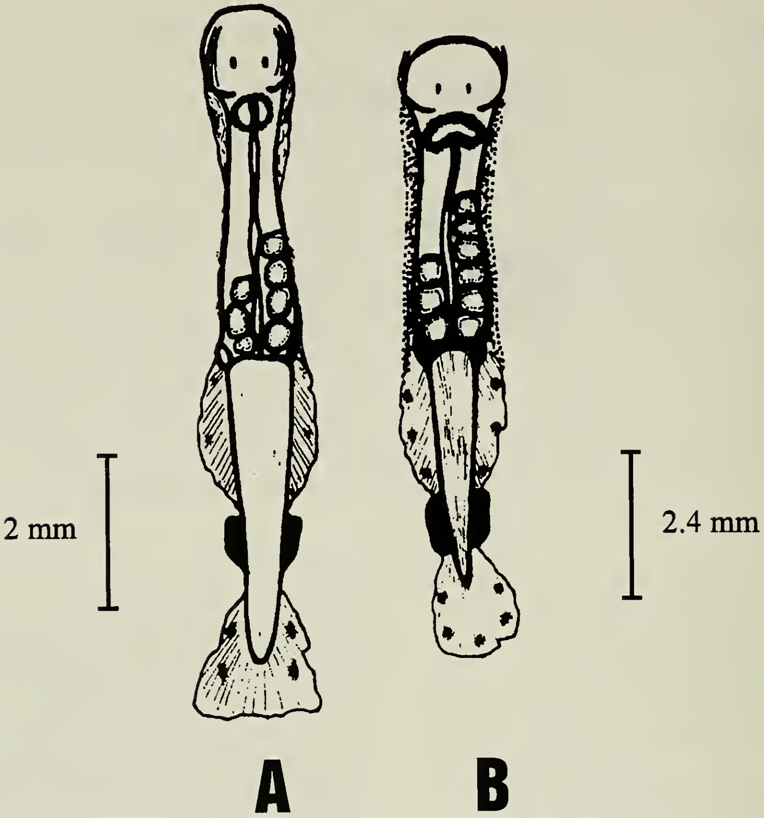

Fig. 2. Selected specimens from the samples. A, *Spadella* aff. *ledoyeri*; B, *Spadella cephaloptera.*

1989). This species, as in the case of our specimens of *Spadella ledoyeri*, is clearly the descendent of *Paraspadella schizoptera*, the common neritic species of the region, from which it differs in only a few characteristics.

Likewise, *Spadella ledoyeri* is believed to have evolved from either *Spadella cephaloptera*, isolated in the caves of the Mediterranean from submergence during the most recent ice age, or alternatively, from the deep water species, *Spadella birostrata*, isolated in cavities of deeper caves flooded during a prior glaciation (Casanova 1992).

For the first time in the Atlantic Ocean, benthic chaetognaths of the genus *Spadella* from underwater caves are described. In the

Table 1.—Biometric characteristics of stage III specimens of *Spadella* aff. *ledoyeri* on Tenerife. TL = total length, CL = caudal length, %C/T = relative tail length in relation to total length.

	TL (mm)	CL (mm)	%C/T
Stage I	3.0	1.5	50.0
n = 1			
Stage II	3.0–4.5	1.5–2.5	42.9–55.6
n = 23	average: 3.9	average: 2.0	average: 50.0
Stage III	4.0–4.5	2.0–2.5	44.4–55.6
n = 18	average: 4.3	average: 2.2	average: 51.5

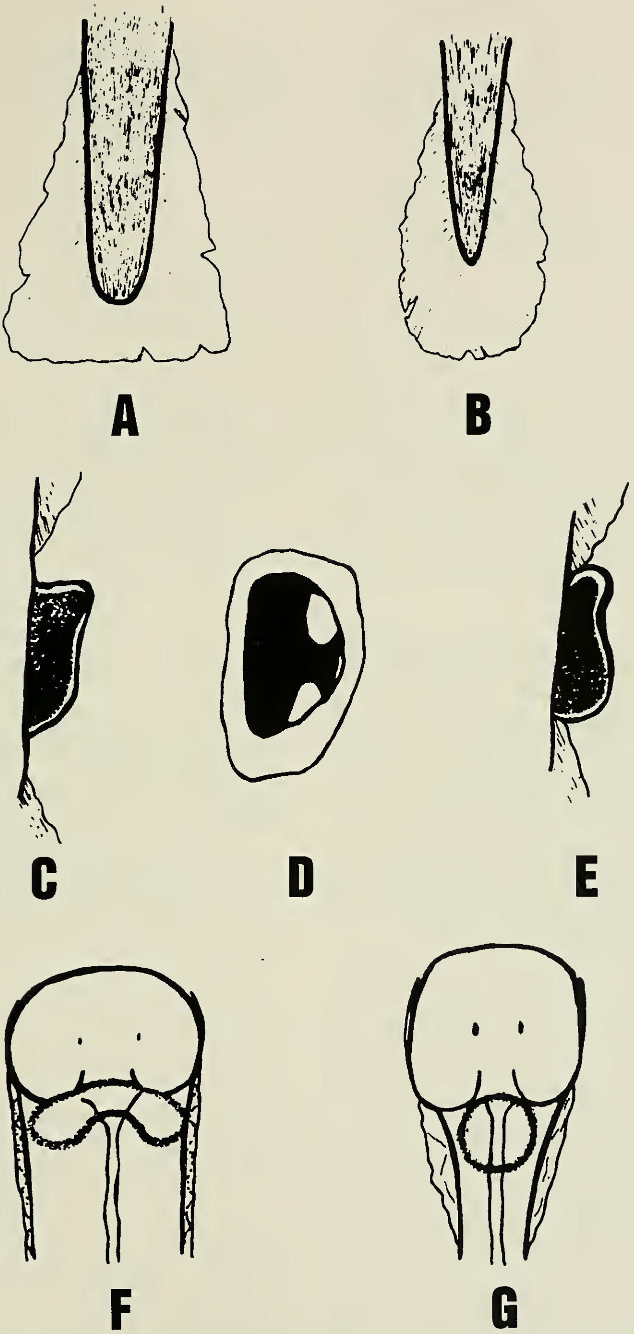

Fig. 3. *Spadella* aff. *ledoyeri.* A, caudal fin; B, seminal vesicle; C, ocular pigment; D, head and neck. *Spadella cephaloptera.* E, caudal fin; F, seminal vesicle; G, head and neck.

Table 2.—Comparison of total length (TL) for stage III specimens of *Spadella* aff. *ledoyeri* from Gran Canaria and Tenerife.

TL (mm)	Island	Month	Habitat
5.5	Gran Canaria	April	seagrass
4.0	Tenerife	April	seagrass
3.5	Tenerife	December	seagrass
4.5	Tenerife	April	cave

Canary Islands, therefore, as is the case in the Mediterranean (Casanova 1992, genus *Spadella*) and the Bahamas (Bowman & Bieri 1989, genus *Paraspadella*), these animals exist in the biotope of submarine caves, where, according to the above mentioned authors, there are original populations.

New collections will be done, at different times of the year, extending the study to other caves in the islands, in order to investigate the biological cycle and to clarify certain aspects, which are debated in the Mediterranean, of the origin of the cave dwelling species and make accurate comparisons between *Spadella* aff. *ledoyeri* and the coastal species *Spadella cephaloptera* from waters surrounding the Islands.

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The discovery of *Glyphocrangon stenolepis* Chace (Decapoda: Caridea: Glyphocrangonidae) from Taiwan and Japan, with notes on individual variation

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Abstract.—Abundant material of *Glyphocrangon stenolepis* Chace was found off Taiwan. Supplementary specimens from the South China Sea and Japan have made possible to redescribe this poorly known species. Remarkable sexual differences in body sculpture and coloration are found in this species. The paratype from the Sulu Sea has proven to represent a different as yet undetermined species. Other morphological variations are discussed, and the coloration is illustrated.

In his report on the glyphocrangonid and crangonid shrimps collected by the Philippine *Albatross* Expedition 1907–1910, Chace (1984) described *Glyphocrangon stenolepis*, based on two specimens, one from the South China Sea, off Pratas Islands, and another from north of the Sulu Sea, Philippines. The specimen from the South China Sea is the holotype. The paratype from the Sulu Sea is much smaller than the holotype, and appears to be a juvenile or a young female. Although Chace (1984) noted some differences between the holotype and paratype, he interpreted them as size-related. The species has not been reported since the original description.

Recent investigations by one of us (TYC) has shown that *Glyphocrangon stenolepis* is common in offshore waters of Taiwan. Furthermore, scientists from the Fisheries Research Institute of Taiwan collected four specimens from the type locality, off Pratas Islands in 1996. Through the kind courtesy of Prof. K. Hayashi, a single specimen from the East China Sea, off Japan, has also been made available for examination. All this material has enabled us to diagnose the species more precisely, and to extend its known geographical range northwards to Japan. The study of the material has shown that the species exhibits marked variation in body sculpture in males. Therefore, we provide a full redescription of the species. Some important differences between the holotype and paratype noted by Chace (1984) indicate that the paratype represents another species, though its exact identity is still uncertain.

The specimens, all collected by bottom trawls, are deposited in institutions indicated by the following abbreviations: CBM, Natural History Museum and Institute, Chiba; NUF, National University of Fisheries, Shimonoseki; NTOU, National Taiwan Ocean University, Keelung; TFRI, Taiwan Fisheries Research Institute, Keelung Branch; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. The terminology for the carinae and spines on the carapace follows Holthuis (1971) and Chace (1984). The abbreviation cl indicates postorbital carapace length.

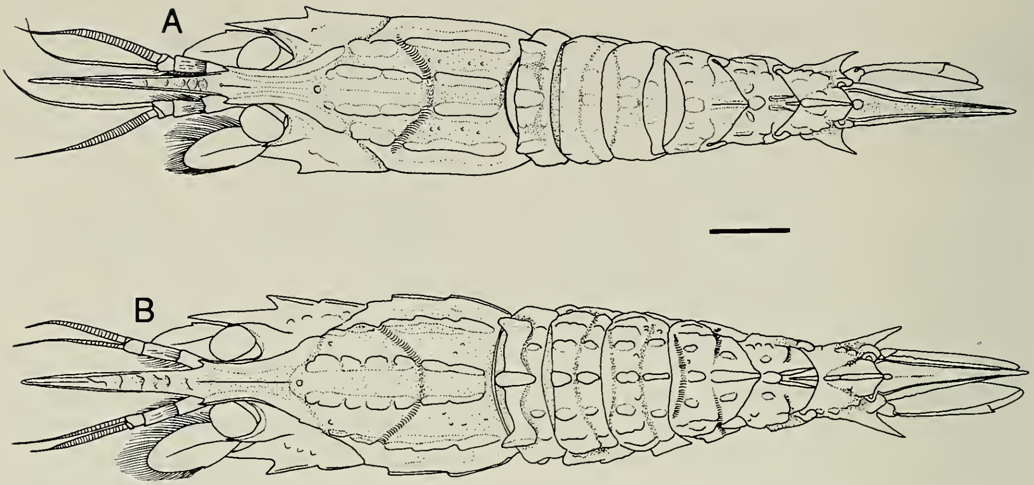

Fig. 1. *Glyphocrangon stenolepis* Chace, 1984. Animals in dorsal view, pereopods omitted. A, male from off Ta-Shi, NE Taiwan, cl 14.1 mm, CBM-ZC 3614; B, female from off Su-Aou, NE Taiwan, cl 14.7 mm, CBM-ZC 2935. Scale bar indicates 5 mm.

Glyphocrangon stenolepis Chace, 1984
(Figs. 1–4)

Glyphocrangon stenolepis Chace, 1984:22 (part), fig. 5 (not fig. 6; =*Glyphocrangon* sp.).

Type material.—South China Sea. Pratas Islands (Tungsha Tao), *Albatross* Stn 5300, 20°31′N, 115°49′E, 485 m, 8 Aug 1908, 1 male (cl 11.3 mm), holotype (USNM 205091).

Other material.—South China Sea. R.V. *Fisheries Research I*, 19°49.2′N, 114°09.3′E, 512 m, 23 Apr 1996, 1 male (cl 11.1 mm) (TFRI); exact position unknown, 1996, 3 males (cl 13.6–14.8 mm) (TFRI).

Taiwan. Fishing pots, commercial trawlers, 300–500 m, sandy mud bottoms: Ta-

Fig. 2. *Glyphocrangon stenolepis* Chace, 1984. Animals in lateral view, pereopods and pleopods omitted. A, male from off Ta-Shi, NE Taiwan, cl 14.1 mm, CBM-ZC 3614; B, female from off Su-Aou, NE Taiwan, cl 14.7 mm, CBM-ZC 2935. Scale bar indicates 5 mm.

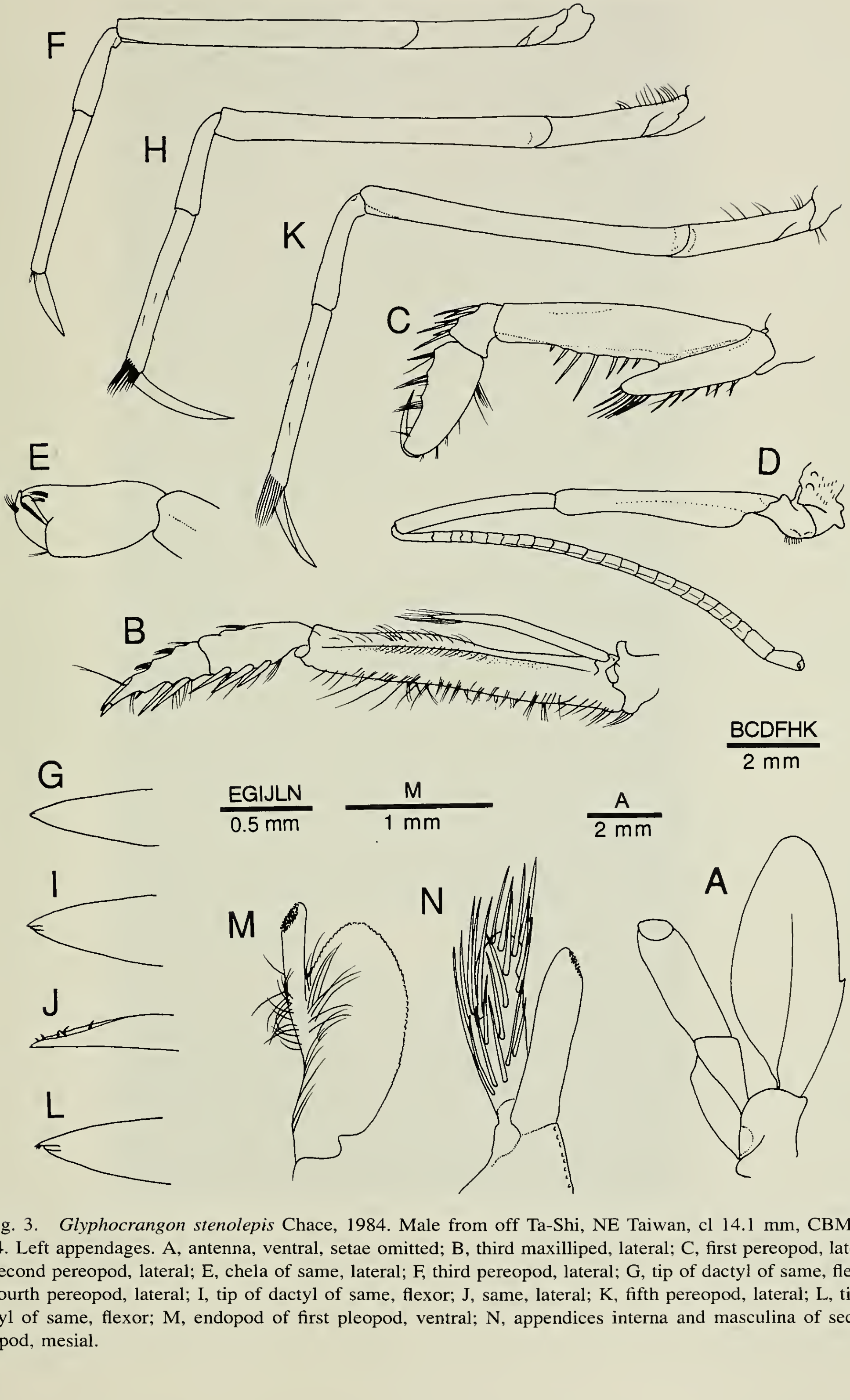

Fig. 3. *Glyphocrangon stenolepis* Chace, 1984. Male from off Ta-Shi, NE Taiwan, cl 14.1 mm, CBM-ZC 3614. Left appendages. A, antenna, ventral, setae omitted; B, third maxilliped, lateral; C, first pereopod, lateral; D, second pereopod, lateral; E, chela of same, lateral; F, third pereopod, lateral; G, tip of dactyl of same, flexor; H, fourth pereopod, lateral; I, tip of dactyl of same, flexor; J, same, lateral; K, fifth pereopod, lateral; L, tip of dactyl of same, flexor; M, endopod of first pleopod, ventral; N, appendices interna and masculina of second pleopod, mesial.

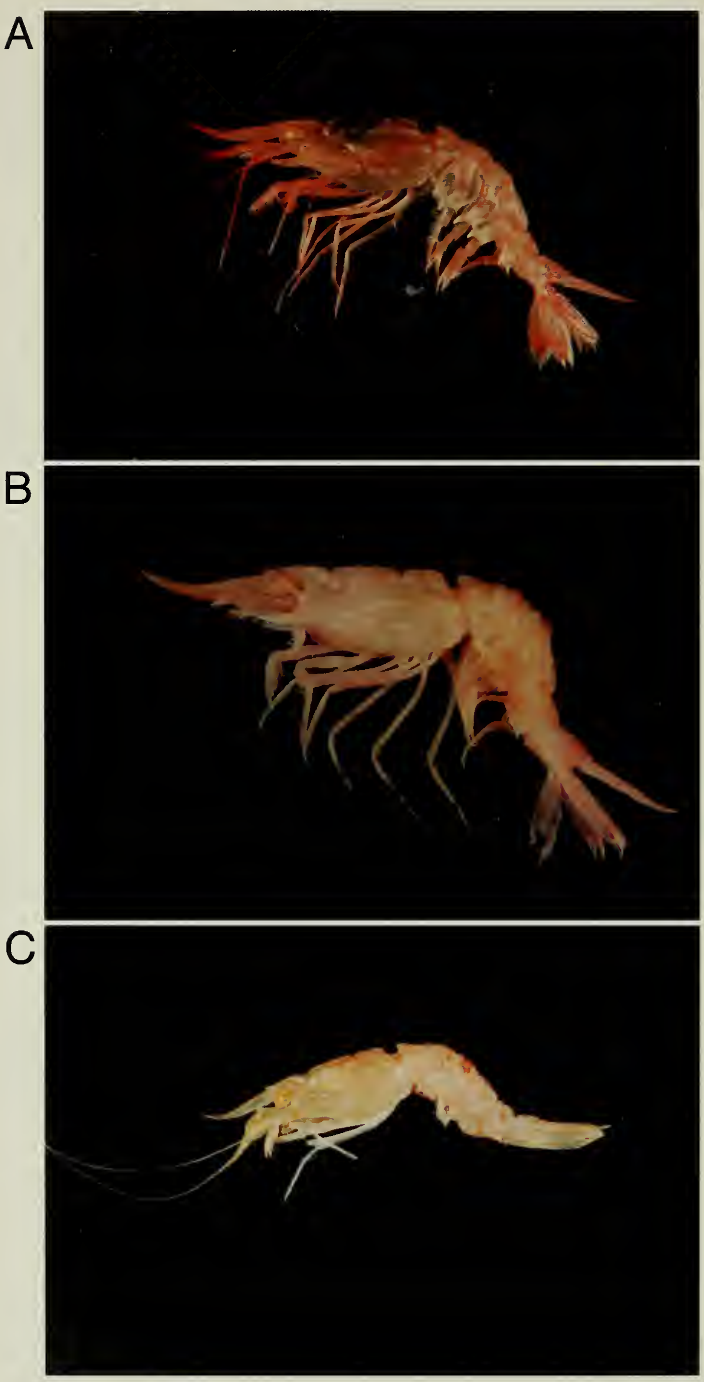

Fig. 4. *Glyphocrangon stenolepis* Chace, 1984. A, ovigerous female from Taiwan; B, male from Taiwan; C, male from Pratas Islands, South China Sea.

Shi, I-Lan County (northeastern coast), 25 Nov 1994, 3 males (cl 12.1–13.2 mm), 4 ovig. females (cl 12.2–14.5 mm) (NTOU); 27 Apr 1995, 1 ovig. female (cl 13.9 mm), 1 female (cl 15.4 mm) (NTOU); 13 June 1995, 2 males (cl 13.3, 14.5 mm), 1 ovig. female (cl 15.0 mm) (CBM-ZC 3614); 3 July 1995, 2 ovig. females (cl 13.6, 14.6 mm); 11 Mar 1997, 18 males (cl 11.4–16.1 mm), 35 ovig. females (cl 12.3–16.0 mm), 12 females (cl 11.0–16.0 mm) (NTOU); 10 males (cl 11.8–16.7 mm), 7 ovig. females (cl 13.6–17.5 mm), 3 females (CL 13.0–13.4 mm) (CBM-ZC 3918); 25 Feb 1997, 1 ovig. female (cl 14.2 mm) (NTOU); 4 Dec 1997, 1 female (cl 11.7 mm) (CBM-ZC 3882); 1 June 1998, 3 males (cl 9.2–13.0 mm), 1 ovig. female (cl 15.7 mm) (NTOU). Su-Aou, I-Lan County (northeastern coast), 20 Apr 1985, 5 males (cl 12.4–15.0 mm), 4 ovig. females (cl 13.0–16.0 mm) (CBM-ZC 3615); 2 May 1985, 4 males (cl 12.5–13.1 mm), 5 ovig. females (cl 12.4–13.3 mm), 1 female (cl 11.4 mm) (NTOU); 6 Aug 1996, 1 male (cl 13.9 mm), 2 females (cl 14.7, 15.3 mm) (CBM-ZC 2935); 7 Aug 1996, 1 male (cl 16.6 mm) (NTOU); 18 Nov 1997, 1 male (cl 9.5 mm) (NTOU); 5 Dec 1997, 7 males (cl 10.3–14.4 mm), 1 ovig. female (cl 15.2 mm) (CBM-ZC 3901). Tong-Kong, Ping-Tong County (southwestern coast), 25 Feb 1995, 1 male (cl 12.5 mm) (NTOU); 30 May 1997, 1 male (cl 10.5 mm) (NTOU).

East China Sea. R. V. *Tennyo-Maru*, west of Tokara Islands, southern Japan, Stn T-2, 29°20′N, 127°26′E, 488 m, 1 male (cl 12.8 mm) (NUF).

Redescription.—Integument not pubescent. Rostrum (Figs. 1, 2) curved dorsad anteriorly, 0.95–1.23 times as long as carapace, armed with 2 pairs of lateral teeth, posterior pair (arising from posterior to level of posterior margin of orbit) more or less reduced, sometimes barely discernible, never acute; series of distinct transverse septa on anterior part of dorsal surface, median carina present on distal portion and posterior portion between eyes. Carapace (Figs. 1, 2) with anterior first (submedian) carina varying from slightly uneven to distinctly 5-lobed; median area anterior to submedian carina with single tubercle in midline; posterior first (submedian carina) composed of 2 elongate ridges. Anterior second (intermediate) carina composed of 3 obtuse lobes; posterior second (intermediate) carina also 3- or 4-lobed. Intercarinal space between posterior first and second carinae usually with row of tubercles. Hepatic region with 2 or 3 tubercles; posterior third (antennal) carina 3- or 4-lobed. Anterior fourth (lateral) carina forming bilobate, wing-like expansion, terminating anteriorly in sharp point independent of branchiostegal spine, arising from posterior to level of orbit, posterior lobe in line with non-dentate anterior portion; posterior fourth (lateral) carina interrupted posteriorly, most part neither dentate nor lobate. Anterior fifth (sublateral) carina not prominent, nearly linear; posterior fifth (sublateral) carina very short. Sixth (submarginal) carina absent anteriorly, indistinct posteriorly. Margins of carinae faintly erose. Antennal spines unarmed marginally, less than 0.5 as long as and diverging little more than anteriorly directed branchiostegal spines.

Abdomen (Figs. 1, 2) with ridges and tubercles on dorsal surface blunt or obsolete; prominence of ridges and tubercles variable in males, well developed in females. First somite with distinct submedian tubercles on posterior section of tergum in females, sometimes faint in males; median carina obsolete to distinct; transverse groove moderately shallow to faint. Broad median, submedian and lateral carinae on second and third somites interrupted by transverse groove, distinct in females, sometimes obsolete or absent in males; median carina on fourth somite distinct in both sexes, more or less notched at anterior 0.3; fifth somite with prominent anterior tubercle and sharp carina posteriorly along midline, latter flanked by posteriorly divergent sharp carinae; sixth somite with median carina divided in 2 by shallow, sometimes very

Table 1.—*Glyphocrangon stenolepis* Chace, 1984. Branchial formula.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	1	1	1	1	1
Arthrobranchs	—	—	2	1	1	1	1	—
Podobranch	—	—	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	1	—	—	—	—	—

weak, notch anteriorly. Second somite with pleuron bearing 2 short, sometimes blunt teeth and inconspicuous anterior lobe; pleura of third, fourth and fifth somites each with 2 moderately short marginal teeth.

Eyes (Figs. 1, 2) moderately large for genus, cornea lightly pigmented.

Antennular peduncle (Figs. 1, 2) overreaching distal margin of scaphocerite by 0.2–0.3 length of intermediate segment; outer flagellum longer and thicker in males than in females. Scaphocerite (Fig. 3A) elongate oval, 1.95–2.37 times longer than wide, with small lateral tooth arising slightly posterior to level of mid-length, marginal setae confined to blade distal to lateral tooth; carpocerite not overreaching distal margin of blade.

Mouthparts typical of species in genus. Third maxilliped (Fig. 3B) moderately stout, reaching or overreaching distal margin of scaphocerite; antepenultimate segment distinctly carinate dorsolaterally.

First pereopod (Fig. 3C) incompletely subchelate; ischium with distoventral portion strongly produced. Second pereopods (Fig. 3D) nearly equal, each with 23–27 carpal articles; chela (Fig. 3E) flattened, with short fixed finger and strongly oblique cutting edge. Third to fifth pereopods (Fig. 3F, H, K) moderately slender, each with subspatulate dactyl and merus longer than carpus and propodus combined. Third pereopod (Fig. 3F) with dactyl 0.4–0.5 times as long as propodus, terminating in simple unguis (Fig. 3G); propodus with terminal or subterminal setae. Fourth pereopod (Fig. 3H) with dactyl 0.6 times as long as propodus, terminating in small lobe mesiad to small subterminal spine, bearing few short bristles on extensor surface distally (Fig. 3J); propodus with distal setae. Fifth pereopod (Fig. 3K, L) generally similar to fourth pereopod; dactyl 0.4–0.5 times as long as propodi, lacking bristles on extensor surface.

Thoracic sternite deeply depressed in both sexes, anterior part of sixth thoracic sternite produced anteriorly as subtriangular lobe; eighth sternite posteriorly with obtuse median tubercle in males, unarmed in females.

Interlocking mechanism of carapace and thoracic sternum well developed.

First pleopod of male with well-developed appendix interna on endopod (Fig. 3M), bearing rows of long setae basally. Appendix masculina of second pleopod (Fig. 3N) reaching or slightly overreaching appendix interna, bearing numerous long bristles terminally and mesially.

Branchial formula as shown in Table 1.

Eggs large and elongate oval, ranging from 1.2 to 1.5 and 2.2 to 2.5 mm in short axis and long axis respectively.

Coloration.—Females with body orange brown, ridges and carinae somewhat orange to reddish. Antennular and antennal flagella, distal parts of pereopods, posterior margin of abdominal tergites and posterior parts of tail-fan reddish. Meri of posterior pereopods and ventral parts of abdominal pleura slightly whitish. Eyes golden brown. Eggs blue, and developed ovaries visible inside carapace deep blue. Males with body light brown to slightly whitish, and generally with color paler than females, particularly those with less developed abdominal sculpture.

Size.—Males: cl 9.2–16.7 mm; females: cl 11.0–17.5 mm; ovigerous females: cl 12.2–17.5 mm.

Distribution.—East and South China Seas; 300–512 m; inhabiting soft bottoms.

Remarks.—As previously mentioned, *Glyphocrangon stenolepis* was described based on two specimens, the holotype from off Pratas Islands, South China Sea, and the paratype from the Sulu Sea, the Philippines. The present material extends its geographical range to southern Japan. Furthermore, this species is a common by-catch of the deep-sea commercial trawlers in Taiwan.

This study has shown that the sculpture of the carapace and abdomen of the species is generally similar in females, whereas it is rather variable in males. In females, teeth, tubercles, carinae and grooves on the carapace and body are distinct (Figs. 1B, 2B), whereas in males, these structures are frequently obsolete to faint (Figs. 1A, 2A), or occasionally as distinct as in females. Also, there seems to be a relationship between body color and degree of development of abdominal sculpture in this species. The coloration of females is always orange to orange brown (Fig. 4A). In males, however, those with distinct abdominal sculpture have a similar coloration as in females, although those with eroded sculpture have a much paler coloration (Fig. 4B), and those of intermediate sculpture have intermediate coloration. The holotype represents an example of variation with least developed body sculpture, with short longitudinal ridges on the anterior abdominal tergites completely eroded, and the median carina of the fourth abdominal tergite not interrupted (see Chace 1984:fig. 5). Although the least sculptured Taiwanese specimens still have some traces of short longitudinal ridges on the abdominal tergites (Fig. 1A) and a small notch on the median carina of the fourth abdominal tergite, the abdominal sculpture of the three larger specimens from the type locality Pratas Islands (similar to those shown in Figs. 1A, 2A) fit well within the range observed in the Taiwanese material. In addition, the coloration of the small Pratas male is very similar to that of some males from Taiwan (Fig. 4B, C). Therefore, it is concluded that the Taiwanese and South China Sea specimens are conspecific. Nevertheless, it seems that for similar size males, those from Taiwan are generally more sculptured than those from the South China Sea. Perhaps more specimens, particularly females, from the South China Sea, will provide better insights on the geographical variations of this species. In addition to the variability of the body sculpture, the material reported herein displays variation in other important features: the proportional length of the rostrum varies from 0.95 to 1.23 times as long as the carapace; the posterior pair of the lateral rostral teeth are sometimes barely discernible, as noted by Chace (1984), or are sometimes more prominent, showing as dentiform tubercles (Fig. 2B); the posterior fourth carina is usually interrupted at near the posterior end, and is rarely continuous.

As mentioned by Chace (1984), the elongate oval antennal scaphocerite, the configuration of the anterior fourth (lateral) carina, the long branchiostegal spine and the septate rostrum immediately separate *G. stenolepis* from most other species of the genus. Chace (1984) also noted that the juvenile or female paratype was different from the holotype in the more outstanding anterior tooth on the anterior fourth (lateral) carina, the more strongly lobate posterior first, second and third carinae, and the more strongly sculptured abdomen. Except for the sculpture of the abdomen, the present study found that those differences are constant between the paratype and the present material of *G. stenolepis*, not associated with growth as Chace suggested. The smallest specimen in the present material is a male of cl 9.2 mm from Taiwan, slightly larger than the paratype (cl 8.1 mm, USNM 205091). The smallest Taiwanese male has a well developed abdominal sculpture as in females, and the appendix masculina of the second pleopod is only slightly shorter than the appendix interna. Therefore, if the paratype belongs to the same species as the holotype, it should be a female. However, none of the abundant females examined in the present study show a prominent anterior tooth on the anterior fourth carina as in the paratype. In addition to above differences, the posterior part of the third abdominal somite is more strongly elevated in the paratype than in the holotype or all other specimens of *G. stenolepis.* These differences indicate that the paratype represents a different species. More material from the Sulu Sea is needed to determine the exact identity of Chace's (1984) paratype.

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A new stomatopod (Crustacea: Malacostraca) of the genus *Harpiosquilla* Holthuis, 1964 from Taiwan and Australia

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Abstract.—A new stomatopod, *Harpiosquilla ocellata*, is described from Taiwan and Australia. *Harpiosquilla ocellata* is closely related to *H. annandalei* (Kemp, 1911), but differs in bearing unarmed submedian carinae on the fifth abdominal somite and in reaching a much larger size. The two species closely resemble each other in color pattern, but differ in the markings of the telson and uropods.

The genus *Harpiosquilla* Holthuis, 1964, includes large squilloids bearing erect spines on the opposable margin of the propodus of the raptorial claw, and a deeply excavate posterolateral margin of the carapace. All species of *Harpiosquilla* are restricted to the tropical Indo-West Pacific and are associated with soft, level substrates. Manning (1995) recognized 11 species of *Harpiosquilla* and provided a key to the species. As part of ongoing study of the stomatopod faunas of Taiwan and Australia, we independently discovered a new species of *Harpiosquilla* from these two regions, which is described below.

Specimens are deposited at the National Taiwan Ocean University, Keelung (NTOU), The Taiwan Museum, Taipei (TMCS) and the Australian Museum, Sydney (AM). All measurements are in millimeters (mm). Terminology and size descriptors generally follow the conventions of Manning (1969b, 1977), supplemented by some abbreviations proposed by Makarov (1979). Total length (TL) is measured along the midline between the apex of the rostral plate and the apices of the submedian teeth of the telson. Carapace length (CL) is measured along the midline and excludes the rostral plate. Corneal index (CI) is given as 100CL/cornea width. Uropod segments are measured dorsally, along the midline. Dorsal carinae are abbreviated as follows: median (MD); submedian (SM); intermediate (IM); lateral (LT); and marginal (MG). The following abbreviations are also used: collector (coll.); antennule (A1), antenna (A2), abdominal somite (AS); thoracic somite (TS); maxilliped (MXP); Fisheries Research Vessel (FRV).

Systematic Account

Harpiosquillidae Manning, 1980
Harpiosquilla Holthuis, 1964
Harpiosquilla ocellata, new species

Figs. 1a–g, 2a–b.

Harpiosquilla annandalei.—Graham et al. 1993a:69; 1993b:73 [not *H. annandalei* (Kemp, 1911)].

Material examined.—Holotype. Taiwan, southwestern coast, Tong-Kong, Ping-Tong County, on sandy mud substrate, depth about 200 m, commercial trawler, 2 Dec 1995, male TL 157 mm (NTOU H-1995-12-2).

Paratypes. Taiwan: on sandy-mud substrate, depth about 200 m, commercial

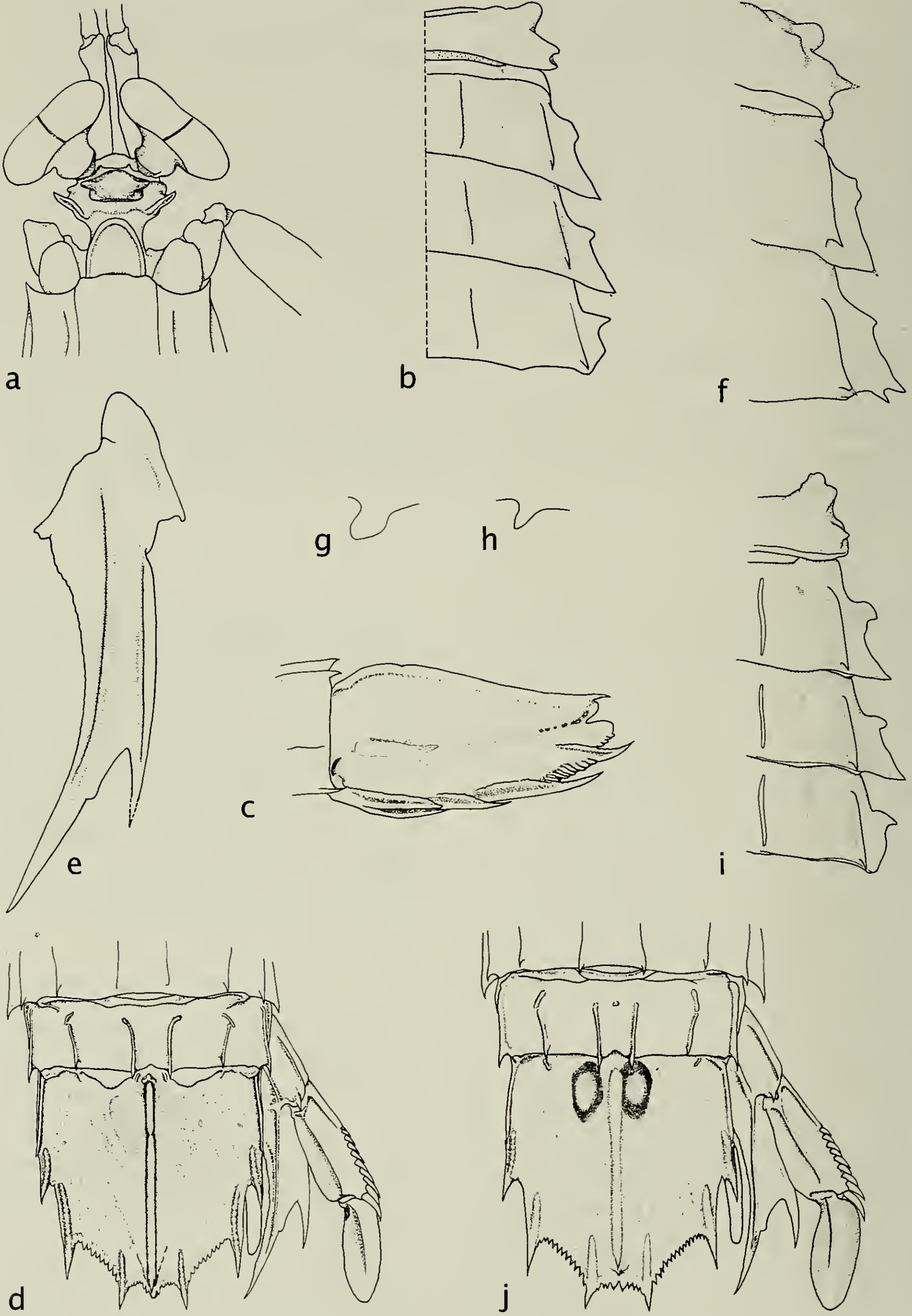

Fig. 1. a–g: *Harpiosquilla ocellata*, new species: a–e, holotype male, TL 157 mm, Taiwan, (NTOU H-1995-12-2); f. male, TL 159 mm, Australia (AM P41823); g. paratype male TL 200 mm, Taiwan (AM P51185). h–j: *H. annandalei* (Kemp. 1911): h–i, male, TL 111 mm. Taiwan (AM); j. male, TL 128 mm, Taiwan (NTOU). a. anterior cephalon; b, i TS5–8, right dorsal; c. telson, left lateral view; d, j. posterior abdominal somites and telson e. uropodal protopod, left ventral view; f. TS5–7 right dorsal; g, h. TS8 sternal keel, right lateral view.

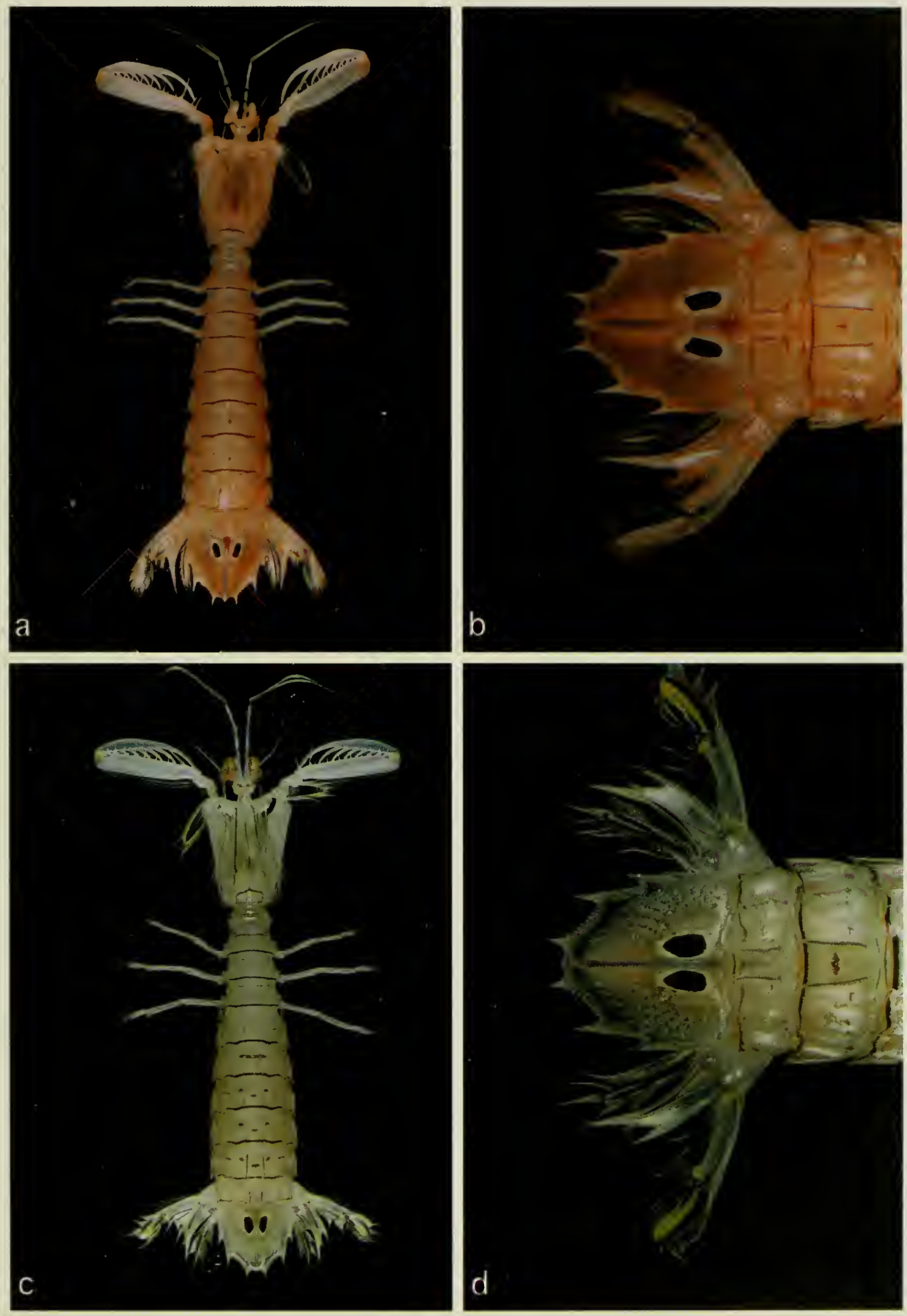

Fig. 2. a–b: *Harpiosquilla ocellata*, new species, male paratype, Taiwan; c–d: *H. annandalei* (Kemp, 1911), Taiwan. a, c. dorsal view; b, d. posterior abdominal somites and telson.

trawlers. Northeastern coast, Su-Aou, I-Lan County, 16 May 1991, 1 female TL 198 mm (TMCS-0103); 9 Nov 1995, 1 male TL 154 mm, 1 female TL 195 mm (NTOU P-1995-11-9), 1 male TL 155 mm (AM P51184).—Northeastern coast, Ta-Shi, I-Lan County, 25 May 1998, 1 female TL 176 mm (AM P53156).—Southwestern coast, Tong-Kong, Ping-Tong County, 26 Jan 1994, 1 female TL 232 mm (NTOU P-1994-1-26); 2 Dec 1994, 2 males TL 157–180 mm (NTOU P-1995-12-2); 5 Aug 1996, 1 male TL 197 mm (NTOU P-1996-8-5), 1 male TL 200 mm (AM P51185).

Other material. Australia: East of Port Hunter, Newcastle New South Wales, FRV Kapala, coll. K. Graham, [32°55′S, 151°57′], depth 72 m, 13 Apr 1992, 1 male TL 145 mm (AM P41785); [32°55′S, 151°57′], depth 65–72 m, 2 Nov 1995, 1 female TL 148 mm (AM P49681); [32°54′S, 151°59′E], depth 73 m, 5 Sep 1991, 1 male TL 159 mm (AM P41823).—East of Swains Reef, Queensland, commercial trawler, coll. J. K. Lowry & K. Dempsey [22°28.34′S, 152°59.45′E to 22°26.75′S, 153°09.17′E], depth 137 m, 8–9 Sep 1995, 4 females TL 171–206 mm (AM P49682-49685).

Diagnosis.—A1 peduncle longer than CL, but shorter than CL and rostral plate combined. Rostral plate apex broadly rounded, lacking anterior projection. Carapace with MD carina. Raptorial claw dactylus with 8 teeth. TS5 intermediate carina produced to a single short spine, directed laterally. TS6–8 (rarely only 7–8) with distinct SM and armed IM carinae. TS8 sternal keel broad with angular apex, inclined posteriorly. AS1–6 SM carinae distinct. Abdominal carinae spined posteriorly as follows: SM 6; IM 1–6; LT 1–6; MG 1–5. Telson MG carina approximately twice length of carina of lateral tooth; MD carina with pair of large, dark, white-margined "eye spots" proximally. Exopod of uropod with distal segment black on inner half only.

Description.—TL of adults to 232 mm. Dorsal surface lightly pitted.

Eye large, cornea strongly bilobed; CI 278–362 (294–311 in Taiwanese material, 278–336 in Australian material). Ophthalmic somite with anterior margin broadly rounded.

A1 peduncle 0.99–1.07 CL, but shorter than CL and rostral plate combined. A1 somite with slender dorsal processes, with acute apices, directed anterolaterally. A2 scale length 0.71–0.80 CL.

Rostral plate slightly broader than long; apex broadly rounded; margins convex; lacking anterior projection or dorsal carina.

Carapace anterior width 0.40–0.45 CL; anterolateral spines not extending to base of rostral plate; with MD, IM, LT and MG carinae; MD carina distinct, lacking branches of anterior bifurcation; posterior margin medially concave.

Raptorial claw dactylus with 8 teeth; outer margin broadly curved, slightly angular in adult males; propodus opposable margin with 1–2 smaller spines and several minute denticles between largest spines.

Mandibular palp 3-segmented. MXP1–5 with subcircular epipod. MXP5 basal segment unarmed.

Pereiopods 1–3 basal segment unarmed; endopod 2-segmented, distal segment styliform.

TS6–8 (rarely only 7–8) with distinct, divergent SM and armed IM carinae.

TS5 intermediate carina produced to a single short spine, spinular or triangular, directed laterally; ventral spine triangular, directed anteroventrally.

TS6–7 lateral process bilobed; anterior lobe very small and low, apex blunt; posterior lobe broad and triangular, apex acute or secondarily bifurcate.

TS8 anterolateral angle triangular; sternal keel broad with angular apex, inclined posteriorly.

AS1–6 with normal complement of carinae; SM carinae distinct, subparallel or faintly divergent. AS6 posterior margin faintly crenulate adjacent to submedian spines; with sharp ventrolateral spine anterior to uropodal articulation. Abdominal carinae spined as follows: SM 6; IM 1–6; LT 1–6; MG 1–5.

Telson longer than broad; submedian, intermediate and lateral teeth slender, with tuberculate dorsal carinae and apices deflected dorsally. MG carina approximately twice length of carina of lateral tooth. Submedian and intermediate denticles triangular; some apices spiniform; lateral denticle rounded. Denticles: 5–9, 9–15, 1. MD carina high, uninterrupted proximally; posteriorly armed with short apical spine overhanging several blunt tubercles; with pair of large, dark, white-margined "eye spots" proximally. Telson dorsolateral surface rugose, with curved rows of very shallow pits. Telson ventral surface with tuberculate postanal carina, extending half distance between anus and posterior margin.

Uropod protopod with small, flattened, ventral lobe anterior to endopod articulation; inner margin crenulate. Terminal spines of uropod protopod with blunt lobe on outer margin of inner spine, margin concave. Uropod exopod proximal segment outer margin with 8–9 (usually 9) graded movable spines, distalmost longest, not exceeding midlength of distal segment; distal margin with stout ventral spine. Uropod exopod distal segment slightly longer than proximal segment; black on inner half only.

Color in life.—(Fig. 2a, b) Eye with cornea metallic green. Overall dorsal color light golden brown. Second and third segments of A1 peduncle with one proximal and one distal black spot. Black transverse bar present between A1 and ophthalmic somites. Carapace with anterolateral and posterior margins, carinae and grooves outlined in dark pigment. Merus of raptorial claw with inner distal black spot and yellow meral depression. Propodus of raptorial claw yellow distally. Posterior margin of thoracic and abdominal somites black. AS2 with black median transverse bar. AS1 and AS3–5 with traces of broken transverse bar. SM carinae of thoracic and abdominal somites pale purple. Telson with pair of large, dark, white-margined, "eye spots" proximally; MD carina and carinae of marginal teeth maroon. Spines of uropodal protopod pinkish. Uropodal endopod yellowish, blackish distally. Uropodal exopod distal segment yellow on outer half and black on inner half.

Size.—Taiwanese material: males ($n = 7$) TL 154–200 mm; females ($n = 4$) TL 176–232 mm. Australian material: males ($n = 2$) TL 145–159 mm; females ($n = 5$) TL 148–206 mm.

Etymology.—Latin, *ocellata*, marked with spots, from *ocellus*, diminutive of *oculus*, eye, in allusion to the large, eye-like pigment spots of the telson.

Remarks.—With the exception of *Harpiosquilla annandalei* (Kemp, 1911), *H. ocellata* can be immediately distinguished from all known species of the genus by the combination of the short, apically rounded rostral plate and armed IM carinae of the exposed thoracic somites (Fig. 1b, f, i).

This new species closely resembles *H. annandalei* in most characters, including coloration. Comparison of *H. ocellata* with the accounts of *H. annandalei* in Manning (1969a, 1995) and 20 Taiwanese specimens in the collections of the NTOU (2 specimens transferred to AM) show the following differences between the two species: in *H. ocellata* the SM carinae of AS5 are unarmed (Fig. 1d) whereas they are always armed in *H. annandalei* (Fig. 1j); in *H. ocellata* the TS8 sternal keel is broad with an angular apex (Fig. 1g) whereas in *H. annandalei* the keel is hooked (Fig. 1h); *H. ocellata* attains a much larger size (TL to 232 mm) than *H. annandalei* (TL to 150 mm (Manning, 1969a), and to TL 130 mm in the 20 Taiwanese specimens examined). Although coloration of the two species is very similar, the body of *H. annandalei* is generally lighter, the margins of the "eye spots" on the telson of both the white and black circles are more sharply defined (Fig. 2c, d) and the MD carina of the telson is colored like the rest of the telson. In contrast, the body of *H. ocellata* is light golden brown, the margins of the "eye spots" are somewhat diffuse, and the MD carina of the telson is purplish (Fig. 2a, b). In addition, in *H. annandalei* the distal segment of the uropodal exopod is blackish with a yellowish madrib (Fig. 2d), whereas it is blackish on the inner half and yellowish on the outer half in *H. ocellata* (Fig. 2b). Although, *H. ocellata* could easily be confused with *H. annandalei*, the aforementioned differences will readily separate the two species.

Secondary sexual dimorphism is much less evident in *H. ocellata* than most other species of the genus. As in *H. annandalei*, the margins of the telson and MD carina are not inflated, the outer margin of the dactylus of the raptorial claw is faintly sinuous and the bases of the dactylar teeth are only slightly inflated.

Meristic counts and corneal indices overlap between Taiwanese and Australian material. Only minor morphological differences were noted between Taiwanese and Australian material of *H. ocellata.* Thus, the apices of the posterior lobes of the lateral processes of TS6–7 usually terminate in an acute spine, but are secondarily bifurcate in two specimens from Australia, resembling the condition reported by Manning (1969a) for some specimens of *H. annandalei.* In all Australian specimens, the IM carinae of TS6–8 are armed posteriorly, whereas in three of the 11 Taiwanese specimens, the IM carinae of TS6 are unarmed. Nevertheless, TS7–8 are armed in all Taiwanese specimens.

The precise habitat of *H. ocellata* is unknown although all material was taken on sand and mud substrates with benthic trawls. *Harpiosquilla ocellata* is presently known only from Taiwan and eastern Australia in relatively deep water. This, apparently disjunct distribution, likely reflects sampling effort but may also result from confusion of *H. ocellata* with *H. annandalei* by previous workers, especially in preserved material lacking pigmentation. Further, the bathymetric range of *H. ocellata* (63 to about 200 m) coincides with that reported by Manning (1969a) for *H. annandalei* (15–206 m).

Distribution.—Western Pacific. Known with certainty from Taiwan (eastern and southern coasts) and eastern Australia (central Queensland south to the Newcastle Bight, New South Wales) at depths of 63 to about 200 m, on soft substrata.

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A new species of the genus *Bellator* (Pisces: Triglidae), with comments on the trigloids of the Galápagos Islands

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Abstract.—A new, endemic species, *Bellator farrago*, is described from the Galápagos Islands. It differs from its congeners by a combination of characters including absence of a supplemental preopercular spine, short first dorsal fin spine, produced rostral spines, and lack of scales on the breast and interpelvic area. The Galápagos trigloid fauna comprises: *B. farrago*, *Prionotus miles*, *Pr. stephanophrys*, and *Peristedion crustosum.*

The fishes of the New World genus *Bellator* were revised by Miller & Richards (1991); they treated four Atlantic species and three eastern Pacific species. Recent collecting in and around the Galápagos by the submersible *Johnson Sea-Link* revealed the presence of an undescribed species. The submersible captured one specimen and another was found in the California Academy of Sciences Fish Collection. Prior to this study only one *Bellator* was known from the Galápagos based on Gruchy (1970), who added *Prionotus loxias* (=*Bellator loxias*) to the Galápagos fauna. A re-examination of the Gruchy specimens reveals that they also are this undescribed species and not *B. loxias.* This new species is diagnosed and described, and details of its habitat are provided based on observations made from the submersible. The submersible also captured three specimens of *Peristedion crustosum* Garman which is a new record of this species from the Galápagos.

Methods.—Counts and measurements follow Miller & Richards (1991).

Bellator farrago, new species
(Figs. 1–3, Tables 1–3)

[non] *Prionotus loxias:* Gruchy 1970:526 (misidentification). Miller & Richards 1991:646 (distribution, following Gruchy 1970). Bussing 1995:1646 (distribution).

Material examined.—Holotype: CAS 54562 (103.9 mm SL), southeastern Pacific, Ecuador, Galápagos Islands, Isla Santa Cruz, Academy Bay, R/V *Te Vega* Field No. TV24-VIII-68. 24 Aug 1968. Paratypes: CAS 86564 (96.2 mm SL), southeastern Pacific Ocean, Ecuador, Galápagos Islands, Isla Genovesa (Tower). 0°21.8′S, 89°58.2′W, JSL dive 3974, 462 m, coll. J. E. McCosker et al., 24 Nov 1995. NMC 69-78, 2 (75.5–112.4 mm SL), southeastern Pacific Ocean, Ecuador, Galápagos Islands, Isla Isabella, mouth of Tagus Cove, coll. Barr et al. 8 Mar 1968.

Diagnosis.—A species of *Bellator* with opercular spine short, breast and interpelvic area lacking scales, belly scaled, first dorsal spine shorter than second, supplementary preopercular spine weak or absent, anal rays 11, pored lateral line scales 50–52.

Description.—Morphometric data are in Table 1, meristic data in Table 2, and comparison with other eastern Pacific *Bellator* in Table 3. Head moderate with produced rostrum with small spines on distal edge; small spines on lateral edge of first, second, and third infraorbital bones; no nasal spine,

Fig. 1. Lateral view and dorsal view of head of *Bellator farrago*, new species, paratype CAS 86564, 96 mm SL. Illustration by Molly Brown.

although all head bones with very small spines giving rough texture; prominent spines on anterior and posterior edge of orbit; prominent nuchal, parietal, opercular and preopercular spines, but supplemental preopercular spine absent in three specimens and very weakly developed in one. Cleithral spine short, not prominent. First spine of the first dorsal fin shorter than second spine, serrate anteriorly. Base of first ray of second dorsal fin with serrate anterior edge. Teeth present on premaxillaries, dentaries, head of vomer, extending posteriorly from head of vomer on palatines. Nape, prepectoral area, opercle, breast, interpelvic area scaleless. Belly with scales. Lateral line with 50–52 scales bearing pores, body scales small, with cteni, with 10 rows above the lateral line and 24–34 rows below. Gill rakers on first arch include small rudiments on epibranchial and hypobranchial with short rakers on epibranchial and ceratobranchial (Table 2). First dorsal, second dorsal and anal fins with 11 elements each. Pectoral fin with 12–13 connected rays, 3 free rays. (Connected pectoral rays difficult to count.) Vertebrae 26 (9 + 17 on holotype and paratype CAS 86564). Swimbladder with extrinsic and intrinsic musculature. One papilla present on each eye at one o'clock on the following specimens: CAS 86564, NMC 69-78 (right eye only of 112.4 mm SL specimen). No papillae on eyes of holotype. Mandible with flat ridge about ⅔ its length.

Coloration.—Two prominent dark saddles below each dorsal fin and less distinct dark area on dorsal surface of caudal peduncle. Small, irregular, dark spots on dorsal surface of head. Dark areas on margin of interspinous membrane of first dorsal fin; dark margin on anterior edge of membrane of second dorsal fin. Trunk area below lateral line, and anal and caudal fins lack any dark areas, being basically pale. Pectoral fin with middle rays dark from base to tip. From color photograph of a specimen approximately 1 hour after death (Fig. 2): specimen bright red with dorsal saddles appearing as deep red, margin of first few interspinous membranes of first dorsal black, as well as ventral edge of caudal peduncle extending onto lower caudal rays. Dorsal fins and anal fin red with scattered yellow

Figs. 2–3. 2, Photograph of a paratype of *Bellator farrago*, new species (CAS 86564), taken approximately one hour after death. 3, Photograph of *Peristedion crustosum* taken form submersible *Johnson Sea-Link* at 486 m, seamount SE of Isla San Cristobal, Galápagos.

spots on second dorsal fin. Dark spots not visible on head but faint indication of yellow spots. Medial rays of caudal also yellowish. Pectoral fin with black medial rays extending to tip. Lower flank and bottom of head white.

Etymology.—From the Latin *farrago*, a medley or mixture, in reference to the new species' combination of its congeners' characters, here considered a noun in apposition.

Discussion.—This new species is endem-

Table 1.—Morphometric characters of *Bellator farrago,* new species.

	Specimens							
	CAS 54562		CAS 54564		NMC 69-78		NMC 69-78	
Character	(mm)	%SL	(mm)	%SL	(mm)	%SL	(mm)	%SL
Standard length	103.9		96.2		112.5		75.5	
Head length	37.5	36.1	33.7	35.0	38.8	34.5	24.8	32.8
Rostral length	3.1	3.0	2.8	2.9	1.9	1.7	2.1	2.8
Rostral width	4.0	3.8	3.9	4.1	3.6	3.2	3.1	4.1
Snout length	16.5	15.9	15.8	16.4	14.3	12.7	9.3	12.3
Premaxillary length	15.5	14.9	12.7	13.2	15.3	13.6	9.8	13.0
Orbit length	10.4	10.0	8.3	8.6	11.3	10.0	7.0	9.3
Orbit depth	10.9	10.5	7.5	7.8	11.6	10.3	6.0	7.9
Interorbital width	3.9	3.8	3.8	4.0	4.9	4.4	3.8	5.0
Cheek height	8.7	8.4	8.5	8.8	8.9	7.9	5.6	7.4
Opercular spine length	10.1	9.7	9.8	10.2	11.3	10.0	7.2	9.5
Preopercular spine length	9.9	9.5	9.0	9.4	9.2	8.2	7.2	9.5
Cleithral spine length	8.3	8.0	7.9	8.2	7.6	6.8	7.0	9.3
1st Dorsal spine length	8.3	8.0	8.2	8.5	10.4	9.2	8.0	10.6
2nd Dorsal spine length	13.3	12.8	12.2	12.7	13.2	11.7	10.5	13.9
3rd Dorsal spine length	14.4	13.9	13.8	14.3	17.3	15.4	11.2	14.8
2nd Dorsal fin base length	25.5	24.5	25.7	26.7	28.4	25.2	18.5	24.5
Anal fin base length	30.9	29.7	29.3	30.5	33.2	29.5	22.6	29.9
Pectoral fin length	34.7	33.4	31.8	33.1	34.5	30.7	24.2	32.1
1st Free pectoral ray length	32.8	31.6	24.2	25.2	32.5	28.9	19.1	25.3
2nd Free pectoral ray length	28.1	27.0	21.5	22.3	28.6	25.4	16.9	22.4
3rd Free pectoral ray length	25.4	24.4	19.0	19.8	24.5	21.8	13.2	17.5
Pelvic fin length	30.6	29.5	28.1	29.2	32.2	28.6	21.9	29.0
Body depth	28.9	27.8	23.6	24.5	27.2	24.2	19.1	25.3
Least depth of caudal peduncle	7.3	7.0	7.1	7.4	8.4	7.5	6.1	8.1
Gill raker length	2.8	2.6	2.4	2.5	4.4	3.9	1.8	2.4
Snout angle (degrees)	43.0		28.0		34.0		33.0	

Table 2.—Meristic characters of *Bellator farrago* new species.

	Specimens			
Character	CAS 54562	CAS 54564	NMC 69-78	NMC 69-78
Std. length (mm)	103.9	96.2	112.5	75.5
1st Dorsal fin rays	11	11	11	11
2nd Dorsal fin rays	11	11	11	11
Anal rays	11	11	11	11
Pectoral fin rays	13+3	12+3	12+3	12+3
Gill rakers				
Epibranchials	2r	2r	1+1r	1+1r
Ceratobranchials	7+3r	10+1r	10	10
Hypobranchials	3r	3r	3r	3r
Total gill rakers	7	10	11	11
Squamation				
Lateral line scales	52	52	52	50
Scale rows above lateral line	10	9	10	10
Scale rows below lateral line	30	27	34	24

Table 3.—Characters for distinguishing the eastern Pacific species of *Bellator.*

	Species			
Characters	*gymnostethus*	*loxias*	*xenisma*	*farrago*
Supplemental preopercular spine	present	absent	present	absent
First dorsal spine	shorter than 2nd	longer than 2nd	longer than 2nd	shorter than 2nd
Breast & interpelvic area	naked	scaled	scaled	naked
Rostral spines	produced	not produced	produced	produced

ic to the Galápagos Islands and is easily distinguished from its congeners. Its possesses character states present in other Pacific *Bellator* (see Table 3); however, in combination it differs from each. Its coloration is most like that of *B. loxias* Jordan (in Gilbert 1896) and it has a similar but notably different preopercular spine condition, but differs in squamation and rostral spine condition. The new species' reduced first anterior dorsal spine is like that of *B. gymnostethus* Gilbert 1891, from which if differs in its coloration and preopercular spine condition. *Bellator farrago* is similar to *B. xenisma* (Jordan & Bollman, 1890) in coloration and in its rostral spine condition, but differs in its preopercular spine state, its first dorsal spine condition, and in lacking scales on the breast. Its exact relationship to other species of *Bellator* cannot be determined at this time as character polarity for the genus has not been developed nor have cladistic analyses been made. It is premature to speculate further.

A paratype of the new species (CAS 86564) was collected by the junior author while aboard the submersible (JSL). It was captured using the submersible's suction device and photographed at the surface soon after its death (Fig. 2). The water depth at the collection site was 462 m, temperature 8.58°C, and the bottom was largely black volcanic rock overlain with sand patches and small boulders partially encrusted with a thin cover of stony corals and sponges.

As a result of our studies, we conclude that the Galápagos trigloid fauna comprises: *Bellator farrago, Prionotus miles*, and *Pr. stephanophrys* of the family Triglidae and *Peristedion crustosum* Garman, 1899 of the Family Peristediidae. As stated in the introduction, the previous record of *B. loxias* (as *Prionotus loxias*, Gruchy 1970) from the Galápagos was based on material which we describe herein as *B. farrago. Bellator loxias* reaches offshore to the Cocos Island area as noted by Bussing (1995) and a specimen collected by the *Albatross* (MCZ 30779, 81.0 mm SL) which was identified by the senior author. The species of *Prionotus* reported from the Galápagos also deserve explanation. *Prionotus miles* Jenyns, 1842 is an endemic species and has been captured at several locations throughout the islands. Galápagos records of *P. albirostris* Jordan & Bollman (1890) (Gruchy 1970, Bussing 1995, Grove & Lavenberg 1997) are based on misidentifications of *P. stephanophrys* Lockington (1881), as confirmed by the senior author after examination of Gruchy's specimens. Other erroneous records of Galápagos triglids are explained by Gruchy (1970:526): including Jordan & Evermann's (1896:2172) listing of *P. horrens* Richardson (1845) from Galapagos and Teague's (1951:26) mistake in listing the type locality of *P. quiescens* Jordan & Bollman (1890) as the Galápagos Islands rather than the Gulf of Panama.

Grove & Lavenberg (1997:302–303) reported upon a poorly preserved specimen (LACM 20838, 138.5 mm SL) of *Peristedion crustosum* Garman 1899 taken off Daphne Minor, Galápagos, in 1938 by the Allan Hancock Expedition. They suggested that "*Peristedion crustosum* may prove to be a mainland species, which would make the population in the Galápagos a new species." Four specimens of *Peristedion* were collected by the junior author on JSL dives and after comparison with the type material of the two eastern Pacific *Peristedion* by the senior author, we find that the JSL specimens are *P. crustosum.* The specimens are: CAS 86565, 151.6 mm SL, Galápagos Islands, Isla Genovesa (Tower Island), 0°21.8′S, 89°58.2′W, JSL Dive 3974, sand bottom strewn with small volcanic rocks, 372 m; and CAS 86562, 103.1 and 108.8 mm SL, Galápagos Islands, 1°06′S, 89°12.2′W, seamount SE of Isla San Cristobal, JSL Dive 3934, volcanic rock and boulder bottom with sand channels, 486 m (Fig. 3). Other specimens were observed at Isla Fernandina, off Cabo Douglas (JSL Dive 3957, 0°17.5′S, 91°38.9′W), at 431 m resting on a 60° sand slope, and off Isla Floreana (JSL Dive 3944, 1°13′S, 90°23′W), above a flat sand bottom at 305 m, the single specimen collected and deposited at the Instituto Nacional de Pesca in Quayaquil.

Collection records for both species of *Peristedion* are unknown other than the material upon which Garman based his original description. *Peristedion crustosum* was illustrated by Garman in color, but the other species, *P. barbiger*, was not. The two species can be easily separated by the nature of the chin and lip barbels and rostral spine shape. In *P. barbiger* the barbels are unusually thick and closely spaced giving a thick bearded appearance. In *P. crustosum* the barbels are slimmer and fewer in number. *Peristedion crustosum* has a well developed nasal spine but this spine is weak or absent in *P. barbiger.* The striking difference is the form of the rostral spines. In *P. crustosum* these spines project forward nearly parallel, wherein *P. barbiger* these spines project forward in a convergent direction, though their tips do not touch. There were indications of thickening of these bones which possibly could be hyperostosis, a condition found in a few trigloid fishes.

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A new species of *Polyipnus* (Teleostei: Stomiiformes) from the western Indian Ocean, with comments on sternoptychid ecology

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Abstract.—*Polyipnus limatulus* is described based on material collected in the Gulf of Aden and immediately adjacent areas of the northwestern Indian Ocean. These collections were made during midwater fish surveys conducted from three vessels, R/V *Beinta* (1987), R/V *Malcolm Baldridge* (1995), and R/V *Tyro* (1992). Like other species in this genus *P. limatulus* appears to occur in association with the continental slope and/or various types of sea floor rises. *Polyipnus limatulus* shares certain apomorphic characters with the *P. spinosus* species group; among these are a multispinose posttemporal, and the occurrence of numerous spine-like denticles on the modified scales covering many of the ventral photophores. These denticles are lacking on the ACB photophore scales, a character which distinguishes the new species from a putatively closely related species, *P. asper* (eastern Indian ocean). *Polyipnus indicus* (western Indian Ocean) has somewhat similar scale denticulation but has a relatively unmodified parietal, among other differences. The new species was found to occur in relatively warm, saline, low oxygen water associated with Red Sea outflow, whereas the other *Polyipnus* species collected during the R/V *Tyro* survey, *P. omphus* Baird, 1971 was collected in the colder, less saline, higher oxygen water associated with the Somali Current.

The Stomiiformes are mainly meso- and bathypelagic fishes, found in all oceans but more diverse in the tropics and subtropics (Harold & Weitzman 1996, Harold 1998). Among the Sternoptychidae or hatchetfishes one genus in particular, *Polyipnus*, contains more species than any of the other nine genera in the family (Weitzman 1974, Harold 1994). *Polyipnus* has been the subject of several revisionary studies (Schultz 1938, 1961, 1964; Baird 1971; Borodulina 1979; Harold 1994) and a series of recent species descriptions (Harold 1989, 1990a; Aizawa 1990; Last & Harold 1994). The most diverse clade of this genus, the *Polyipnus spinosus* species group, was phylogenetically diagnosed by Harold (1994:455–458) and at that time contained 14 named species. More recently, Last & Harold (1994) described *P. latirastrus* from the Coral Sea and added it to the group, based on the presence of synapomorphies proposed by Harold (1994).

We describe here a new species belonging to *Polyipnus*, based on collections made in the Gulf of Aden and vicinity by three vessels, R/V *Beinta* (January and March 1987), R/V *Malcolm Baldridge* (August 1995), and R/V *Tyro* (August 1992 and January 1993, as part of the Somali Ecosystem Study [SES], Netherlands Indian Ocean Program [NIOP]). A total of 192 specimens were examined, ranging in standard length from 6.5 to 45.7 mm. For the first time a reasonably complete series of larval through adult specimens is available for a species of the *P. spinosus* species group and we therefore illustrate and briefly describe the larva.

Materials and Methods

Specimen body size is standard length (SL) in all cases. Morphometric, meristic, photophore and other characters were determined following the methods and terminology of Harold (1994). Values for the holotype are given in parentheses in the description. Terminology of the photophores is repeated here for convenience, and because the terms now in use replace those of Schultz (1961) that occur in much of the sternoptychid literature. The abbreviation for each photophore cluster and its verbal descriptor, as defined by Schultz (1961), are given in parentheses: ACA (SAN, supra-anal), ACB (AN, anal), ACC (SC, subcaudal), BR (BR, branchiostegal), IP (IS, isthmus), L (L, lateral), OP (PRO, preopercular + SO, subopercular + PTO, postorbital), ORB (PO, preorbital), OVA (SP, suprapectoral), OVB (SAB, supra-abdominal), PV (AB, abdominal), and VAV (PAN, preanal). Specimens were cleared and counterstained for bone and cartilage following the methods outlined by Pothoff (1984) and Taylor and Van Dyke (1985). Observations on osteology and dentition of *P. limatulus* were based on two cleared and stained adult specimens (USNM 345149, 31.8–38.0 mm SL). Institutional abbreviations are as listed in Leviton et al. (1985).

Acronyms used for various "Subareas" of the Somali Ecosystem Study are defined as follows: GAD (Gulf of Aden), between 12°20′ and 12°45′N, 38°08′ and 50°05′E; SWL (Great Swirl, an eddy created by the Somali Current), between 6°10′ and 12°05′N, 53°40′ and 55°00′E; USI (Upper Somali Current Inshore), between 7°30′ and 10°50′N, 50°21′ and 52°05′E; LSI (Lower Somali Current Inshore), between 0°06′ and 3°22′N, 44°56′ and 48°26′E; LSO (Lower Somali Current Offshore), 1°55′N, 53°34′E, represented by a single station.

Ecological comparisons were made between *P. limatulus* and other sternoptychids with which it was collected. A mathematical formula, the "weighted hydrographic index" (modified, after Wessel 1997) was used to summarize hydrographic conditions with which each species is associated. The analysis is based on 17 hauls of a rectangular midwater trawl.

Weighted hydrographic index.—To allow comparisons between species, hauls, stations, subareas, day/night occurrence and season, a weighted hydrographic index was devised to best represent the average conditions of capture for specimens of a given species under stated capture criteria (e.g., day vs. night; summer vs. winter). Construction of this index involved two steps: computation of an integrated average for each hydrographic parameter for each discrete depth segment sampled, and combination of this average with proportionate capture information for each species for each set of capture criteria. The hydrographic average was constructed as the integral average of the hydrocast data within each sampling depth segment by the method of trapezoidal approximation, evaluated for all hydrographic data points (up to N = 9 discrete values) within a sampling segment (i.e., one "haul"), such that:

$$V_x = \sum_{i=1}^{N} \left(\left(\left(\frac{|V_{i+1} - V_i|}{2} \right) + V_L \right) \times \left(\frac{D_{i+1} - D_i}{D_z - D_1} \right) \right)$$

where

V_x = computed integral average for a given hydrographic parameter (temperature, salinity, dissolved oxygen, etc.) for a given haul segment.

V_{i+1}, V_i = two sequentially successive measurements of that value within that segment.

V_L = the smaller of the two values, V_{i+1} or V_i, for each comparison.

D_{i+1}, D_i = depth at which the two measurements, V_{i+1}, V_i, respectively, was made; where $D_{i+1} > D_i$.

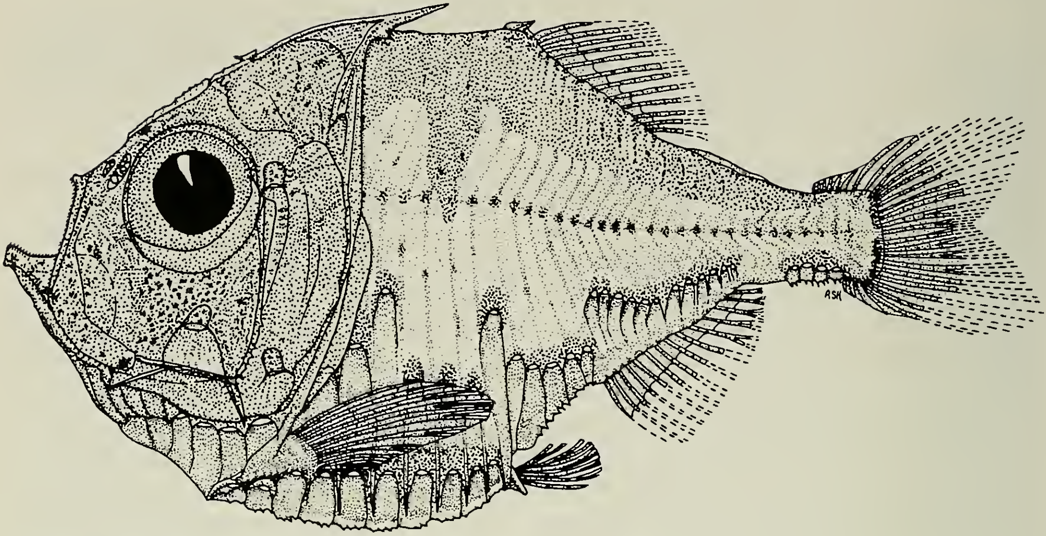


Fig. 1. *Polyipnus limatulus*, holotype, USNM 316316, 39.0 mm SL.

D_1 = shallowest depth of measurement for segment.

D_z = deepest depth of measurement for segment.

Comparisons between species (for given evaluation criteria) were then facilitated by weighting the integral average of the hydrographic values for each haul (successful in capturing the species) by proportionate capture of the species over all hauls successful in capturing the species, such that, for species A:

$$INV_A = \frac{\sum_{i=1}^{H} \left(V_{A_i} \times \frac{n_i}{N} \right)}{N}$$

where

INV_A = weighted hydrographic index for species A, as restricted by preset criteria (e.g., day vs. night, summer vs. winter).

H = number of hauls in which species A was captured.

V_{A_i} = integral average of hydrographic value for haul i.

n_i = number of specimens of species A taken in haul i.

N = total number of specimens of species A taken in all (=H) hauls.

Polyipnus limatulus Harold & Wessel, new species

Figs. 1–4, Tables 1 & 2

Polyipnus cf. *indicus* Harold, 1994:437, 450, 511 (USNM 293986, 301277, 316316; fig. 16B, pectoral girdle morphology).

Type material.—Holotype: USNM 316316, (1, 39.0 mm), 11°12′12″N, 47°57′30″E, (0-)315 m, R/V *Beinta*, Cr. 18, Sta. 4, 8 Jan 1987. Paratypes: MCZ 150026, (1, 28.5 mm), 14°05′00″N, 50°42′36″E, 0–1000 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-50 (1), 9 Aug 1995. MCZ 150036, (1, 27.4 mm), 14°05′00″N, 50°42′36″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-50 (4), 9 Aug 1995. USNM 293986, (3, 42.6–45.7 mm), 12°01′00″N, 51°16′36″E, (0-)375–393 m, R/V *Beinta* Cr. 20, Sta. 18, 1600 h, 12 Mar 1987. USNM 301277, (5; 2, 26.4–31.8

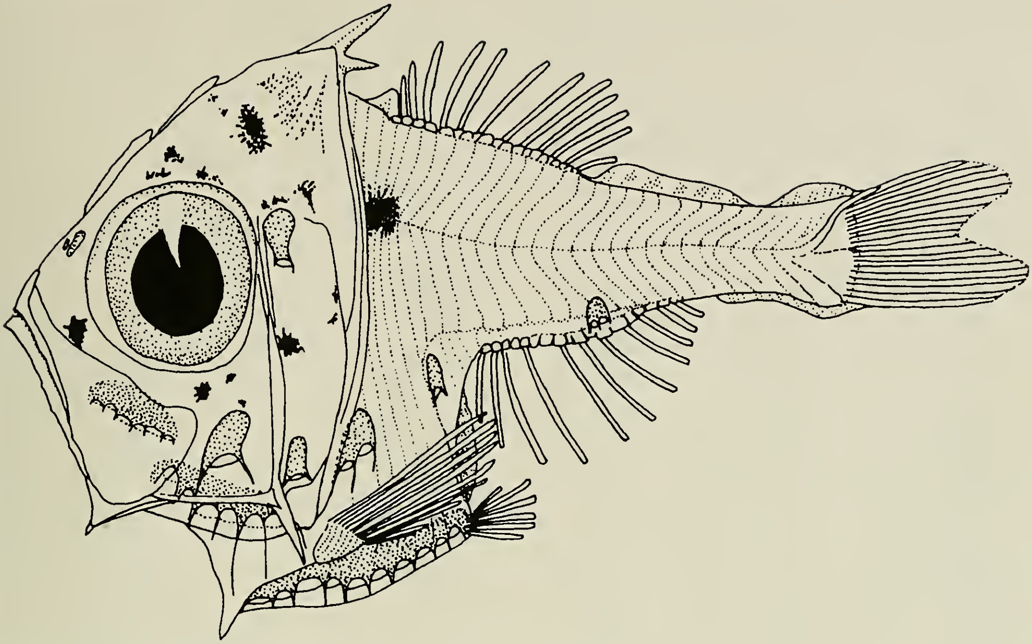


Fig. 2. *Polyipnus limatulus*, larva, MCZ 150024, 6.5 mm SL.

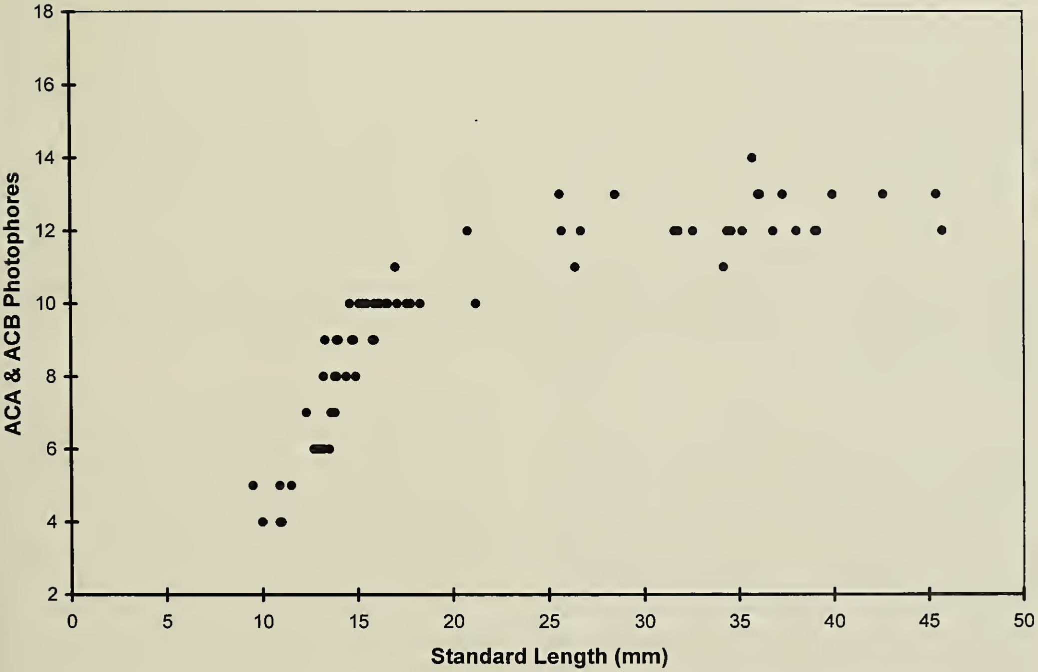


Fig. 3. Plot of ACA + ACB photophore count (combined) versus SL for *Polyipnus limatulus*.

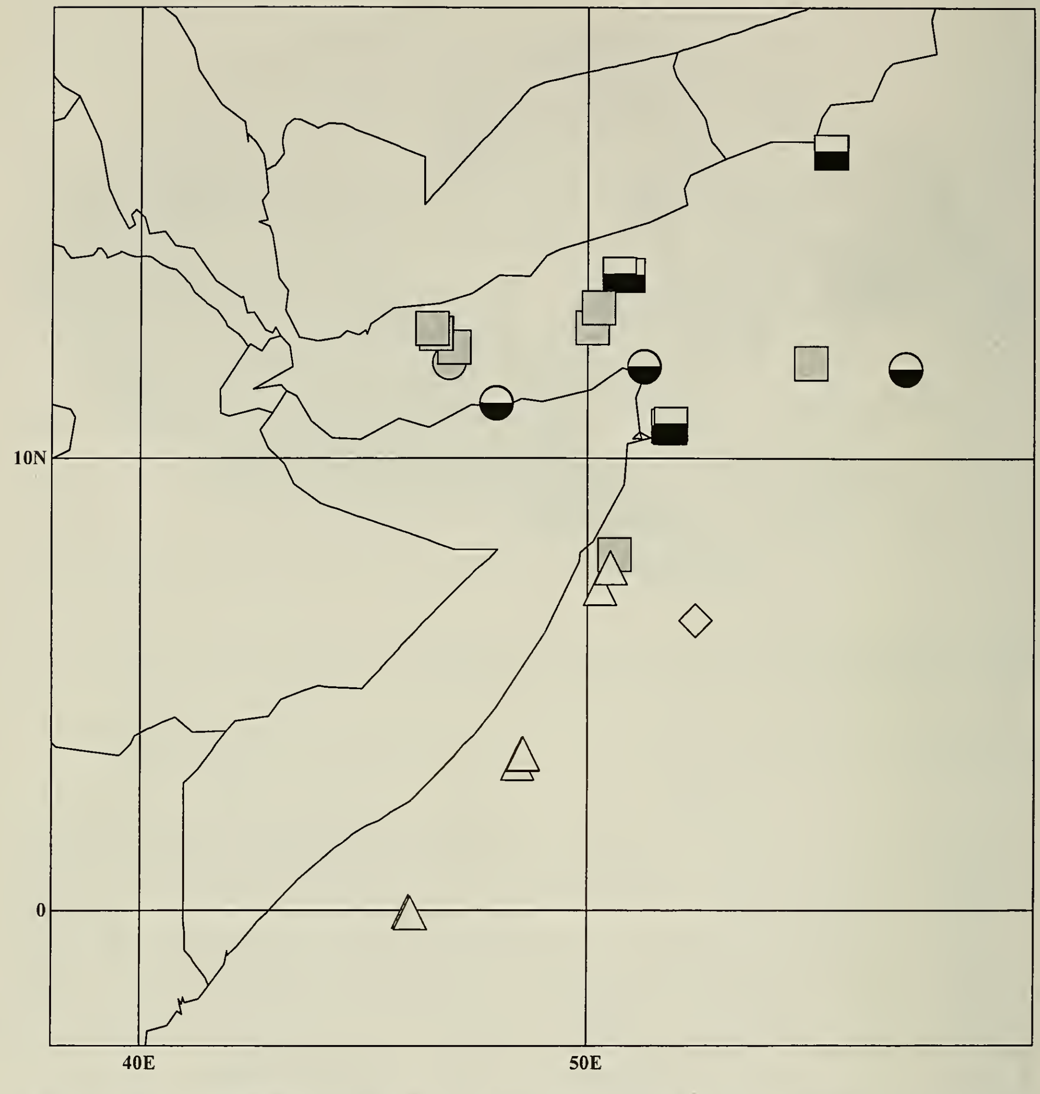


Fig. 4. Map of northwestern Indian Ocean, off east Africa, showing collection stations of *Polyipnus limatulus. Polyipnus limatulus:* half-filled circle = R/V *Beinta* stations, half-filled square = R/V *Malcolm Baldridge* stations, shaded circle = R/V *Tyro* cruise B1 stations (summer), shaded square = R/V *Tyro* cruise B2 stations (winter). *Polyipnus omphus:* open triangle = R/V *Tyro* cruise B1 stations (summer), open diamond = R/V *Tyro* cruise B2 stations (winter).

mm), 11°57′30″N, 51°07′30″E, (0-)366 m, R/V *Beinta*, Cr. 20, Sta. 11, 11 Mar 1987. USNM 345149, (56; 14, 32.6–39.9 mm; 2 cleared and stained, 31.8–38.0 mm), collected with holotype. ZMA 121.797, (3, 26.7–31.6 mm), 12°07′00″N, 46°54′00″E, 202–300 m, *Tyro*, Cr. B1, Seq. 582, Sta. GA2, 2304–2353 h, 5 Aug 1992. ZMA 121.798, (2, 25.6–25.7 mm), 12°46′00″N, 46°36′36″E, 200–300 m, *Tyro*, Cr. B2, Seq. 1129, Sta. GA2, 2134–2244 h, 29 Jan 1993.

Non-type larval material: MCZ 150020, (4), 16°46′24″N, 55°27′00″E, 0–1000 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-48 (1), 7 Aug 1995. MCZ 150021, (1), 16°46′24″N, 55°27′00″E, 500–300 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10–48 (3), 7 Aug 1995. MCZ 150022, (2),

Table 1.—Morphometric characters expressed as percentages of head length (2 to 6) or standard length (all others) for *Polyipnus limatulus* holotype (USNM 316316) and 26 paratypes: MCZ 150026(1), 150036(1), USNM 293986(3), 301277(2), 345149(14), ZMA 121.797 (3), and 121.798 (2).

		Paratypes		
	Holotype	Min.	Max.	Mean
1. Standard length	39	25.6	45.7	35
2. Posttemporal spine length	25.7	25.7	35.3	30.5
3. Preopercular spine length	13.9	10.1	19.2	15.0
4. Head length	36.9	33.7	38.9	35.6
5. Orbit diameter	45.8	41.1	53.2	46.1
6. Snout length	18.8	17.4	25	21.0
7. Body depth	61.3	58.5	69.5	63.3
8. Caudal peduncle length	18.7	14.5	18.8	16.5
9. Caudal peduncle depth	10.8	9.6	12.1	10.8
10. Dorsal fin length	17.9	17.6	21.9	19.5
11. Anal fin length	21.3	20.9	24.8	22.9
12. Preanal length	70.8	67.1	72.6	70.4
13. Predorsal length	59.7	58.2	64.4	60.9
14. Prepelvic length	65.6	60.6	69.1	65.1
15. Postdorsal length	47.7	44	51.9	47.4
16. Postanal length	40	36.1	42.7	39.4
17. Dorsal-pelvic length	52.8	51.6	57.3	54.9
18. ACC length (left)	6.4	5.8	9.2	6.7
19. ACC length (right)	0	5.8	7	6.4
20. ACB-ACC length (left)	5.6	2.4	5.6	3.8
21. ACB-ACC length (right)	4.6	3.5	4.6	4.1

16°46′24″N, 55°27′00″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-48 (4), 7 Aug 1995. MCZ 150023, (6), 16°47′24″N, 55°27′00″E, 0–100 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-49 (1), 7 Aug 1995. MCZ 150024, (1), 16°47′00″N, 55°27′06″E, 500–300 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-49 (3), 7 Aug 1995. MCZ 150025, (1), 16°47′00″N, 55°27′06″E, 150–0 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-49 (5), 7 Aug 1995. MCZ 150027, (2), 14°03′24″N, 50°54′12″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-51 (4), 9 Aug 1995. MCZ 150028, (10), 10°40′48″N, 51°51′24″E, 0–900 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-52 (1), 11 Aug 1995. MCZ 150030, (6), 10°40′48″N, 51°51′24″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-52 (4), 11 Aug 1995. MCZ 150031, (2), 10°42′18″N, 51°49′06″E, 0–900 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-53 (1), 11 Aug 1995. MCZ 150032, (16), 10°42′18″N, 51°49′06″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-53 (4), 11 Aug 1995. MCZ 150033, (1), 10°45′18″N, 51°52′54″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-54 (4), 12 Aug 1995. MCZ 150035, (1), 10°45′00″N, 51°52′18″E, 300–150 m, R/V *Malcolm Baldridge*, Cr. 9506, Sta. 10-55 (4), 13 Aug 1995. MCZ 153593, (6), collected with MCZ 150036 (paratype). ZMA 121.799, (1), 07°53′N, 50°37′E, 200–300 m, *Tyro*, Cr. B2, Sta. US1, 2253–2343 h,

Table 2.—Frequency distribution of the number of ACB photophores in species of *Polyipnus* with two posttemporal spines.

	ACB photophores					
Species	6	7	8	9	10	11
Polyipnus asper			21	8		
Polyipnus indicus		1	14	4		
Polyipnus limatulus			2	14	9	1
Polyipnus nuttingi		1	22	6		
Polyipnus oluolus	1					

18 Jan 1993. ZMA 121.800, (1), 10°57′N, 52°01′E, 200–300 m, *Tyro*, Cr. B2, Sta. US2, 2121–2204 h, 20 Jan 1993. ZMA 121.801, (2), 12°06′N, 55°01′E, 300–500 m, *Tyro*, Cr. B2, Sta. SI, 1158–1251 h, 24 Jan 1993. ZMA 121.802, (1), 12°53′N, 50°07′E, 100–300 m, *Tyro*, Cr. B2, Sta. GA1, 0930–1018 h, 27 Jan 1993. ZMA 121.803, (7), 13°20′N, 50°15′E, 200–300 m, *Tyro*, Cr. B2, Sta. GA1, 2313–0005 h, 27 Jan 1993. ZMA 121.804, (12), 12°27′N, 47°00′E, 100–300 m, *Tyro*, Cr. B2, Sta. GA2, 0844–0947 h, 29 Jan 1993. ZMA 121.805, (29), collected with ZMA 121.798 (paratypes). ZMA 121.806, (8), 12°52′N, 46°31′E, 300–500 m, *Tyro*, Cr. B2, Sta. GA2, 2331–0030 h, 29 Jan 1993.

Diagnosis.—Characters, in combination, which serve to distinguish *Polyipnus limatulus*: Lateral pigment bar tapered and long, approaching or reaching lateral midline. Two posttemporal spines: dorsal spine long, basal spine length less than half of that of dorsal spine. Photophore scale denticles restricted to PV, VAV, and ACC clusters; no denticles on ACB photophore scales. ACB photophores 8–10. ACC photophores closely juxtaposed, with the separating interspaces much less than one half of the width of one ACC photophore. Longitudinal parietal keel or crest terminating posteriorly with a disjunct portion bearing two spines, one directed anteriorly and one directed posteriorly. Autapomorphies: none known.

Description.—Moderate-sized species, maximum observed adult body size 45.7 mm SL. D (12) 10–14. A(14)14–17. P(12)11–13. V(6)5–6. GR(11+11) 10+9–11+11 = (22) 19–22. Branchiostegal rays 10 (7 anterior ceratohyal + 3 posterior ceratohyal). Vertebrae (12+21) 12–14+19–21 = (33)32–34. Body covered with slightly imbricated, sheet-like, dorsally elongate scales. Other scales thickened and modified in association with photophores (see Harold 1994). Body profile anterior of dorsal fin and pelvic fin broadly ovate, posteriorly tapering at a 60° angle to caudal peduncle. Profile of caudal peduncle slightly elongate, and rectangular.

Orbit circular to slightly ovate with elongation in dorsoventral axis; pronounced aphakic space located ventrally to lens. Ventral margin of dentary with two keels; lateral-most keel smooth or sparsely serrate, ventromedial keel with 9–15 fine serrae. Premaxillary teeth minute and conical, uniserial over posterior half of bone and with up to three rows anteriorly; about 55 to 60 teeth in longest series. Maxillary teeth minute and conical, uniserial with 45 to 48 teeth. Dentary teeth minute; conical and uniserial over posterior half of bone, and slightly recurved in up to four rows anteriorly; 27 to 33 teeth in longest series. Palatine and mesopterygoid teeth absent. Vomerine teeth minute and conical, in five to seven longitudinal rows arranged in a transverse patch across the anterior wing-like process; no teeth present on posteromedian process. Parietal crest discontinuous; anterior portion keel-like, posterior region with two conical spines in the medial plane, directed anteriorly and posteriorly. Posttemporal dorsal limbs smooth or ornamented with two or three weak serrae. Two posttemporal spines: dorsal spine without serrae, elongate, ranging from 25.7 to 35.3% HL ($n = 10$), posterodorsally directed; ventral spine short, also unornamented (usually about one quarter of the length of the dorsal spine), ventrolaterally directed. Ventral margin of pectoral shield with five to 12 small conical spines, anterior spine slightly deflected laterally. Vertical and anteroventral rami of preopercle each with two parallel, deeply serrate lateral ridges, the numbers of serrae highly variable. Preopercle with two spines: ventral spine longest, ranging from 10.1 to 19.2% HL ($n = 10$), anteriorly curved, directed anteroventrally; dorsal spine minute, similar to adjacent serrae of adjacent lateral ridge, directed ventrolaterally. Dorsal spinous process smooth, exposed length and height about equal, terminating posterodorsally as two conical dorsolaterally-directed spines (one per side). Anal-fin pterygiophore spines absent. Morphometric characters summarized in Table 1.

Ventral margins of photophore scales smooth, except those of PV, VAV, and ACC clusters which have numerous denticles. OVB 1 + 1 + 1, variably positioned, but most commonly found in an anteriorly-inclined straight line (in holotype elevation of central OVB slightly ventral to that of first and third OVB). ACA #1 and #2 isolated, #3 joined to ACB forming continuous cluster. ACB (9)8–11, usually 9 or 10 (Table 2), with dorsal step between #3 and #4.

Color in preservative.—Dark brown pigment saddle with an elongate and narrow predorsal notch and a moderately long lateral pigment bar tapering toward and usually reaching lateral midline. Dark brown to black chromatophores delineating myosepta and lateral midline. Two prominent, vertically elongate patches of dark brown pigment at base of caudal fin rays immediately dorsal and ventral to lateral midline, especially distinct in juveniles and larvae. Central portion of caudal peduncle with internal rectangular patch of dark brown pigment in association with vertical septum.

Larval morphology.—Overall larval morphology similar to that described and illustrated by Ahlstrom et al. (1984) for *Polyipnus polli* Schultz, 1961; smallest specimen of *P. limatulus* examined (6.5 mm SL; Fig. 2) is slightly deeper bodied in the thoracic and abdominal regions than the illustration of the 5.2 mm specimen of *P. polli*, in addition to much greater development of the median fin rays and some photophore groups. Evidently, photophore development is relatively protracted in *P. polli*. For example in *P. polli* the first photophores to appear in the SAB (=OVB) cluster do so at a standard length of between 9.0 and 9.6 mm whereas in *P. limatulus* they are beginning to develop at 7.6 mm. Similarly in *P. polli* the AN (=ACB) photophores begin to appear between 7.5 and 9.0 mm SL whereas in *P. limatulus* there are two well-developed ACB photophores present on each side in 6.5 and 6.8 mm specimens. In *P. limatulus*, the combined linear cluster ACA + ACB reaches its full adult complement (11–14) at standard lengths between about 25 and 30 mm (Fig. 3). According to the occurrence of small photophore buds on the posterior margin of the ACB cluster *Polyipnus polli* adds photophores to this cluster at a standard length of 23.5 mm so the two species may be similar in the size at which the full complement is attained. These observations are in general agreement with other congeners for which photophore development has been reported, except for *P. fraseri* (*P. spinosus* species group) which has paedomorphic development of the ACB cluster (Harold 1990b).

The adults of *P. limatulus* have two vertically elongate patches of dark pigment near the base of the caudal fin rays, as described and illustrated (Fig. 1). In well-developed larvae and juveniles (9.5 + mm SL) these patches appear as two distinct black spots, one at the base of the ventral caudal-fin rays and one at the base of the dorsal caudal-fin rays, on each side of the fin base. Smaller larvae (6.5–7.6 mm SL) lack the caudal spots (Fig. 2) and any other pigmentation in the caudal region.

Etymology.—The specific name *limatulus* is based on the diminutive form of the Latin adjective *limatus*, meaning filed, polished or smoothed, in reference to the characteristic lack of denticles on the scales covering the ACB photophores.

Distribution.—*Polyipnus limatulus* is known to occur only in the Gulf of Aden and immediately adjacent areas in the northwestern Indian Ocean (Fig. 4).

Ecology.—Deep-bodied sternoptychids (Sternoptychini, sensu Baird 1986) were represented in the Somali Ecosystem Study (SES) region collections of R/V *Tyro* (1992, 1993) by 809 specimens allocated among six species: *Argyropelecus affinis* (*n* = 336), *A. hemigymnus* (*n* = 41), *A. sladeni* (*n* = 312), *Polyipnus limatulus* (*n* = 66), *P. omphus*. (*n* = 21), and *Sternoptyx obscura* (*n* = 33). *Polyipnus limatulus* was

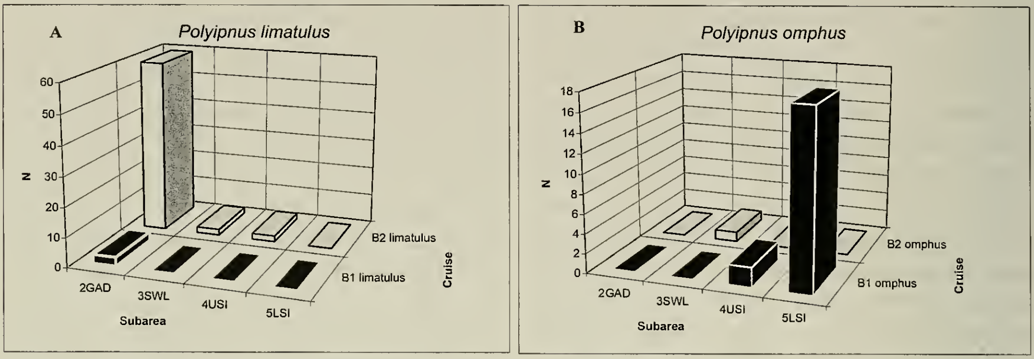


Fig. 5. Seasonal and spatial distribution of captures (n = number of specimens) of two species of *Polyipnus*, *P. limatulus* and *P. omphus*. Seasonal distribution indicated by B1 (summer) captures and B2 (winter) captures. Spatial distribution indicated by subarea (2GAD = Gulf of Aden, 3SWL = Great Swirl, 4USI = Upper Somali Inshore, 5LSI = Lower Somali Inshore; definition of subareas provided in Materials and Methods).

taken at five stations (Fig. 4: GA2, GA1 (subregion GAD); SI (subregion SWL); US2, US1 (subregion USI)) and in three SES subregions: GAD (n = 62), SWL (n = 2), USI (n = 1). Despite a nearly even distribution of effort among stations by season, geography and depth, *P. limatulus* was unequally represented in the winter (n = 62) vs. summer (n = 3) cruises. *Polyipnus omphus* was taken at four stations (Fig. 4: SB2, subregion SWL; US1, subregion USI; US0, SB1, subregion LSI) and in three SES subregions: SWL (n = 1), USI (n = 2) and LSI (n = 18). *Polyipnus omphus* was similarly unequally represented in summer (n = 20) vs. winter (n = 1) cruise stations.

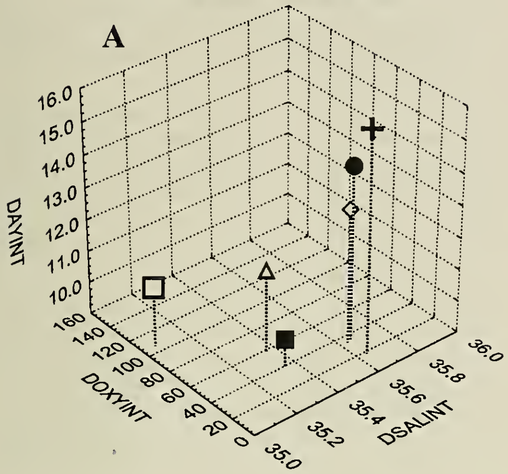
A comparison of geographic (Figs. 4, 5) and seasonal (Fig. 5) captures of the two *Polyipnus* species reveals that within the SES area their occurrences are nearly opposite, with highest captures of *P. limatulus* in the north and in winter (especially GAD subregion), and highest captures of *P. omphus* in the south and in summer (especially LSI subregion).

Vertical distributional records are nearly the same in our material, with most specimens taken at night (51:15 for *P. limatulus*, 17:4 for *P. omphus*) and mostly within the 200 to 300 m depth stratum (68% of all specimens of *P. limatulus*, 71% of all specimens of *P. omphus*). All captures, day and night, are within the 100 to 500 m range. There is no evidence for diel vertical migration in our data. This conclusion is corroborated by the consistency (Fig. 6A, B) for day vs. night values for weighted-integral values of temperature, salinity and dissolved oxygen (see Wessel & Johnson 1998 and Wessel 1997 for treatment of "weight-integral" values for hydrographic data associated with SES net captures of mesopelagic fishes).

With comparison to each other and in comparison with other reported SES sternoptychids (Fig. 6A, B), *P. limatulus* and *P. omphus* are again distributional opposites. *P. limatulus* is consistently associated with warm, relatively saline, low oxygen water; *P. omphus* is associated with colder, less saline, higher oxygen water. This probably reflects the influence of Red Sea outflow water on *P. limatulus* vs. the summer intrusive occurrence of *P. omphus* in the SES area, associated with the summertime development of marked coastal and offshore upwelling in concert with development of the monsoonal Somali Current flow.

Remarks.—The parietal structure of specimens here ascribed to *P. limatulus* was noted by Harold (1994:511) as an indication that material listed in that study as *P.* cf. *indicus* from the Gulf of Aden, the

DAY HAULS:
DSALINT vs. DOXYINT vs. DAYINT



NIGHT HAULS:
NSALINT vs. NOXYINT vs. NIGHTINT

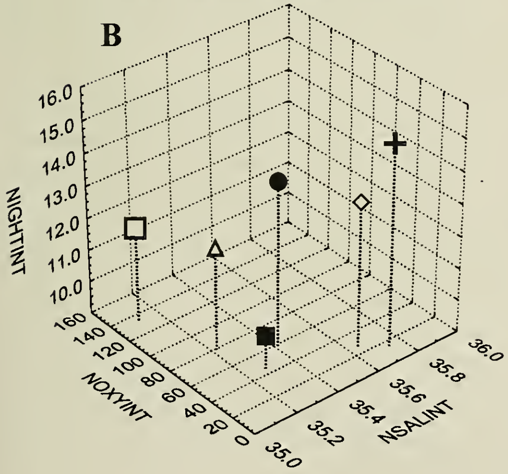


Fig. 6. Comparison of weighted integral-mean values of temperature, salinity, and dissolved oxygen for day (respectively: DAYINT, DSALINT, DOXYINT) and night (respectively: NIGHTINT, NSALINT, NOXYINT) captures of six species of sternoptychids in the Somali Current Ecosystem Area (see Materials and Methods for explanation of weighted integral-mean values). Open diamond = *Argyropelecus affinis*, open triangle = *A. hemigymnus*, filled circle = *A. sladeni*, cross = *Polyipnus limatulus*, open square = *P. omphus.*, filled square = *Sternoptyx obscura*.

northern portion of the geographic range of *P. indicus* Schultz, 1961, may represent an undescribed species. Further study of material available at that time, as well as new collections from the region (R/V *Malcolm Baldridge* and R/V *Tyro*), has indicated to us that the northern, *P.* cf. *indicus* material, should be recognized as a distinct species.

Five species of the *P. spinosus* species group have posttemporal bones with two spines: *P. limatulus*, *P. asper* Harold, 1994 (Andaman Sea, eastern Indian Ocean), *P. indicus* (western Indian Ocean), *P. nuttingi* Gilbert, 1905 (Hawaiian Islands), and *P. oluolus* Baird, 1971 (Marshall Islands). *Polyipnus limatulus* is most similar to the two other Indian Ocean species, *P. indicus* and *P. asper* (couplet 15 of Key to the Species of *Polyipnus*, in Harold 1994:470–475) in regard to body shape, and fin-ray counts. The new species is more similar to *P. asper* in regard to the presence of denticles on the ACB photophore scales. *Polyipnus limatulus* and *P. indicus*, which are both known to occur off east Africa, can be readily distinguished on the basis of the form of the parietal crest. The new species has the bispinate parietal morphology as is typical of *P. asper* and more derived species (see Harold 1994:436, fig. 6D), whereas in *P. indicus*, like *P. nuttingi*, and *P. oluolus*, the parietal crest is a simple blade lacking the posterior ornamentation (Harold 1994:436, fig. 6C). An important feature separating *P. limatulus* from *P. asper* is the lack of denticles on the ACB photophore scales in *P. limatulus*. The new species often has more ACB photophores than any of these four other species (Table 2). The other two species with two posttemporal spines, *P. nuttingi*, and *P. oluolus*, are also readily distinguished from *P. limatulus*. *Polyipnus nuttingi*, an apparent endemic of the Hawaiian Islands, has relatively high gill raker counts (21–25, usually 23 or 24) compared with *P. limatulus* (18–21, usually 19). The remaining species, *P. oluolus* (known from a single specimen from the Marshall Islands; Baird 1971), has an overall photophore configuration, which includes only six ACB, that is unusual for members of the *P. spinosus* group (Harold 1994:515–517, fig. 52).

Phylogenetic relationships of *Polyipnus* species were proposed by Harold (1994). All those species of the *P. spinosus* group with only two posttemporal spines, of which *P. limatulus* is one, appear to be basal, although not comprising a monophyletic group. Little else can be said of the relationships of the new species until a survey of the characters utilized by Harold (1994) is completed for *P. limatulus* and *P. latirastrus.*

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A review of western north Atlantic species of *Bembrops*, with descriptions of three new species, and additional comments on two eastern Atlantic species (Pisces: Percophidae)

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Abstract.—The Atlantic members of the genus *Bembrops* were examined from approximately 700 specimens. Meristic, morphometric, and pigment characters were used to redescribe six species, *B. anatirostris*, *B. gobioides*, *B. greyi*, *B. heterurus*, *B. macromma*, and *B. magnisquamis*. Three species, *Bembrops ocellatus*, *B. quadrisella*, and *B. raneyi* are described as new. New information on sexual dimorphism, the cephalic canal system and vertebral number is presented. Distribution maps for all nine species are shown. *Bembrops ocellatus* and *B. quadrisella* are widespread in the Caribbean Sea. *Bembrops raneyi* is known only from the Bahama Islands. The three new species are illustrated.

The American members of the genus *Bembrops* were reviewed by Ginsburg (1955); three of the four species he described as new; in addition, he reviewed the literature and characterized the family Percophidae (=Percophididae). The family was also characterized by Grey (1959) and detailed descriptions of *B. anatirostris*, *B. gobioides*, and *B. macromma* were presented, along with figures of *B. anatirostris* and *B. macromma.*

More recently, Das & Nelson (1996) presented a world-wide revision of the percophid genus *Bembrops*, recognizing a new species from the eastern Atlantic. They reviewed the eighteen nominal species in the genus, relegating five into synonymy.

A wealth of unstudied material of the various species is available from Cornell University (CU); Tulane University, Museum of Natural History (TU); University of Florida (UF); and United States National Museum (USNM) and we present additional data on the four species known to Ginsburg, plus data on two eastern Atlantic species, and describe three new species from the western north Atlantic.

During this study we have become aware that much remains to be done in systematics, life history, sexual dimorphism, and distribution of the species within the genus *Bembrops.* We intend to pursue the study of Atlantic populations and expand our study to include related Indian and Pacific Ocean species. However, because of practical considerations the main purpose of this paper is to provide names for the three new forms.

We follow Ginsburg's (1955) placement of *Bembrops* in the family Percophidae (=Percophididae). Future research may prove the necessity of elevating the subfamily Bembropinae (Nelson 1976, 1984, 1994) to family status. The new species described herein fit the characters for the family and genus as given by Ginsburg (1955), Nelson (1976, 1978, 1984, 1994) and Das & Nelson (1996).

Methods and Materials

Ginsburg (1955) pointed out the difficulties involved in studying the species of

Bembrops because most are captured in bottom trawls and often specimens suffer broken fin rays and loss of some or most of their body scales. Difficulties in measuring and making some counts are increased when specimens have twisted, contorted bodies, and widely flared branchiocranial structures. Some of our lateral-line scale counts are estimates based on counts of scale "pockets" and some of the variation presented in the morphometrics is due to the use of distorted specimens.

We follow Ginsburg (1955) and Hubbs & Lagler (1958, 1964) in fin ray and gill raker counts. We counted rudimentary elements on both upper and lower limbs of the first left gill arch, and the raker at the angle of the arch was included in the count of the lower limb. Although Das & Nelson (1996) cited Hubbs & Lagler (1964) in their Methods and Materials section, our gill raker and fin ray counts do not always agree.

Depth of body was measured at the origin of first dorsal fin. Caudal peduncle was measured at its least depth. The head was measured from the anterior point of the rounded lobe near the end of the snout rather than from the indented midpoint to the posterior end of the extended fleshy opercle. The snout was measured from this same point to the anterior rim of the orbit. The eye (orbit) was measured horizontally between the most anterior and posterior fleshy rims of the orbit. The interorbital measurement is the least bony interorbital distance. Upper jaw length was measured from its anterior tip to the bony posterior tip of maxilla (not including tentacle). The lower jaw measurement was interpreted as the distance between anterior tip of dentary to the posterior bony tip of maxilla (not including tentacle).

Left and right tentacles are seldom of equal length and so we measured both whenever feasible, especially for species of which we had few specimens. The tentacles are quite elastic and before measurement each tentacle was gently stretched straight with a fine forceps, allowed to contract, then measured.

Pigmentation patterns in the first dorsal fin were determined for the nine Atlantic species of *Bembrops* included in our study (Fig. 1). Pigmentation on other fins and on body is also described.

Vertebral counts were made from radiographs of 333 specimens taken primarily by the Radiology Department, Louisiana State University School of Veterinary Medicine.

Counts were made on 113 *Bembrops anatirostris*, 178 *B. gobioides*, 60 *B. greyi*, 75 *B. heterurus*, 67 *B. macromma*, 8 *B. magnisquamis*, 39 *B. ocellatus*, 123 *B. quadrisella*, and 29 *B. raneyi.*

Measurements were made on 50 *B. anatirostris*, 50 *B. gobioides*, 62 *B. greyi*, 50 *B. heterurus*, 45 *B. macromma*, 6 *B. magnisquamis*, 14 *B. ocellatus*, 16 *B. quadrisella*, and 19 *B. raneyi.* Proportional measurements were made with a needle-point dial calipers and recorded to the nearest 0.1 mm.

Meristic data are presented in Tables 1-4 and morphometrics are presented in Tables 5-10. In Tables 5-7 and 10 the proportional measurements are expressed in thousandths of standard length (SL). Table 8 shows frequency distributions of ratios of head width divided by head depth, Table 9 contains frequency distributions of snout length divided by orbit length. Table 11 presents a summary of typical fin pigmentation patterns for the nine Atlantic species with sexual dimorphism noted.

We investigated the full extent of the cephalic portion of the lateral-line sensory system, which was only briefly mentioned by Ginsburg (1955) and Grey (1959). The supracleithrum and posttemporal bone were dissected from the right side of five species (*B. anatirostris*, *B. gobioides*, *B. greyi*, *B. heterurus*, and *B. macromma*) and measured, and expressed as percent of SL. The connection of the cephalic canal system to the lateral-line was examined to determined to what degree the canal is enclosed by bone.

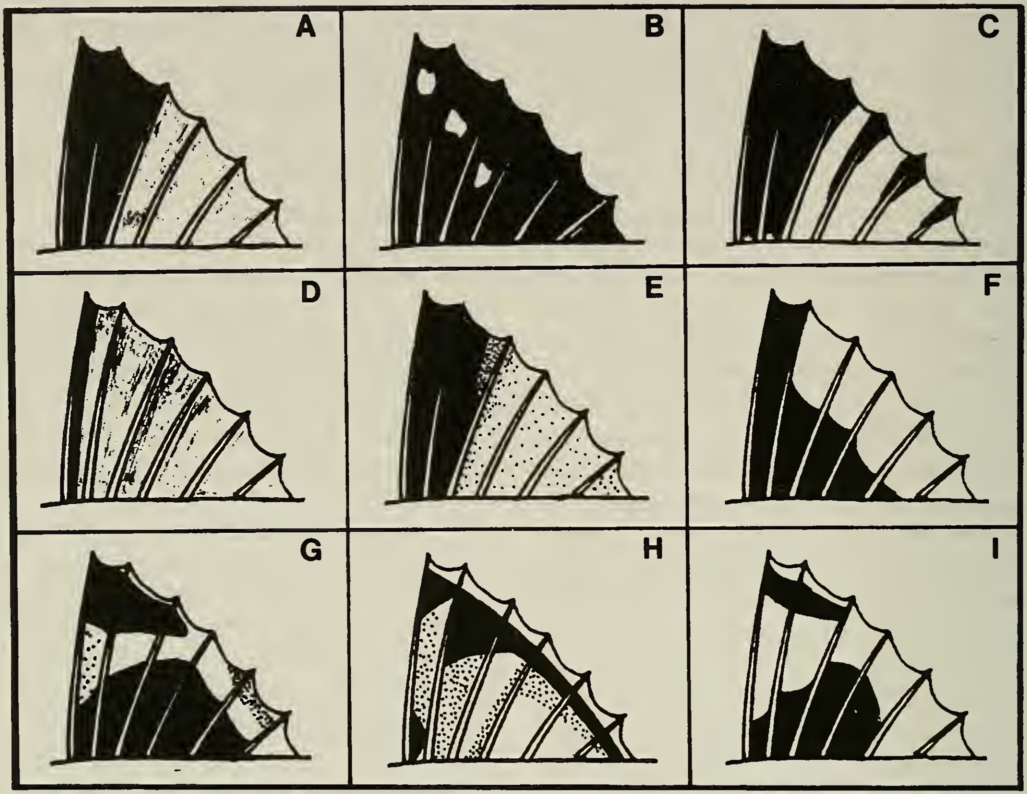

Fig. 1. Spinous dorsal fin pigment pattern in nine Atlantic *Bembrops:* A) *B. anatirostris*, B) *B. greyi*, C) *B. gobioides*, D) *B. heterurus*, E) *B. macromma*, F) *B. magnisquamis*, G) *B. ocellatus*, H) *B. quadrisella*, and I) *B. raneyi*.

The alimentary tract was dissected on 3–4 specimens of *B. anatirostris*, *B. gobioides*, *B. greyi*, *B. heterurus*, and *B. macromma* and pyloric caeca measured; length of caeca is given as percent of SL.

Collection depths were obtained from cruise reports and reported in meters (m). Maps in Williams (1968) were used for locating collecting sites of the two eastern Atlantic *Bembrops*.

Table 1.—Frequency distribution of the number of dorsal, anal, and pectoral rays in nine Atlantic species of *Bembrops*.

	Dorsal rays					Anal rays				Pectoral rays								
Species	14	15	16	17	18	16	17	18	19	22	23	24	25	26	27	28	29	30
B. anatirostris	8	105					20	92	1				3	16	59	31	4	
B. gobioides			9	163	6		4	163	9					30	111	33	1	1
B. greyi		10	48	2			26	34					4	44	12			
B. heterurus	6	67	2				1	69	5					25	50			
B. macromma	66						16	50	1			4	45	18				
B. magnisquamis		7	1				8			1	3	4						
B. ocellatus		8	28	2		1	7	29	2				4	23	11	1		
B. quadrisella		17	101	5		1	37	82	3				8	53	54	8		
B. raneyi		3	25	1			9	20					1	3	18	6	1	

Table 2.—Frequency distribution of the number of lateral-line scales in nine Atlantic species of *Bembrops*.

Species	Scales 44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
B. anatirostris															1	5	10	9	20	15	20	11	12	5	2	3	
B. gobioides																	5	4	26	22	32	35	13	20	10	8	1
B. greyi		1	—	5	15	11	17	8	4																		
B. heterurus											2	18	19	19	9	6	2										
B. macromma										8	10	13	10	9	5	3	2	1									
B. magnisquamis	4	1	2	1																							
B. ocellatus												1	1	1	5	5	7	6	7	4	1						
B. quadrisella														2	10	12	27	30	17	17	9	6					
B. raneyi													1	5	3	7	4	4	1								

Species accounts and distribution maps are based almost entirely on our own observations, not compilations of previous published information, so nearly all specimens used in this study have never been published upon. Exceptions are a few specimens from the National Museum of Natural History (USNM) and University of Florida (UF) cited in Das & Nelson (1996). Several Pacific *Bembrops* were examined for comparison to the nine Atlantic species: *B. curvatura* CAS 32808, 32976, 33100, 34393, 34589, and 88698 (25); *B. filifera* CAS 89509 (8); *B. nematopterus* USNM 347251 (1); *B. platyrhynchus* CAS 88685, USNM 345189 (5); *B.* sp. nov. CAS 88680, USNM 345190 (7). We recommend the use of "duckbill" for the common name of members of the genus *Bembrops* to avoid confusion with the commonly used name "flathead" as applied to the family Platycephalidae (Eschmeyer 1990). We suggest common names for the nine Atlantic species.

Genus *Bembrops* Steindachner, 1876

We examined the cephalic sensory pore system in detail in *Bembrops anatirostris*, *B. ocellatus*, and *B. raneyi* and found the general configuration of the canals to be nearly identical. We found that canals and pores were more discernible on those specimens that had lost patches of scales and pigmented skin from the head. Figure 2A is a composite sketch representing several specimens.

The most anterior pore is on either side near anterior tip of snout and the canals extending posteriorly from these two pores gradually converge toward the anterior portion of interorbital area. These two canals (left and right) pass medial to the anterior and posterior nares, respectively, and the second set of pores project laterally at this place and may easily be confused with the narial openings. The third set of pores is in a staggered arrangement, with respect to each other, at the anterior interorbital area

Table 3.—Frequency distribution of the number of gill rakers in nine Atlantic species of *Bembrops*.

	Upper limb				Lower limb							Total, both limbs								
Species	3	4	5	6	12	13	14	15	16	17	18	15	16	17	18	19	20	21	22	23
B. anatirostris		12	97	4			22	82	9						4	25	73	10	1	
B. gobioides		22	151	3		1	49	107	18	1				1	5	57	95	16	2	
B. greyi	6	49	5		4	17	39					1	6	14	36	3				
B. heterurus		18	57			2	25	45	3					1	10	24	37	2		
B. macromma		2	54	3	4	2	17	36					1	4	1	16	35	2		
B. magnisquamis		1	7			2	1	2	3						2	1	3	2		
B. ocellatus		1	33	1			12	18	5						1	11	18	4	1	
B. quadrisella			106				18	41	27	19	1					18	41	27	19	1
B. raneyi		2	24	3		6	18	5						2	4	15	8			

where the two canals (left and right) are separate but adjacent to each other. Between the anterior and posterior interorbital areas the two canals seem to join to form a single canal and at the posterior interorbital area there is a centrally located single pore. We do not know that this arrangement is typical, however an air jet placed at the single pore forced liquid out of both pores at the anterior interorbital area and the pores near the narial openings.

Immediately posterior to the single, interorbital pore the canal divides into a left and right branch and respectively circles around posterior rim of orbit. About half way around the posterior rim of orbit there is a branch canal that courses posteriorly and at the occipital area a short side branch projects medially, but right and left side branches do not join across the occiput. After the small side branch, the main (branch) canal continues to extend posteriorly and connects with the anterior end of each lateral-line canal. The two systems meet or join under the tip of a diagonally directed spine (posttemporal of some authors) and the anterior keeled lateral-line scale. The number of pores in the infraorbital canal posterior to the orbit varies in several species, having either 3 or 4 pores.

Table 4.—Frequency distribution of the number of vertebrae in nine Atlantic species of *Bembrops*.

Species	27	28	29	30	N	$\bar{X}$	*SD*
B. anatirostris	1	41			42	27.98	0.15
B. gobioides			2	35	37	29.95	0.23
B. greyi			8	46	54	29.85	0.36
B. heterurus		49	1		50	28.02	0.14
B. macromma	3	59			62	27.95	0.22
B. magnisquamis			8		8	29.00	—
B. ocellatus			2	12	14	29.87	0.34
B. quadrisella			6	31	37	29.83	0.37
B. raneyi			4	25	29	29.86	0.35

There is also a mucous canal and pore system associated with the preoperculomandibular area. This system is not connected with the cephalic system described above. The preoperculomandibular system extends from upper end of preopercle, ventrally and then anteriorly to anterior tip of lower jaw. The number of pores seem to be variable. Figure 2B illustrates the right preoperculomandibular canal of a *B. ocellatus* with nine pores. Thus we find the cephalic lateral-line system of *Bembrops* is somewhat abbreviated in comparison to that of the genus *Acanthaphritis*, subfamily Hemerocoetinae (Suzuki & Nakabo 1996) with *Bembrops* having the infraorbital canal very short, extending less than halfway to the anterior margin of the orbit and the preoperculomandibular branch not connecting with the lateral-line canal (Fig. 2A, B).

The cephalic canal system that passes through the posttemporal bone (ptt) and along the top of the supracleithrum (scl) in connecting with the lateral-line varies among the five Atlantic species examined. The size of each bone, expressed as percent of SL, and the degree to which the canal is

Table 5.—Proportional measurements (expressed in thousandths of standard length) for four western north Atlantic species of *Bembrops.*

Proportion	*B. anatirostris* n = 50 Range	$\bar{X}$	*SD*	*B. gobioides* n = 50 Range	$\bar{X}$	*SD*	*B. macromma* n = 45 Range	$\bar{X}$	*SD*	*B. magnisquamis* n = 6 Range	$\bar{X}$	*SD*
SL mm	65.8–246.0	157.7	46.18	84.6–217.4	162.3	33.53	77.3–190.0	117.9	23.15	72.0–104.2	91.8	12.33
Body depth	108–171	126	12.00	94–144	112	9.39	105–155	131	10.56	97–113	105	5.53
Caudal peduncle depth	48–59	53	2.59	45–53	48	2.33	52–64	59	2.78	55–60	57	2.17
Head length	329–426	382	16.86	325–371	346	10.98	331–424	385	12.34	359–386	376	10.40
Head depth	97–139	111	8.49	93–122	100	6.00	113–134	124	5.42	97–103	99	2.45
Head width	133–172	149	8.11	119–147	133	7.09	150–184	166	7.94	147–156	151	3.54
Interorbital width	6–10	9	1.16	6–11	8	1.13	7–13	10	1.28	8–10	9	0.82
Snout length	109–139	119	6.75	90–122	105	6.64	95–110	103	3.73	96–102	99	2.48
Orbit length	76–105	87	5.50	83–108	90	4.37	93–129	111	10.01	98–110	103	5.35
Upper jaw length	136–168	148	7.43	125–149	135	7.27	132–164	150	7.40	131–148	139	5.61
Lower jaw length	155–187	168	8.41	139–161	149	5.62	145–179	164	8.43	150–160	155	3.56
Postorbital length	158–197	174	9.40	136–160	150	5.45	161–189	170	15.55	164–184	175	6.76

enclosed by bone differs as follows: *B. anatirostris*—canal partly enclosed, longest ptt and scl, 6.5% and 5.7% (Fig. 3A); *B. gobioides*—canal an open groove, shortest ptt and scl, 5.3% and 4.2% (Fig. 3B); *B. greyi*, *B. heterurus*, and *B. macromma* are very similar with canal more or less completely enclosed with a single pore along length, intermediate-sized ptt and scl, 6.8% and 5.3%, 6.4% and 5.2%, 6.5% and 5.5%, respectively (Fig. 3C–E). There is a single large, exposed spine projecting posteriorly from the rear of the posttemporal just dorsal of the cephalic canal.

Bembrops anatirostris Ginsburg, 1955
Longnose duckbill

Dorsal fin in 113 specimens has VI, 14 or 15 soft rays, nearly all with 15 rays. Anal fin has 17 or 18 rays with a strong mode of 18. Pectoral fin rays range from 25 to 29 with the mode at 27 (Table 1).

Lateral-line scales range from 58 to 69, $\bar{X}$ = 63.3 (Table 2). Gill rakers range from 4 to 6 on upper limb, 14 to 16 on lower limb and total counts range from 18 to 22 (Table 3). Number of vertebrae is almost always 28, only a single count of 27 (Table 4).

Bembrops anatirostris has the longest snout of the nine Atlantic species, with all specimens examined having the snout length greater than the orbit length (Tables 5, 9). *Bembrops anatirostris* has a long thin triangular maxillary tentacle, attenuate at tip. It has the longest tentacle of the nine species considered in this study (Table 10). Richards (1990) shows a rudimentary tentacle on a 9.4 mm SL *B. anatirostris* and a well-formed tentacle on a 15 mm SL (although there is a possibility these figures may be *B. raneyi*, also known from the Straits of Florida).

Bembrops anatirostris is the only one of the nine species in this study that has any prolonged dorsal spines; the second dorsal spine is prolonged in large males. We cannot confirm Das & Nelson's (1996) report-

Table 6.—Proportional measurements (expressed in thousandths of standard length) for two eastern Atlantic species of *Bembrops.*

	B. greyi $n = 62$			*B. heterurus* $n = 50$		
Proportion	Range	$\bar{X}$	*SD*	Range	$\bar{X}$	*SD*
SL mm	54.9–223.4	125.6	42.27	80.7–214.5	145.8	35.03
Body depth	96–156	118	13.14	121–167	137	11.07
Caudal peduncle depth	48–63	55	3.32	51–66	57	3.17
Head length	366–428	388	13.59	351–398	377	10.07
Head depth	96–137	114	8.60	109–156	124	9.78
Head width	138–172	153	7.36	133–191	162	12.82
Interorbital width	5–10	7	1.18	7–12	10	1.18
Snout length	82–122	105	10.35	106–124	114	4.05
Orbit length	100–125	112	6.75	74–103	93	5.88
Upper jaw length	138–175	155	10.86	140–160	152	5.47
Lower jaw length	152–191	171	10.79	158–187	173	6.85
Postorbital length	156–190	174	8.20	148–178	167	5.69

ing elongation of the third spine of first dorsal of this species since all males examined in this study had only the second spine elongated. There is a moderate correlation between length of specimen and length of spine. Twenty-one males that range from 147 to 230 mm in standard length have second dorsal spines (expressed in thousandths of standard length) that range from 172 to 381, $\bar{X} = 265$. The elongate spine possesses a narrow "flag" of black epidermis along the posterior margin from the margin of the fin to the tip of the spine.

The first two membranes of the spinous dorsal fin of *B. anatirostris* are a dull black, the remaining membranes are typically clear (Fig. 1A). Small specimens have an upper basal caudal spot but neither adult males nor females retain a distinct caudal spot.

Bembrops anatirostris has three long pyloric caeca, 12.5, 13.2, and 14.1 (left to right) % of SL. The caeca extend past the posterior end of the undistended stomach.

Distribution/Depth.—Northern Gulf of Mexico; Gulf of Campeche; also from northwestern edge of Little Bahamas Bank, western Caribbean Sea off Rosalind Bank and southern Nicaragua; southwestern Caribbean Sea off Panama; western end of Puerto Rico and Atlantic Ocean east of Dominica. Off South America—Colombia, eastern Venezuela, Guyana, and Suriname (Fig. 4). Additional records in Ginsburg (1955), Grey (1959), Uyeno et al. (1983), Boschung (1992), and Das & Nelson (1996). *Bembrops anatirostris* is the shallowest occurring species of the genus in the Atlantic. The depth range of our *B. anatirostris* is 82–549 m, with most specimens from 320 m or less. Ginsburg (1955) reported the species from 110–366 m, while Grey (1959) listed her material from 139–366 m, with most specimens from 220 m or less. Bullis & Struhsaker (1970) reported the highest density of *B. anatirostris* from 185–274 m, with few specimens from deeper waters. Das & Nelson (1996) listed the species from 100 to over 350 m. We examined one collection of *B. anatirostris* taken with *B. magnisquamis* off Costa Rica and one collection taken with *B. quadrisella* off Venezuela.

Material examined.—TU 26887 (1): Oregon 156; 27°22′N, 96°08′W; 180 m; 27 Nov 1950. TU 2732 (10): Oregon 278; 29°49′N, 85°45′W; 205 m; 24 Feb 1950. TU 10689 (7): Anna Inez 644; 28°52′N, 88°59′W; no depth recorded; 7 Jul 1955 [pyloric caeca dissection]. TU 10995 (4): Oregon 1094; 27°10′N, 96°20′W; 274 m; 5 Jun 1954. TU 12891 (4): Oregon 1095; 27°10′N, 96°17′W; 320 m; 5 Jun 1954. TU 12896 (2): Oregon 1093; 27°03′N,

Table 7.—Proportional measurements (expressed in thousandths of standard length) for three new species of *Bembrops.*

Proportion	*B. ocellatus* $n = 14$				*B. quadrisella* $n = 16$				*B. raneyi* $n = 19$			
	Holotype	Range	$\bar{X}$	*SD*	Holotype	Range	$\bar{X}$	*SD*	Holotype	Range	$\bar{X}$	*SD*
SL mm	135.3	90.9–190.0	128.5	23.89	195.0	127.5–235.3	182.6	30.39	136.0	69.1–167.3	124.2	26.79
Body depth	120	91–121	106	9.19	107	96–128	112	9.20	98	97–136	110	10.58
Caudal peduncle depth	51	44–58	50	3.72	48	47–55	50	2.22	47	45–55	50	3.09
Head length	363	349–387	369	10.93	373	340–404	376	15.46	370	348–390	369	11.49
Head depth	117	92–117	104	6.42	105	96–127	108	7.97	98	89–116	102	6.33
Head width	155	139–157	147	4.92	145	134–165	150	9.45	152	139–178	152	8.96
Interorbital width	7	5–10	7	1.40	8	5–9	8	1.31	9	6–11	8	1.26
Snout length	107	99–116	103	4.72	105	105–126	113	4.98	104	90–116	101	6.75
Orbit length	98	92–113	103	7.23	103	92–120	103	8.70	112	88–116	105	7.94
Upper jaw length	138	136–158	145	7.13	150	139–160	151	6.56	144	133–149	141	3.87
Lower jaw length	149	147–170	156	7.74	161	154–175	164	7.43	157	142–161	152	5.82
Postorbital length	159	155–172	164	4.80	164	150–218	168	14.35	163	156–178	166	5.99

96°16′W; 384 m; 4 Jun 1954. TU 12962 (1): Oregon 895; 28°47′N, 85°19′W; 117 m; 7 Mar 1953. TU 12981 (2): Oregon 864; 29°19′N, 86°04′W; 150 m; 31 Oct 1953. TU 17609 (3): Oregon 2000; 07°55′N, 57°30′W; 82 m; 5 Nov 1957. TU 90207 (1): Oregon-II 13167; 29°15.7′N, 88°09′W; 128 m; 3 May 1973. TU 90224 (1): 29°14.7′N, 88°08.5′W; 165 m; 3 May 1973. TU 90241 (8): Oregon-II 13170; 29°14′N, 88°09.3′W; 183 m; 3 May 1973. TU 180139 (7): Oregon 1985; 09°41′N, 59°47′W; 274 m; 3 Nov 1957. TU 180140 (5): Oregon 2012; 07°34′N, 54°19′W; 274 m; 8 Nov 1957. TU 180141 (4): Oregon 2203; 29°13.5′N, 88°12′W; 229 m; 26 Jun 1958. TU 180142 (1): Silver Bay 441; 27°39′N, 79°15′W; 503–549 m; 9 Jun 1958. TU 180337 (3): Oregon 1984; 09°45′N, 59°45′W; 366 m; 3 Nov 1957. TU 180338 (8): Oregon 1989; 09°45′N, 59°45′W; 366 m; 4 Nov 1957. TU 180339 (10): Oregon 2005; 07°37′N, 54°50′W; 366 m; 6 Nov 1957. TU 180340 (1): Oregon 2023; 07°15′N, 53°21′W; 247 m; 9 Nov 1957. TU 180341 (1): Silver Bay 175; 28°05′N, 90°52′W; 183 m; 20 Sep 1957. TU 180342 (5): Oregon 2022; 07°15′N, 53°25′W; 210 m; 9 Nov 1957. TU 180343 (8): Oregon 1983; 09°53′N, 59°53′W; 229 m; 3 Nov 1957. TU 180344 (2): Oregon 1981; 10°03′N, 60°01′W; 366 m; 3 Nov 1957. TU 180345 (2): Silver Bay 154; 28°58′N, 84°44′W; 139–148 m; 22 Aug 1957. TU 180346 (1): Oregon 1884; 16°53′N, 81°22′W; 411 m; 23 Aug 1957. TU 180347 (1): Silver Bay 100; 29°10′N, 85°48′W; 101–130 m; 26 Jul 1957. TU 180348 (1): Oregon 1986; 09°39′N, 59°47′W; 183 m; 4 Nov 1957. USNM 304921 (2): Oregon 4838; 11°09′N, 74°24′W; 329 m; 16 May 1965. USNM 343811 (2): Oregon 2658; 18°26′N, 67°11.5′W; 320 m; 7 Oct 1959. Examined for distribution information (Fig. 4): USNM 231943 (2), 278482 (4), 308117 (4), 347203 (6), 347222 (1), 347274 (1), 347275 (2), 347276 (2), 347277 (3), 347278 (1), 347279 (2), 347280 (5),

Table 8.—Frequency distribution of head width divided by head depth in nine Atlantic species of *Bembrops.*

Species	Standard length in mm	*n*	Ratio 1.1	1.2	1.3	1.4	1.5	1.6	1.7
B. anatirostris	65.8–246.0	50		9	20	18	3		
B. gobioides	84.6–217.4	50		6	25	15	4		
B. greyi	54.9–223.4	62	1	7	32	17	3	2	
B. heterurus	80.7–214.5	50	1	9	27	12	1		
B. macromma	77.3–190.0	45		2	29	14			
B. magnisquamis	72.0–104.2	6		1	—	1	3	1	
B. ocellatus	90.9–190.0	14			1	9	3	1	
B. quadrisella	127.5–235.3	16		1	4	7	4		
B. raneyi	69.1–167.3	19				4	11	3	1

347281 (4), 347282 (4), 347283 (3), 347284 (2), 347285 (8), 347286 (1).

Bembrops gobioides (Goode, 1880)
Goby duckbill

Dorsal fin in 178 specimens has VI, 16–18 soft rays, with a strong mode of 17 rays. Anal fin rays vary in number from 17 to 19, mostly 18. Pectoral fin rays range from 26 to 30, with a strong mode of 27 (Table 1). Lateral-line scales range from 60 to 70, $\bar{X}$ = 64.6 (Table 2). Gill rakers range from 4 to 6 on upper limb, 13 to 17 on lower limb, and total counts range from 17 to 22, usually 19 or 20 (Table 3). Number of vertebrae is almost always 30 (35 of 37), two counts of 29 (Table 4).

Based on 50 specimens ranging from 84.6 to 217.4 mm in SL, five have the orbit length equal to the length of snout but most specimens have the snout longer than the eye (Tables 5, 9). An additional small specimen (84 mm SL) not included in Tables 5 and 9 has the orbit slightly greater in length than length of snout. This observation matches that presented by Ginsburg (1955, Table 4) for an 81 mm SL specimen.

Bembrops gobioides typically has 17 soft dorsal rays, 18 anal rays, 27 or 28 pectoral rays, more than 60 lateral-line scales, and 30 vertebrae all among the highest values for these characters for the nine Atlantic species. Its 30 vertebrae contrasts with *B. anatirostris* which typically has 28 vertebrae. The caudal peduncle of *B. gobioides* is less deep than that in *B. anatirostris.* There is a more pronounced change in relative size of orbit and snout with respect to size of specimen than was observed for *B. anatirostris.* No small specimens of *B. anatirostris* has the orbit exceeding or equal to length of snout, whereas *B. gobioides* specimens between 80 to 85 mm in SL have the orbit equal to or greater than length of

Table 9.—Frequency distribution of snout length divided by orbit length in nine Atlantic species of *Bembrops.*

Species	Standard length in mm	*n*	Ratio 0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6
B. anatirostris	65.8–246.0	50					2	5	14	18	10	1
B. gobioides	84.6–217.4	50				5	17	21	7			
B. greyi	54.9–223.4	62	5	11	15	19	12					
B. heterurus	80.7–214.5	50					10	24	11	4	1	
B. macromma	77.3–190.0	45	1	10	12	18	4					
B. magnisquamis	72.0–104.2	6			3	3						
B. ocellatus	90.9–190.0	33			11	14	6					
B. quadrisella	127.5–235.3	94			6	50	18	17	3			
B. raneyi	69.1–167.3	19		3	8	3	4	1				

Table 10.—Maxillary tentacle length (expressed in thousandths of standard length) in nine Atlantic species of *Bembrops.*

Species	*n*	Range	$\bar{X}$	*SD*
B. anatirostris	53	33–71	51	9.42
B. gobioides	48	20–37	28	4.20
B. greyi	121	15–51	33	7.78
B. heterurus	98	12–50	30	8.83
B. macromma	87	7-27	18	4.60
B. magnisquamis	12	17–49	37	9.70
B. ocellatus	27	19–39	26	5.33
B. quadrisella	30	14–27	21	3.50
B. raneyi	38	31–59	41	7.47

snout. The maxillary tentacle of *B. gobioides* is small to moderate in length and is triangular in shape, whereas *B. anatirostris* has a very long tentacle that has an attenuate distal portion.

The spinous dorsal fin pigmentation of *B. gobioides* is similar in some respects to that described for *B. anatirostris*; the first two membranes are blackened, however there are additional wedges of black pigmentation at the distal ends of spines 3–6 (Fig. 1C).

Bembrops gobiodes has three short pyloric caeca, 6.0, 5.4, and 6.2 (left to right) % of SL.

Distribution/Depth.—Northwestern, northcentral and northeastern Gulf of Mexico; Dry Tortugas; southern Gulf of Mexico, north of Yucatan; off east coast of Florida; western Little Bahamas Bank; no records from Caribbean Sea (Fig. 5). Additional records in Ginsburg (1955), Grey (1959), Boschung (1992), and Das & Nelson (1996). The depth range of our *Bembrops gobiodes* is 329–549 m, with most specimens taken between 350 to 450 m. Ginsburg (1955) listed this species from 119–512 m and Grey (1959) reported it between 338 and 438 m. Das & Nelson (1996) reported it from about 100 to over 700 m. Bullis & Struhsaker (1970) reported the highest densities of *B. gobiodes* from the western Caribbean in two depth ranges, 276–366 m and 459–549 m, but these probably represent a composite of two of our new species since we have no valid records of this species from the Caribbean Sea.

Material examined.–TU 1709 (6): Oregon 61; 29°04′N, 88°30′W; 357 m; 2 Aug 1950. TU 2692 (1): Oregon 62; 29°01′N, 88°30′; 424 m; 2 Aug 1950. TU 2729 (4): Oregon 162; 27°18′N, 96°09′W; 366 m; 28 Nov 1950. TU 2730 (5): Oregon 163; 27°15′N, 96°00′W; 430 m; 28 Nov 1950. TU 11714 (8): Oregon 1520-80; 29°10′N, 88°10′W; 366–457 m; 16–19 May 1956. TU 12869 (4): Oregon 1107; 29°03′N, 88°25′W; 384–430 m; 15 Jun 1954. TU 12897 (5): Oregon 1093; 27°03′N, 96°16′W; 384 m; 4 Jun 1954. TU 12943 (13): Oregon 1091; 26°41′N, 96°20′W; 366–384 m; 3 Jun 1954. TU 14779 (2): Pelican 60; 28°29′N, 79°54′W; 293–347 m; 11 Jun 1956. TU 14810 (1): Pelican 66; 28°33′N, 79°52′W; 357–371 m; 13 Jun 1956. TU 17073 (25): Combat 332; 28°55′N, 79°56′W; 329 m; 31 May 1957 [pyloric caeca dissection]. TU 35788 (3): Oregon 4367; 24°31′N, 83°30′W; 375 m; 5 Aug 1963. TU 35802 (3): Oregon 4367; 24°31′N, 83°30′W; 375 m; 5 Aug 1963. TU 35803 (5): Oregon 4368; 24°31′N, 83°30′W; 375 m; 5 Aug 1963. TU 35805 (5): Oregon 4368; 24°28′N, 83°26′W; 384 m; 5 Aug 1963. TU 35832 (3): Oregon 4371; 24°28′N, 83°27′W; 375 m; 6 Aug 1963. TU 35863 (2): Oregon 4372; 24°29′N, 83°32′W; 375 m; 6 Aug 1963. TU 90280 (1): Oregon-II 13208; 29°16.1′N, 87°38.4′W; 457 m; 4 May 1973. TU 90300 (2): Oregon-II 13210; 29°15.6′N, 87°45.0′W; 411 m; 4 May 1973. TU 90320 (1): Oregon-II 13218; 29°14.5′N, 87°44′W; 494 m; 5 May 1973. TU 90342 (6): Oregon-II 13222; 29°10.4′N, 88°07.9′W; 366 m; 5 May 1973. TU 90398 (7): Oregon-II 13254; 28°54.7′N, 88°45.6′W; 347 m; 7 May 1973. TU 90406 (18): Oregon-II 13256; 29°00′N, 88°35.5′W; 347 m; 7 May 1973. TU 90425 (10): Oregon-II 13260; 28°55.2′N, 88°40′W; 411 m; 7 May 1973. TU 90468 (5): Oregon-II 13332; 24°23.4′N, 83°24.1′W; 402 m; 21 May 1973. TU 90485 (17): Oregon-II 13338; 24°20.1′N,

Table 11.—Summary of fin pigment patterns for nine Atlantic species of *Bembrops.*

Fin/species	Spinous dorsal	Second dorsal	Anal	Caudal	Pectoral	Pelvic
anatirostris	memb 1 & 2 dark grey; other memb light grey to clear; with black filament on spine 2	distal ½ of fin dark; basal ½ clear; pigment on entire length of rays	distal ½–⅔ of fin black; males with dusky base, females with base clear	uniform grey wash over entire fin	pigment along rays, most at base of center rays; blotch at dorsal base of rays 2–3	slight duskiness on post ½ of fin
greyi	♀: memb black, several clear spots memb 1–3; ♂: black at base & top of fin, clear center	2 dark bands, one distal, one basal, along entire fin	♀: clear fin; ♂: dusky or clear fin	♀: strong ocellus at dorsal fin base; ♂: lacks ocellus, some diffuse pigment at base; 2 dark bands & mottling at posterior ½	dark pigment along rays; fin with dark crescent at fin base on medial side of fin	post ½ dusky, ant ½ clear
gobioides	memb 1 & 2 dark; distal margins of other memb black; some with black at base of memb 2–4	2 dark bands; distal one along entire fin, basal band widely interrupted by clear areas	usually clear; some ♂♂ with slight duskiness	ventral and post margins black; ♀ with ocellus or dark blotch, ♂ lack ocellus	melanophores on rays, mostly on ventral ⅓ of fin; dark crescent at fin base	slight duskiness on post ½ of fin
heterurus	ant ½ of memb 1 dark; rest of fin with grey wash	clear to light brown-grey wash; no distinct pattern	single black band on distal ½ of entire fin length	slight grey-brown wash; no distinct pattern	melanophores along rays, darker at base of center rays	some with duskiness on post ½ of fin
macromma	memb 1 & 2 (sometimes part of 3) black; rest of fin clear or slightly dusky	distal fifth of fin with black band	♀: very thin black band or clear fin; ♂: black band on distal ¼ of fin	post ¼–⅓ black	slight scattering of melanophores on rays	small melanophores on rays and memb at edge of rays
magnisquamis	basal black blotch memb 2–4; memb 1 all black	basal black along length of fin; slight distal black band	slight black at distal margin; most of fin clear	dusky across fin; 2 distinct black spots	pigment on rays concentrated at base on both sides of fin	pigment on membranes and edge of rays 3–5
ocellatus	basal black blotch in memb 1–5; submarginal black blotch in memb 1–3; melanophores in memb 1, 4, 5	most of fin clear; black at base of rays 1–5 & 9–13 (at saddles); black on distal ¼ of rays	usually clear; few melanophores in some specimens; post rays with slight basal pigment	♀: large ocellus in dorsal fin base; ♂: wedge of black in same location; dorsal, post and ventral margin black	melanophores on rays	small melanophores on rays in post ½ of fin

Table 11.—Continued.

Fin/species	Spinous dorsal	Second dorsal	Anal	Caudal	Pectoral	Pelvic
quadrisella	small basal black blotch in memb 1; submarginal black in all memb with triangular extension in memb 1 & 2; some scattered melanophores in memb	dusky membranes; some black at base of ant memb; white bands in fin	♀: light grey or clear; about distal ½–⅔ of fin black; white pigment on memb	♀: ocellus at dorsal fin base; ♂: no ocellus; post and ventral margins dark	melanophores on rays; white pigment at base of lower rays	post ½ dusky; outer memb darker; white pigment on both surface of fin memb at base of fin
raneyi	submarginal black band in memb 1 & 2; large basal black blotch in membs 2–4, covering ½ of memb 3 & 4	black at base of rays 1–5 & 10–12; distal black band	clear in both sexes	black blotch, often as an ocellus at base of fin extending onto body; ventral and post margins black; post ½ of dorsal margin black; dusky at center of fin	melanophores on rays except ventral 4–5 rays that are clear	few light, scattered melanophores

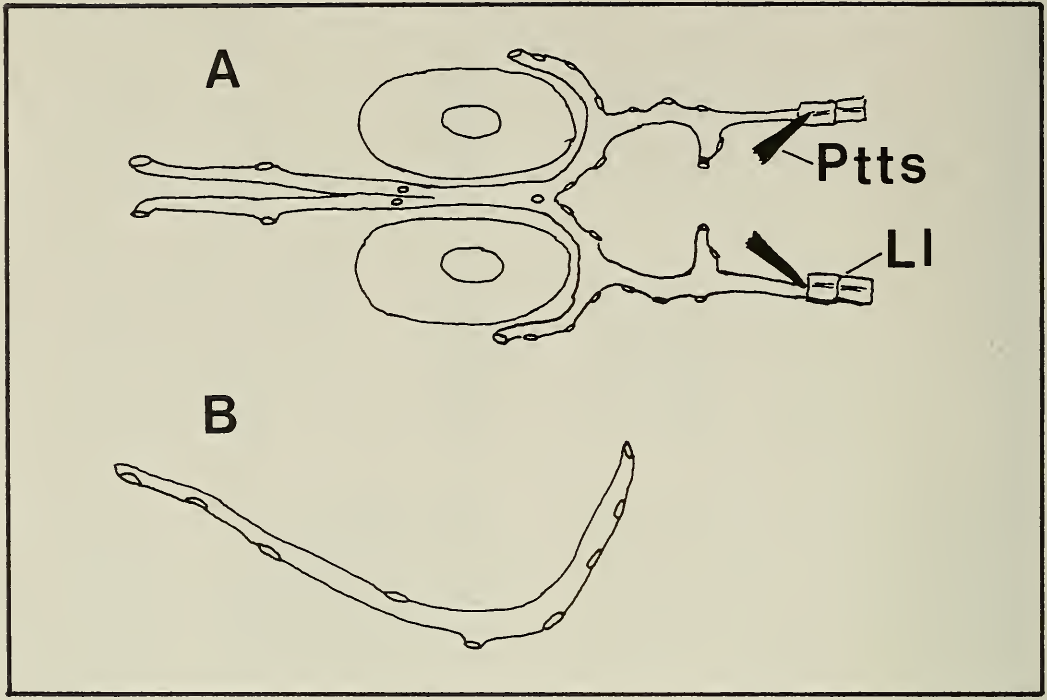

Fig. 2. Cephalic sensory pore system: A. Composite of *Bembrops anatirostris*, *B. ocellatus*, and *B. raneyi*. B. Right preoperculomandibular canal of *B. ocellatus*. Ptts = posttemporal spine, L1 = lateral-line.

83°09.9′W; 402 m; 22 May 1973. TU 90503 (13): Oregon-II 13344; 24°16′N, 82°52.7′W; 402 m; 22 May 1973. TU 90565 (1): Oregon-II 13362; 24°09′N, 82°31′W; 549 m; 23 May 1973. TU 180143 (1): Silver Bay 221; 29°21′N, 80°06′W; 329–347 m; 22 Nov 1957. TU 180144 (1): Silver Bay 212; 29°59′N, 80°07′W; 366 m; 20 Nov 1957. TU 180145 (1): Silver Bay 224; 29°29′N, 80°09′W; 329 m; 24 Nov 1957. TU 180146 (1): Silver Bay 217; 29°41′N, 80°08′W; 329–366 m; 21 Nov 1957. TU 180147 (2): Combat 464; 27°51′N, 79°50′W; 393 m; 29 Jul 1957. TU 180148 (1): Combat 482; 29°28′N, 80°08′W; 347 m; 17 Aug 1957. TU 180149 (5): Combat 317; 29°07′N, 80°04′W; 366 m; 27 Apr 1957. TU 180150 (6): Combat 462; 27°14′N, 79°50′W; 384 m; 29 Jul 1957. TU 180151 (3): Combat 330; 29°08′N, 80°03′W; 347 m; 31 May 1957. TU 180152 (4): Combat 314; 29°38′N, 80°11′W; 329 m; 27 Apr 1957. TU 180153 (5): Combat 467; 28°36′N, 79°54′W; 402 m; 30 Jul 1957. TU 180154 (2): Combat 479; 29°22′N, 80°06′W; 366 m; 17 Aug 1957. TU 180155 (1): Combat 316; 29°20′N, 80°04′W; 393 m; 27 Apr 1957. TU 180156 (3): Combat 463; 27°22′N, 78°50′W; 402 m; 29 Jul 1957. TU 180349 (1): Combat 501; 29°36′N, 80°07′W; 384 m; 12 Sep 1957.

Bembrops greyi Poll, 1959
Blackfin duckbill

Dorsal fin in 60 specimens has VI, 15 to 17 soft rays, with a strong mode of 16 rays. Anal fin has 17 or 18 rays, with a greater frequency of 18 rays. Pectoral fin rays range from 25 to 27 in number, with a mode of 26 (Table 1). Lateral-line scales range from 45 to 52, $\bar{X}$ = 49.2 (Table 2). Gill rakers range from 3 to 5 on upper limb, 12 to 14 on lower limb, and total counts range from 15 to 19, usually 17 or 18 (Table 3).

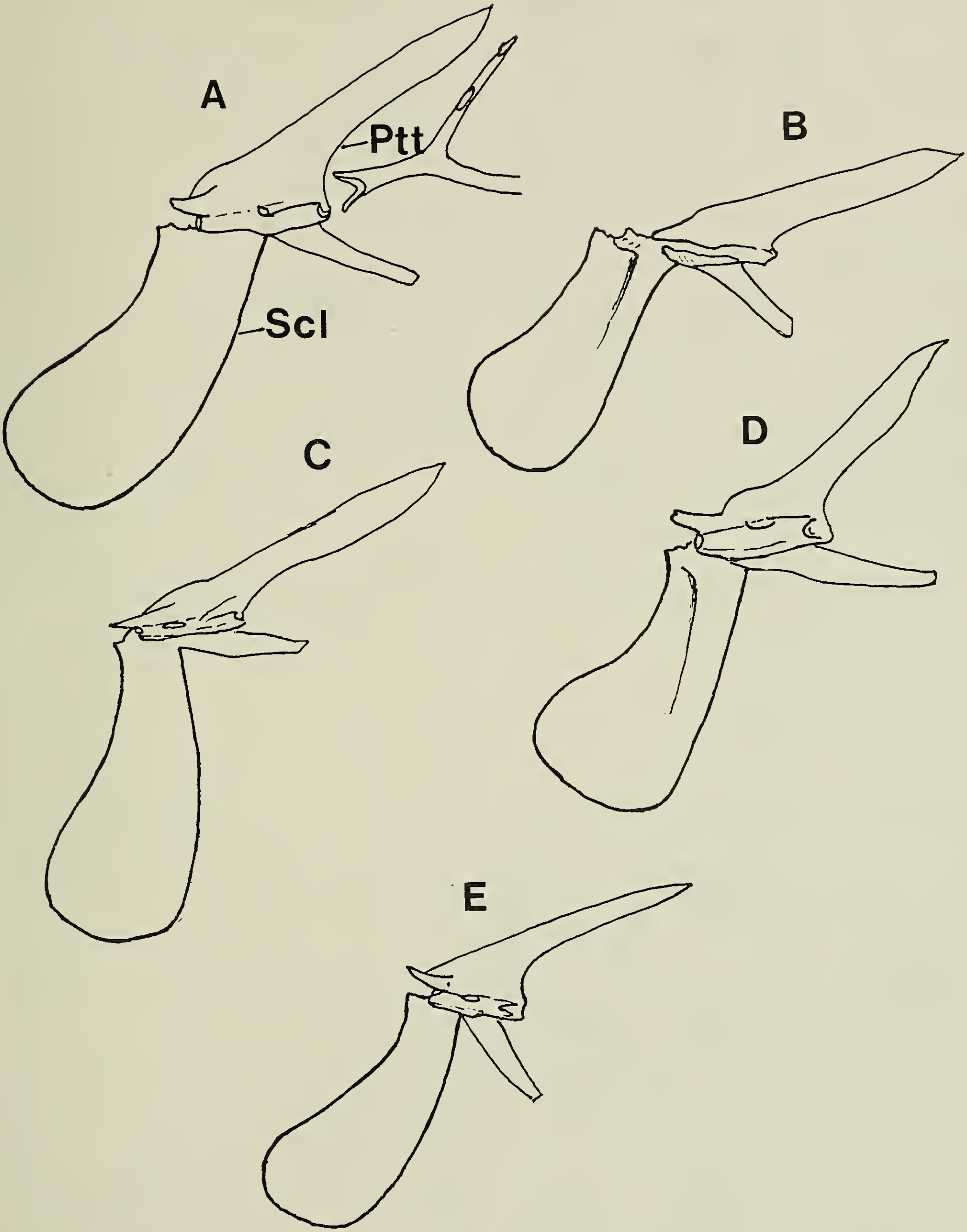

Fig. 3. Posttemporal and supracleithrum of five species of *Bembrops:* A) *B. anatirostris*, B) *B. gobioides*, C) *B. greyi*, D) *B. heterurus*, and E) *B. macromma*. Ptt = posttemporal, Scl = supracleithrum.

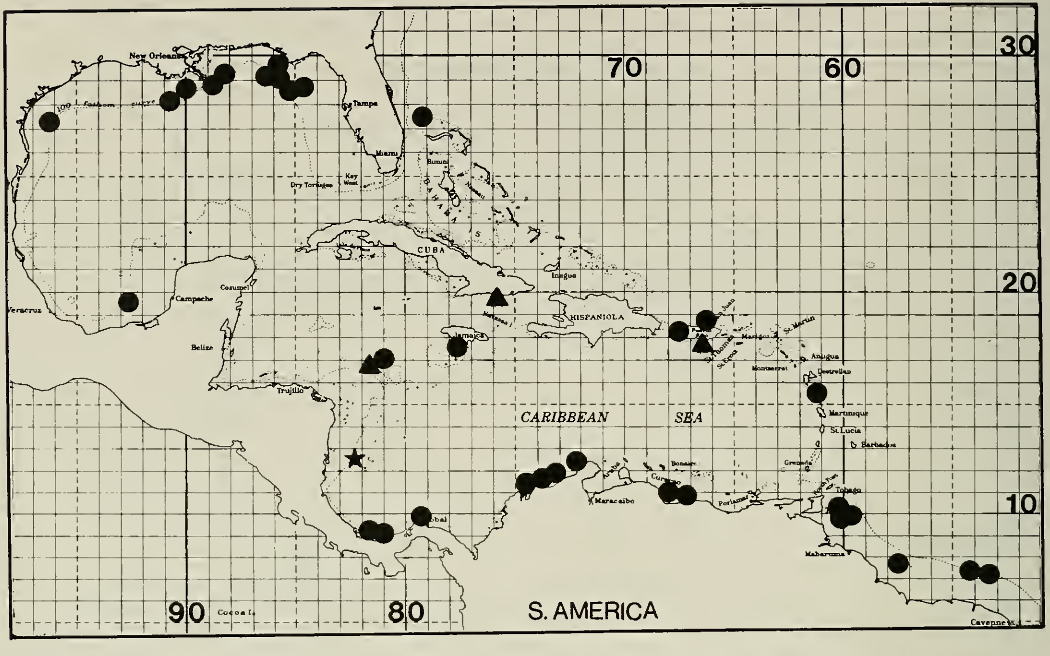

Fig. 4. Distribution of *Bembrops anatirostris* (●), *B. magnisquamis* (▲), and (★) both species.

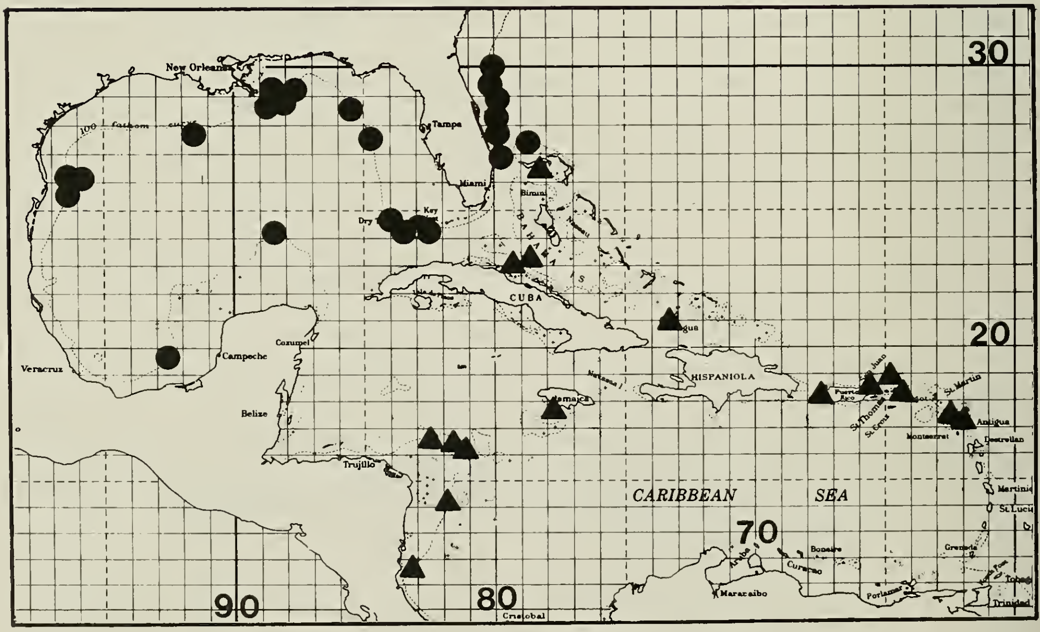

Fig. 5. Distribution of *Bembrops gobioides* (●), *B. macromma* (▲).

Number of vertebrae is typically 30, however eight have 29 (Table 4).

Based on 62 specimens ranging from 54.9 to 223.4 mm SL; half (31 specimens) have the orbit length greater than length of snout; the orbit and snout lengths are equal in 19 specimens; and in 12 specimens the snout length is greater than the orbit length (Table 9).

Based on 121 maxillary tentacle measurements (representing 62 specimens) the tentacle length in *B. greyi* is slightly greater than average among the nine species (Table 10), although *B. anatirostris*, *B. raneyi*, and *B. magnisquamis* have longer tentacles.

In summary, *Bembrops greyi* has a low number of lateral-line scales with only *B. magnisquamis* having as low a lateral-line scale count. *Bembrops greyi* has the lowest average number of gill rakers of the nine species and typically has a high number of vertebrae (30). *Bembrops greyi* has a short snout and a moderately long maxillary tentacle.

The spinous dorsal fin pigmentation in *Bembrops greyi* is unique, in that, except for several small, irregular-shaped clear windows, the entire fin is jet-black (Fig. 1B).

Bembrops greyi has three medium-length pyloric caeca, 6.8, 6.4, and 6.9 (left to right) % of SL.

Distribution/Depth.—Eastern Atlantic Ocean in Gulf of Guinea off Grand-Bassam, Cote D'Ivoire, off Lagos, Nigeria; and from equator near Port Gentil, Gabon southward to Pointe Noire, Congo. We examined three collections with *Bembrops greyi* taken with *B. heterurus* (Fig. 6). Additional records in Poll (1959) and Das & Nelson (1996). Our records of *Bembrops greyi* range from a depth of 101–494 m, with the largest series (19) containing many juveniles at the shallowest depth. Most collections are from 300–400 m. Poll (1959) reported it between 250–420 m, Blache et al. (1970) between 250–400 m, and Das & Nelson (1996) from 250–420 m.

Material examined.—CU 48206 (19): Geronimo 2-199; 01°26′S, 08°24′E; 400 m; 3 Sep 1963. CU 48215 (1): Geronimo 2-220; 03°02′S, 09°21′E; 300 m; 6 Sep 1963. CU 48216 (6): Geronimo 2-205; 01°57′S, 08°47′E; 400 m; 4 Sep 1963. CU 48217 (1): Geronimo 2-238; 04°07′S, 10°23′E; 400 m; 8 Sep 1963. CU 48218 (1): Geronimo 2-179; 00°02′S, 08°50′E; 295 m; 31 Aug 1963. CU 48219 (1): Geronimo 2-237; 04°03′S, 10°22′E; 300 m; 8 Sep 1963. CU 48220 (6): Geronimo 2-246; 04°31′S, 10°53′E; 300 m; 9 Sep 1963. CU 48221 (5): Geronimo 2-204; 01°56′S, 08°47′E; 300 m; 4 Sep 1963. UF 216947 (3): Pillsbury 51; 04°56′N, 05°01′W–04°56′N, 05°03′W; 329–494 m; 31 May 1964 [pyloric caeca dissection]. UF 220549 (19): Pillsbury 236; 05°20′N, 04°45′E–05°19′N, 04°48′E; 101–128 m; 12 May 1965.

Bembrops heterurus (Ribeiro, 1903)
Robust duckbill

Next to *Bembrops macromma*, *B. heterurus* has the lowest number of dorsal soft rays. The dorsal fin formula for *B. heterurus* is VI, 14 to 16 soft rays, with a strong model count of 15. Anal fin rays are usually 18, only six specimens deviate from this count. Pectoral fin ray counts are either 26 or 27, and 27 is the more frequent number (Table 1).

Bembrops heterurus has an intermediate number of lateral-line scales, between the high counts of *B. anatirostris* and *B. gobioides* and the low counts of *B. greyi* and *B. magnisquamis.* Lateral-line scales range from 55 to 60, $\bar{X}$ = 56.5, being most similar to *B. macromma* (Table 2) and overlapping the counts of the three new species.

Bembrops heterurus exceeds *B. greyi* in number of gill rakers; there are either four or five on upper limb, range from 13 to 16 on lower limb, and total counts range from 17 to 21 (Table 3). *Bembrops heterurus* and *B. greyi* differ markedly in number of vertebrae; *B. heterurus* typically has 28 where *B. greyi* typically has 30 vertebrae (Table 4).

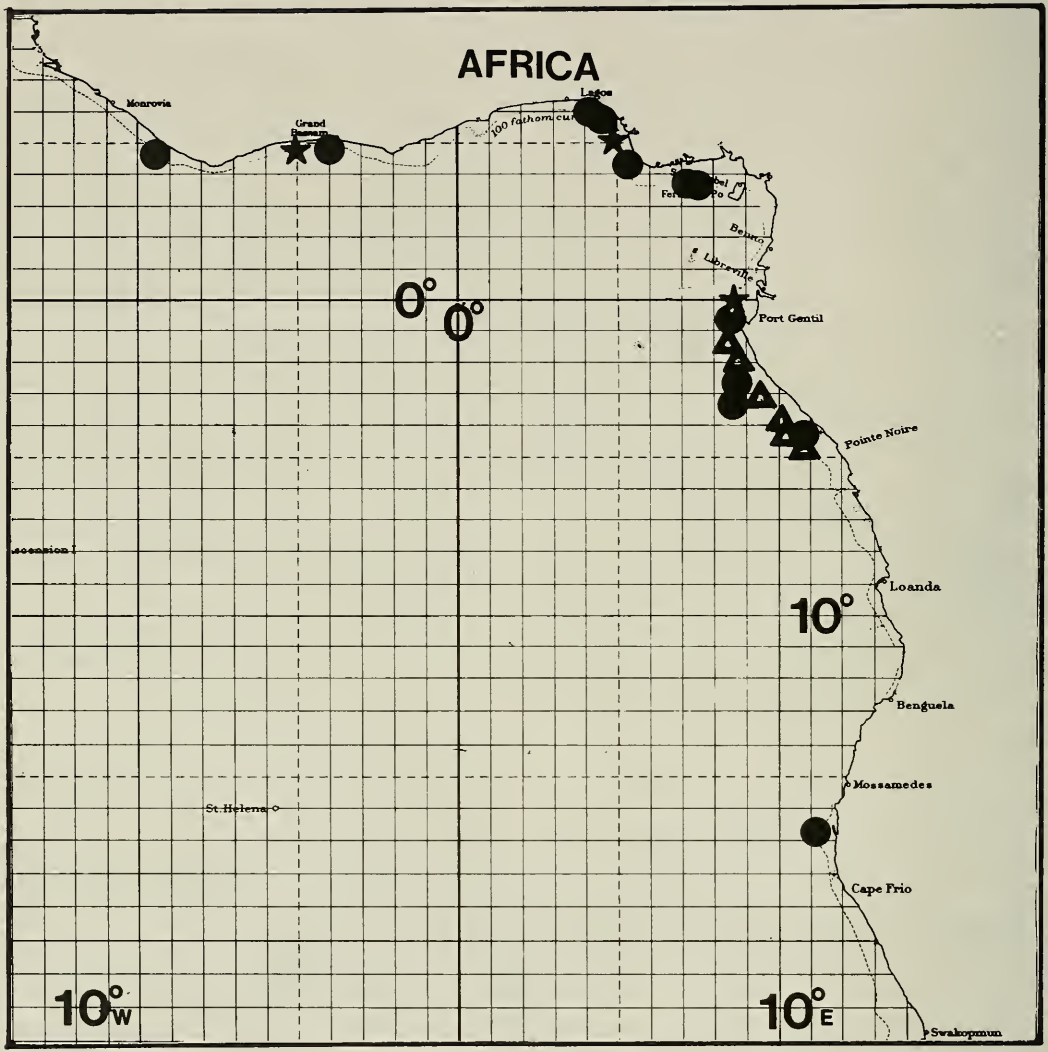

Fig. 6. Distribution of *Bembrops greyi* (△) and *B. heterurus* (●) based on specimens examined in this study. Three syntopic collections (★).

Based on 50 specimens ranging from 80.7 to 214.5 mm SL, all have a snout greater than the eye; with none having the orbit length greater than or equal to length of snout (Tables 6 and 9).

Maxillary tentacle lengths are quite similar in *B. heterurus* and *B. greyi* (Table 10), with *B. heterurus* having the third longest tentacle among the Atlantic species.

The spinous dorsal fin pigmentation in *Bembrops heterurus* contrasts greatly with that described for *B. greyi*. Only the anterior half of the first membrane is blackened in *B. heterurus*, with the rest of the fin clear or slightly dusky (Fig. 1D), whereas, except for small clear areas the entire fin is jet-black in *B. greyi*.

Bembrops heterurus has three moderately-long pyloric caeca, 9.7, 10.1, 9.6 (left to right) % of SL.

Distribution/Depth.—Eastern Atlantic Ocean in Gulf of Guinea off southeastern Liberia; off Cote D'Ivoire in Bight of Benin and Bight of Bonny near Fernando Poo;

southward along African coast from Port Gentil, Gabon to Pointe Noire, Congo; one record near Baia dos Tigres, southern Angola (Fig. 6). We examined three collections that had *Bembrops heterurus* taken with *B. greyi.* Bianchi et al. (1993) reported *Bembrops heterurus* as rare in Namibia its southernmost distribution along the west coast of Africa. Depth for *Bembrops heterurus* used in this study ranged from 64–494 m, with most records between 150 and 300 m. Poll (1959) reported this species between 100 and 300 m. Fager & Longhurst (1968) found *B. heterurus* to be part of a "species group" centered around 200 m depth. Blache et al. (1990) gave a range between 100–400 m. Das & Nelson (1996) reported a depth range for South American specimens of this species from 90–200 m.

Material examined.—CU 48207 (6): Geronimo 2-197; 01°30′S, 08°27′E; 200 m; 3 Sep 1963. CU 48208 (1): Geronimo 2-187; 00°32′S, 08°40′E; 300 m; 1 Sep 1963. CU 48209 (5): Geronimo 2-245; 04°31′S, 10°54′E; 200 m; 9 Sep 1963. CU 48210 (1): Geronimo 2-185; 00°32′S, 08°42′E; 200 m; 1 Sep 1963. CU 48211 (1): Geronimo 2-213; 02°31′S, 08°51′E; 300 m; 5 Sep 1963. CU 48212 (5): Geronimo 2-212; 02°30′S, 08°58′E; 200 m; 5 Sep 1963. CU 48213 (2): Geronimo 2-227; 03°30′S, 08°53′E; 200 m; 7 Sep 1963. CU 48214 (5): Geronimo 2-203; 02°01′S, 08°50′E; 200 m; 4 Sep 1963. TU 180287 (3): Undaunted 252; 16°41′S, 11°21′E; 164–182 m; 18 Mar 1968. UF 47051 (1): Geronimo 2-179; 00°02′S, 08°50′E; 295 m; 31 Aug 1963. UF 216954 (1): Pillsbury 51; 04°56′N, 05°01′W–04°56′30″N, 05°03′W; 329–494 m; 31 May 1964. UF 216958 (1): Pillsbury 82; 04°57′N, 09°30′W–04°58′N, 09°32′W; 146–150 m; 5 Jun 1964. UF 216974 (4): Pillsbury 45; 05°05′N, 04°04′30″W–05°06′N, 04°06′W; 73–97 m; 30 May 1964. UF 220545 (7): Pillsbury 255; 03°49′N, 07°38′E–03°48′N, 07°42′E; 264–269 m; 14 May 1965 [pyloric caeca dissection]. UF 220546 (8): Pillsbury 232; 05°56′N, 04°27′E–05°54′N, 04°27′E; 101–132 m; 11 May 1965. UF 220547 (5): Pillsbury 237; 05°19′N, 04°48′E–05°07′N, 04°55′E; 101 m; 12 May 1965. UF 220548 (2): Pillsbury 236; 05°20′N, 04°45′E–05°19′N, 04°48′E; 101–128 m; 12 May 1965. UF 220551 (7): Pillsbury 245; 04°32′N, 05°07′E–04°31′N, 05°13′E; 64–119 m; 13 May 1965. UF 220552 (11): Pillsbury 254; 03°50′N, 07°08′E–03°51′N, 07°12′E; 148–174 m; 14 May 1965.

Bembrops macromma Ginsburg, 1955
Scaled-eye duckbill

Dorsal fin rays in all specimens are VI, 14. *Bembrops macromma* is unique among the Atlantic species in its consistent low number of dorsal soft rays. The only other species with 14 soft dorsal rays are *B. anatirostris* and *B. heterurus* and this is rare. Anal fin rays are usually 18 in number, but frequently are 17. Pectoral fin rays are usually 25, but frequently 26, rarely 24 (Table 1).

Bembrops macromma is similar to *B. heterurus* in having an intermediate number of lateral-line scales, 53 to 60, $\bar{X} = 56.0$ (Table 2). Gill rakers range from 4 to 6, usually 5, on upper limb, range from 12 to 15, usually 14 or 15, on lower limb, and total counts range from 16 to 21, predominantly 19 or 20 (Table 3).

Bembrops macromma, like *B. anatirostris* and *B. heterurus* has a low number of vertebrae, usually 28, very rarely 27, the lowest vertebral number for Atlantic *Bembrops* (Table 4).

Both *Bembrops macromma* and *B. heterurus* have stocky bodies, illustrated by the greater depth of head, depth of body at origin of first dorsal fin, and depth of caudal peduncle. *Bembrops macromma* has a short snout and large orbit whereas *B. heterurus* has a relatively long snout and a small orbit (Table 9). *Bembrops macromma* also differs from *B. heterurus* in length of maxillary tentacle, having the shortest tentacle of the nine species treated in this study (Table 10).

Bembrops macromma is unique in the

genus in possessing scales on the dorsal surface of the eyes. Adults have 20–35 thin, cycloid scales covering each eye between the pupil and interorbit. Juveniles have fewer scales, but all specimens of this species possess these scales.

In summary, *Bembrops macromma* has a low number of soft dorsal rays, usually 18 anal rays, and usually 25 pectoral rays. It has an intermediate number of lateral-line scales and a low number of vertebrae as does *B. heterurus.* Moreover, both *B. macromma* and *B. heterurus* are relatively stout-bodied forms. However, *B. macromma* has a shorter maxillary tentacle and also has a short snout and large orbit, whereas *B. heterurus* has a relatively long snout and a small orbit. *Bembrops macromma* has most of the anterior two membranes (rarely part of the third) blackened in the spinous dorsal fin (Fig. 1E) and *B. heterurus* has black pigmentation only in the anterior half of the first membrane.

Bembrops macromma has three short pyloric caeca, 5.6, 6.0, and 6.0 (left to right) % of SL, across the dorsal surface of the stomach.

Distribution/Depth.—Western Caribbean Sea on shelf along Honduras, Nicaragua, and Costa Rica; south side of Jamaica; north side of Cuba; three Bahama records—one from just south of Grand Bahama Island, one from southwestern edge of Great Bahama Bank, and one at Great Inagua Island; west and northwest of Puerto Rico (taken with *B. anatirostris*); and from northern Leeward Islands (Fig. 5). We cannot confirm Das & Nelson's (1996) Gulf of Mexico record (Fig. 12); this species appears to be absent from the Gulf of Mexico. Uyeno et al. (1983) include *B. macromma* as one of two species in the family occurring off Suriname and French Guiana. We have not been able to substantiate this, and Das & Nelson (1996) also did not include South America in their range of this species. Specimens of *Bembrops macromma* used in this study ranged from 192–512 m in depth, with most specimens taken between 250 and 400 m. Ginsburg (1955) reported the types of this species from 274 and 549 m and Grey (1959) found it at 438 and 457 m. Das & Nelson (1996) reported it between 150 and 550 m, with "most specimens below 250 m".

Material examined.—TU 12769 (2): Oregon 1341; 22°55′N, 79°16′W; 439 m; 16 Jul 1955. TU 12787 (1): Oregon 1341; 22°55′N, 79°16′W; 439 m; 16 Jul 1955. TU 18781 (3) and UF 202714 (5): Oregon 1879; 16°38′N, 81°39′W; 274 m; 22 Aug 1957 [pyloric caeca dissection]. TU 19933 (1): Oregon 1878; 16°39′N, 81°43′W; 230 m; 22 Aug 1957. TU 180136 (1): Oregon 1902; 11°27′N, 83°11′W; 247 m; 9 Sep 1957. UF 15615 (2): Oregon 3623; 16°08′N, 81°13′W; 192–201 m; 6 Jun 1962. UF 207119 (2): Oregon 2649; 18°12′N, 64°18′W; 274 m; 6 Oct 1959. UF 220555 (1): Gerda 692; 26°35′N, 78°25′W–26°34′N, 78°26′W; 21 Jul 1965. USNM 157983 (2): Oregon 1344, 22°50′N, 79°08′W; 366–411 m; 16 Jul 1955. USNM 304922 (4): Oregon 2658; 18°26′N, 67°11′30″W; 320 m; 7 Oct 1959. UF 47052 (2), USNM 304923 (8), USNM 304928 (2): Oregon 3549; 17°50′N, 77°52′W; 311 m; 16 May 1962. USNM 304925 (3), USNM 347204 (2): Oregon 10559; 23°04′N, 78°46′W; 347–377 m; 15 Dec 1969. USNM 304926 (5): Oregon 6699; 17°38′30″N, 62°16′W; 19 May 1967. USNM 304927 (3), USNM 342603 (2): Oregon 6700; 17°27′N, 62°04′W; 249–285 m; 19 May 1967. USNM 304929 (2): Oregon-II 10195; 14°17′N, 81°55′W; 329 m; 19 Nov 1968. USNM 342604 (1): Oregon 3625; 16°26′N, 81°35′W; 219 m; 6 Jun 1962. USNM 347205 (1): Oregon-II 10849; 20°50′N, 73°20′W; 311 m; 13 Dec 1969. CAS 61007 (2): Oregon-II 46095; 18°13′18″N, 67°19′30″W; 366 m; 21 Aug 1987. CAS 61010 (10): Oregon-II 46096; 18°13′30″N, 67°18′42″W; 357–384 m; 21 Aug 1987. CAS 61011 (1): Oregon-II 46062; 18°30′00″N, 65°42′12″W; 441–512 m; 15 Aug 1987.

Bembrops magnisquamis Ginsburg, 1955
Largescale duckbill

The small number (8) of specimens precludes much discussion and comparison. Dorsal fin formula is typically VI, 15 soft rays; anal fin has 17 rays; and pectoral fin ray counts are low, 22 to 24 (Table 1). Lateral-line scale counts are the lowest for any Atlantic *Bembrops*, ranging from 44 to 47 (Table 2). Gill raker counts are either 4 or 5 on upper limb, range from 13 to 16 on lower limb, and total counts range from 18 to 21 (Table 3). All eight specimens of *Bembrops magnisquamis* have 29 vertebrae, an intermediate number (Table 4). *Bembrops magnisquamis* has a relatively deep caudal peduncle and a very wide head (Table 8). Also, *B. magnisquamis* has a short snout and a large orbit, thus in three of the six specimens the orbit length is equal to length of snout and in the other three specimens the orbit length is greater than the snout (Table 9).

Bembrops magnisquamis has a relatively long maxillary tentacle in comparison to the other eight species considered in this study.

The anterior (first) membrane in the spinous dorsal fin is entirely black or with dark pigment at margin and base, with center of membrane clear. Membranes two and three are black on basal half and the pigmented basal portion is progressively less on succeeding membranes four and five. Membrane six is clear in all specimens examined (Fig. 1F). This spinous dorsal fin pigmentation of *B. magnisquamis* is distinct but has slight resemblance to two of the new forms described below. There is a thin dash of pigment along the midline of the nape just anterior to the spinous dorsal fin in *B. magnisquamis* that is not present in any other Atlantic *Bembrops*.

Distribution/Depth.—Type locality off S coast of Cuba; two sites in western Caribbean Sea, one off Honduras, one off Costa Rica; one locality in eastern Caribbean Sea, S of Puerto Rico (Fig. 4); other records (USNM) re-identified as *B. macromma*. We cannot confirm two records shown in Fig. 9, Das & Nelson (1996). Specimens of *Bembrops magnisquamis* used in this study ranged from 366–622 m. Ginsburg (1955) reported the types of the species from 366 and 465 m. Bullis & Struhsaker (1970) found *B. magnisquamis* between 368 and 640 m, with the highest densities in two depth strata, 368–457 m and 550–640 m. We examined one collection of *B. magnisquamis* taken with *B. anatirostris* off Costa Rica.

Material examined.—USNM 45985 and 108395, holotype and paratype as listed in Ginsburg (1955). TU 180138 (1): Oregon 1883; 16°52′N, 81°30′W; 366 m; 23 Aug 1957. USNM 304924 (4): Oregon 3574; 12°31′N, 82°21′W; 366 m; 23 May 1962. CAS 61008 (1): Oregon-II 46026; 17°44′42″N, 66°12′42″W; 366–622 m; 9 Aug 1987.

Bembrops ocellatus, new species
Ocellate duckbill
Fig. 7

Bembrops anatirostris.—Das & Nelson, 1996 (in part, locality in Caribbean Sea off Nicaragua).

Material.—39 specimens (93.2–187.5 mm SL) from 23 localities. Holotype.—TU 181281, a female 135 mm SL, Atlantic Ocean, off Venezuela, 09°17′N, 59°19′W, 503 m, 4 Nov 1957, Oregon Sta. 1992, 45′ trawl.

Paratypes.—TU 180353 (2): 117–126 mm SL, same data as holotype. TU 181668 (1): 91 mm SL, western Caribbean Sea, 16°41′N, 82°20′W, 549 m, 22 Aug 1957, Oregon Sta. 1872, 40′ flat trawl. CU 43877 (5): 97.0–146.0 mm SL, western Caribbean Sea, no locality data, May or Jun, 1962, Oregon Cruise 78, depth not known. UF 207128(1): 116 mm SL, eastern Caribbean Sea, off Venezuela, 11°36′N, 62°52′W, 394–421 m, 20 Apr 1960, Oregon Sta. 2780. USNM 307592 (3): 95.1–137.3 mm SL, Caribbean Sea off Nicaragua, 14°08′N,

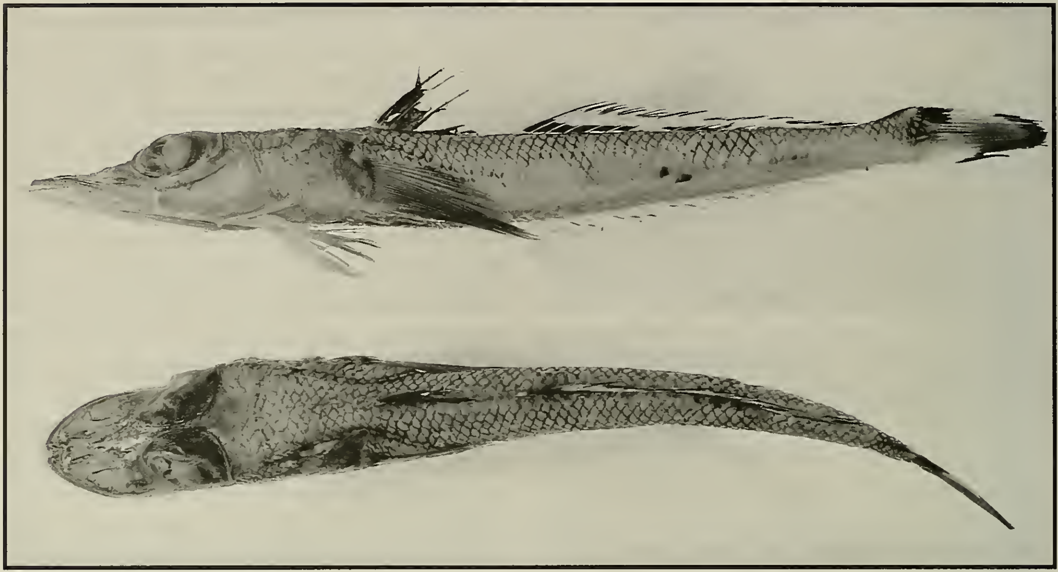

Fig. 7. *Bembrops ocellatus*, paratype, CAS 61006, 187.5 mm SL, female.

81°55′W, 366–439 m, 21 May 1962, Oregon Sta. 3570. USNM 344486 (3): 112.6–128.8 mm SL, Caribbean Sea off Venezuela, 11°49′N, 69°24′W, 549 m, 3 Oct 1963, Oregon Sta. 4412. USNM 347200 (1): 200 mm SL, Atlantic Ocean off Suriname, 07°27′N, 54°30′W, 201 m, 16 May 1962, Oregon-II Sta. 10622. USNM 347201 (1): 125.2 mm SL, Atlantic Ocean off Grenada, 12°01′N, 61°53.5′W, 384–457 m, 26 Sep 1964, Oregon Sta. 5043. USNM 347202 (1): 142.1 mm SL, Caribbean Sea off Nicaragua, 12°26′N, 82°24′W, 503 m, 2 Jun 1962, Oregon Sta. 3609. USNM 347214 (1): 156.5 mm SL, Caribbean Sea off Nicaragua, 13°39′N, 81°52′W, 503 m, 13 Sep 1957, Oregon Sta. 1923. USNM 347215 (2): 145.2–159.7 mm SL, Caribbean Sea off Colombia, 11°26′N, 74°14′W, 576 m, 3 Dec 1968, Oregon-II Sta. 10268. USNM 347216 (1): 169.4 mm SL, Atlantic Ocean N of St. Kitts & Nevis, 17°41′N, 62°50.5′W, 549–585 m, 18 May 1967, Oregon Sta. 6695. USNM 347217 (1): 144.0 mm SL, Atlantic Ocean NE off Dominica, 15°42′N, 61°08′W, 640 m, 1 Dec 1969, Oregon-II Sta. 10825. USNM 347254 (1): 143.0 mm SL, Caribbean Sea NW of Trinidad, 11°36′N, 62°42′W, 430 m, 19 Apr 1960, Oregon Sta. 2776. USNM 347261 (1): 93.2 mm SL, Caribbean Sea S of Jamaica, 17°40′N, 77°55′W, 530 m, 16 May 1962, Oregon Sta. 3552. USNM 347262 (1): 93.5 mm SL, Caribbean Sea W of St. Kitts & Nevis, 17°20′N, 62°52′W, 549–567 m, 30 Sep 1964, Oregon Sta. 5072. CAS 14632 (1): 123.2 mm SL, Caribbean Sea off Venezuela, 11°53′N, 69°28′W, 421 m, 28 Sep 1963, Oregon Sta. 4408, 40′ flat trawl. CAS 61006 (1): 187.5 mm SL, Atlantic Ocean off NE Puerto Rico, 18°31′12″N, 65°40′36″W, 439–512 m, 15 Aug 1987, Oregon-II Sta. 46061. CAS 150896 (1): 118.9 mm SL, Atlantic Ocean off Surinam, 07°34′N, 54°49′W, 411 m, 7 Nov 1957, Oregon 2007, 40′ flat trawl. CAS 98923 (1): 134.0 mm SL, Caribbean Sea, Lesser Antilles off St. Kitts and Nevis, 17°09′00″N, 66°44′48″W, 512–768 m, 4 Aug 1978, Oregon-II Sta. 24263.

Other materials.—USNM 347263 (1): 136.2 mm SL, Caribbean Sea W of Anguilla, 18°07′N, 63°20′W, 658 m, 7 Dec 1969, Oregon-II Sta. 10837. USNM 347264 (1): 140.4 mm SL, Caribbean Sea off Honduras, 16°51′N, 82°14′W, 585 m, 15 Nov

1968, Oregon-II Sta. 10176. USNM 347272 (3): 141.7–210 mm SL, Caribbean Sea off Venezuela, 10°57′N, 67°02′W, 457 m, 12 Oct 1963, Oregon Sta. 4454. USNM 347273 (3): 137.8–162.7 mm SL, SW Caribbean Sea off NW coast of Colombia, 10°16.2′N, 75°54.5′W, 549 m, 25 May 1964, Oregon Sta. 4882.

Diagnosis.—Dorsal fin usually VI-16 (rarely VI-15 or VI-17). Anal fin ranges from 16 to 19, usually 18. Pectoral fin usually 26, but varies from 25 to 27. Lateral-line scales 55–65, most often 58 to 63, $\bar{X} = 60.2$. Gill rakers usually 5 on upper limb, usually 15 on lower limb, and total count usually 20. Vertebral number usually 30 (29 in two). Ratio of head width divided by depth of head ranges from 1.3 to 1.6, usually 1.4, $\bar{X} = 1.43$. Snout short, usually slightly shorter, equal to or slightly longer than length of orbit (eye). Maxillary tentacle short, averaging only 2.6% of SL. The lateral-line has a moderately steep slope, reaching its lowest point under spines 5 or 6 of the first dorsal fin. *Bembrops ocellatus* possesses two (rarely four) wide black dorsal saddles, located under the posterior portion of the second dorsal fin at rays 10–13, and on the posterior part of the caudal peduncle at the start of the secondary caudal fin rays, sharing this character only with *B. quadrisella* and *B. raneyi* in the Atlantic members of the genus, but differing from both *B. quadrisella* and *B. raneyi* in that the anterior two saddles, when present, are usually less defined than the posterior two saddles.

Description.—*Bembrops ocellatus* is most similar to *B. gobioides*, *B. quadrisella*, and *B. raneyi*, having high scale, fin-ray, and vertebral counts (Tables 1–4). *Bembrops ocellatus* lacks the intense black, ‘x’ and ‘v’ secondary scale pigment that characterizes *B. gobioides*. *Bembrops ocellatus* lacks a black band in the anal fin, differing from *B. anatirostris*, *B. heterurus*, *B. macromma*, and *B. quadrisella* whose males have a black band in the anal fin. *Bembrops ocellatus*, similar to *B. raneyi*, but differing from all other Atlantic *Bembrops*, possesses a black “ocellus” spot at the dorsal base of the caudal fin in both sexes, although some males of this species have a basicaudal spot that is not an ocellus. *Bembrops ocellatus* has a black band in the distal part of the second dorsal fin and black at the base of rays 1–5 and 9–13, corresponding to where the dorsal body saddles are located. In larger specimens, the black forms two bands on the fin. This species lacks the elongate dorsal spine found in male *B. anatirostris* and scaled eyes, unique to *B. macromma*. *Bembrops ocellatus* never possesses vertically-oriented lateral markings, sometimes found in *B. greyi*, *B. heterurus*, and *B. macromma*.

The first dorsal fin pigmentation is distinct. There are two separate jet-black blotches, one at distal, anterior part of fin and a larger basal blotch. The wedge-shape, distal blotch is broadest across the first membrane, narrows progressively across second membrane, and its narrowed point extends halfway across the third membrane. The basal blotch broadens progressively from anterior, proximal third of first membrane to posterior half of third membrane, then the distal edge of blotch dips toward the base of the sixth spine, leaving most of the last membrane clear (Fig. 1G).

Bembrops ocellatus tends to have a larger eye in relation to the snout with 82.2% of specimens having snout/eye ratio less than, or equal to, one; whereas *B. quadrisella* has a somewhat longer snout with 93.1% of specimens having a snout/eye ratio greater than, or equal to, one. There is, however, considerable overlap.

Distribution/Depth.—Atlantic Ocean off eastern coast of Venezuela (type locality); widely distributed in the Caribbean Sea: along the coast of Venezuela, off Costa Rica, Nicaragua, and Honduras, near Puerto Rico and along many islands of the Lesser Antilles (Fig. 8). We examined seven collections where *Bembrops ocellatus* was taken with *B. quadrisella*. *Bembrops ocellatus* is found from 394 to 549 m depth.

Etymology.—The genus *Bembrops* is

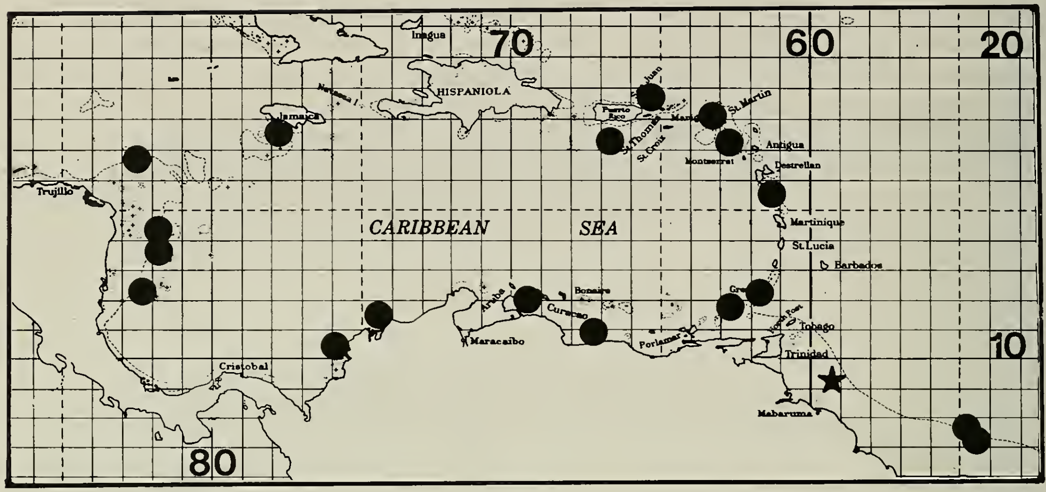

Fig. 8. Distribution of *Bembrops ocellatus* (●) based on specimens examined in this study. Type locality (★).

treated as masculine; the species name *ocellatus* is from the Latin word "ocellus", meaning a little eye (Jaeger 1966) referring to the black spot on the dorsal base of the caudal fin.

Bembrops quadrisella, new species
Saddleback duckbill
Fig. 9

Bembrops anatirostris.—Das & Nelson, 1996 (in part, locality in Caribbean Sea off Nicaragua).

Bembrops gobioides.—Das & Nelson, 1996 (in part, locality in Lesser Antilles).

Material.—123 specimens (101.2–231.0 mm SL) from 32 localities. Holotype.—TU 180351, a female 195 mm in SL, Atlantic Ocean, off Suriname, 07°38′N, 54°43′W, 457 m, 7 Nov 1957, Oregon Sta. 2008, 40′ trawl, bottom listed as "blue mud".

Paratypes.—TU 181667 (1): 178 mm SL, same data as holotype. TU 180350 (1): 159 mm SL, Atlantic Ocean, off Suriname, 07°34′N, 54°49′W, 411 m, 7 Nov 1957, Oregon Sta. 2007. TU 180259 (1): 127 mm SL, western Caribbean Sea, off Nicaragua, 16°39′N, 82°26′W, 457 m, 22 Aug 1957, Oregon Sta. 1871. TU 180353 (1): 145 mm SL, western Caribbean Sea, 16°41′N, 82°20′W, 549 m, 22 Aug 1957, Oregon Sta. 1872. TU 20037 (1): 185 mm SL, eastern Caribbean Sea, 11°35′N, 62°41′W, 388–457 m, 23 Sep 1958, Oregon Sta. 2353. CU 43863 (1): 227 mm SL, western Caribbean Sea, no locality data, May or Jun 1962, Oregon Cruise 78. CU 77466 (1): 163 mm SL, western Caribbean Sea, no locality data, May or Jun 1962, Oregon Cruise 78. USNM 304913 (4): 127.2–211 mm SL, Caribbean Sea off Nicaragua, 12°26′N, 82°24′W, 503 m, 2 Jun 1962, Oregon Sta. 3609. USNM 304917 (2): 192–235 mm SL, Atlantic Ocean NE of Dominica, 15°39′N, 61°10′W, 649 m, 5 Mar 1966, Oregon Sta. 5929. USNM 347206 (4): 139.8–168.0 mm SL, Caribbean Sea off Nicaragua, 14°10′N, 81°55′W, 439–457 m, 21 May 1962, Oregon Sta. 3565. USNM 347207 (3): 154.2–162.6 mm SL, Caribbean Sea off Honduras, 14°10′N, 81°50′W, 549–604 m, 21 May 1962, Oregon Sta. 3571. USNM 347208 and 347258 (2): 182–231 mm SL, Lesser Antilles, 17°06′N, 62°17′W, 589 m, 8 Dec 1969, Oregon-II Sta. 10843. USNM 347209 (1): 222 mm SL, Atlantic Ocean off Dominica, 15°36′N, 61°13′W, 503 m, 4 Mar 1966, Oregon Sta. 5926. USNM 347210 (2): 173–205 mm SL, Caribbean Sea E of

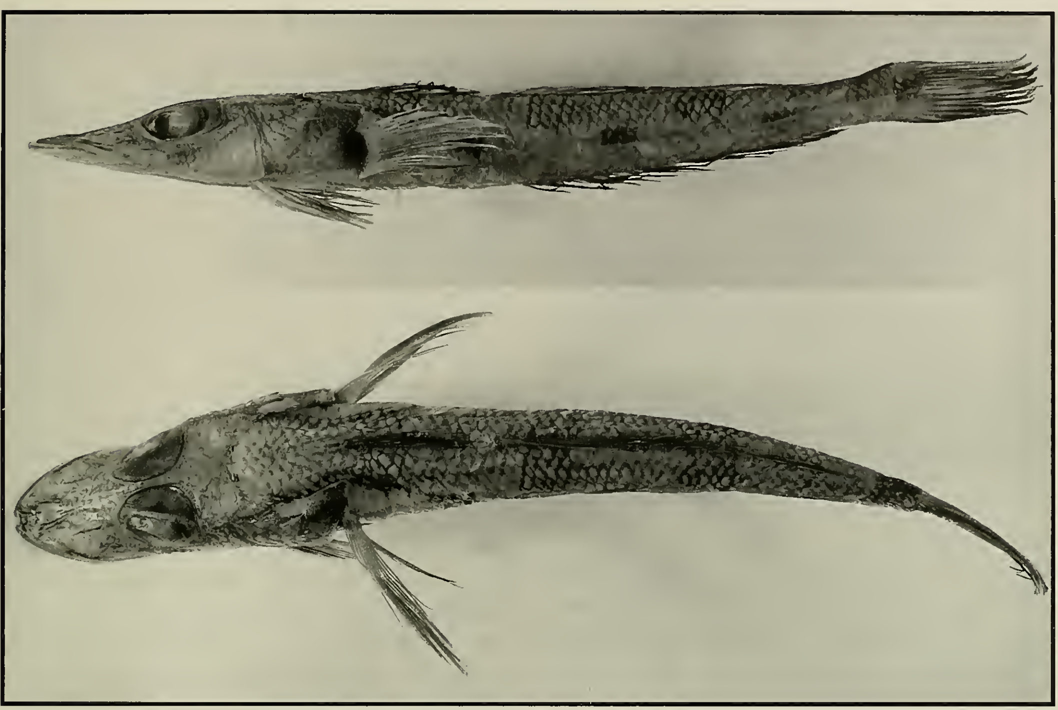

Fig. 9. *Bembrops quadrisella*, paratype, CAS 61004, 197.5 mm SL, male.

St. Croix, 17°42′N, 63°58′W, 741 m, 3 Dec 1969, Oregon-II Sta. 10832. USNM 347211 (2): 200–201 mm SL, eastern Caribbean Sea, 11°40′N, 62°33′W, 585–621 m, 24 Sep 1964, Oregon Sta. 5039. USNM 347218 (11): 101.2–189.5 mm SL, Caribbean Sea off Costa Rica, 12°25′N, 82°15′W, 549–585 m, 23 May 1962, Oregon Sta. 3576. USNM 347219 (1): 192.5 mm SL, Caribbean Sea off Venezuela, 11°53′N, 69°28′W, 421 m, 28 Sep 1963, Oregon Sta. 4408. USNM 347220 (6): 170.4–228 mm SL, Atlantic Ocean NE off Dominica, 15°42′N, 61°08′W, 640 m, 1 Dec 1969, Oregon-II Sta. 10825. USNM 347221 and 347256 (3): 176.0–230 mm SL, Atlantic Ocean N of St. Kitts & Nevis, 17°41′N, 62°50.5′W, 549–585 m, 18 May 1967, Oregon Sta. 6695. USNM 347255 (1): 215 mm SL, Caribbean Sea E of St. Croix, 17°36′N, 63°32′W, 439–476 m, 30 Sep 1959, Oregon Sta. 2636. USNM 347257 (1): 204 mm SL, Atlantic Ocean NE of St. Croix, 18°18′N, 63°24′W, 658 m, 10 Dec 1969, Oregon-II Sta. 10847. USNM 347259 (1): 149.2 mm SL, Caribbean Sea off Venezuela, 10°54′N, 67°08′W, 402 m, 12 Oct 1963, Oregon 4453. USNM 347260 (11): 113.1–190.5 mm SL, Caribbean Sea off Honduras, 16°58′N, 87°53′W, 457–732 m, 10 Jun 1962, Oregon Sta. 3635. USNM 347266 (11): 130.0–188.0 mm SL, Caribbean Sea off Honduras, 16°51′N, 82°14′W, 585 m, 15 Nov 1968, Oregon-II Sta. 10176. USNM 347267 (10): 132.2–162.0 mm SL, Caribbean Sea off Costa Rica, 12°35′N, 82°19′W, 457 m, 23 May 1962, Oregon Sta. 3575. USNM 347268 (5): 130.9–158.1 mm SL, Caribbean Sea off Honduras, 16°44′N, 87°55′W, 347 m, 9 Jun 1962, Oregon Sta. 3634. USNM 347269 (8): 120.0–223 mm SL, Caribbean Sea SE of Puerto Rico, 17°40′N, 63°40′W, 658–695 m, 30 Sep 1959, Oregon Sta. 2637. CAS 56879 (1): 205 mm SL, Caribbean Sea, Lesser Antilles off St. Kitts and Nevis, 17°09′00″N, 66°44′48″W, 512–768 m, 4 Aug 1978, Oregon-II Sta. 24263. CAS 61004 (2): 134.0–197.5 mm SL, Atlantic Ocean, U.S. Virgin Islands, N of St. Thomas Island, 18°32′42″N, 65°42′00″W, 732–777 m, 16 Aug 1987, Oregon-II Sta. 46067, 65′ trawl. CAS 61005 (1): 205 mm SL, Atlantic Ocean, Puerto Rico, NW coast off Bahir de Aquadilla, 18°26′42″N, 67°14′42″W, 658–668 m, 21 Aug 1987, Oregon-II Sta. 46094.

Other materials.—USNM 347270 (3): 147.1–192 mm SL, Caribbean Sea off Venezuela, 11°10′N, 68°08′W, 402 m, 11 Oct 1963, Oregon Sta. 4451. USNM 347271 (17): 114.7–184 mm SL, Caribbean Sea off Nicaragua, 17°02′N, 81°27′W, 549–585 m, 7 Jun 1962, Oregon Sta. 3629. CAS 47193 (1): 175 mm SL, Caribbean Sea off Venezuela, 12°48′N, 70°10′W, 366–914 m, 26 Feb 1973, Oregon-II Sta. 129. CAS 56927 (1): 188 mm SL, Caribbean Sea, Lesser Antilles off St. Kitts and Nevis, 17°15′54″N, 62°16′48″W, 567–640 m, 5 Aug 1978, Oregon-II Sta. 24265.

Diagnosis.—Dorsal fin usually VI-16 (82% of specimens). Anal fin 17 or 18, rarely 16 or 19. Pectoral rays usually 26 or 27, sometimes 25 or 28. Lateral-line scales 57–65, $\bar{X} = 61.1$. Gill rakers always 5 on upper limb, usually 15 or 16 on lower limb, and usually a total count of 20 or 21. Vertebral number usually 30 (29 in six). Ratio of head width divided by depth of head ranges from 1.2 to 1.5, usually 1.4, $\bar{X} = 1.39$. Upper and lower jaw moderately long, and postorbital distance also moderately long. Snout short, equal to or slightly greater than length of orbit (eye). Maxillary tentacle short, averaging only 2.1% SL. The lateral-line has a gentle slope, descending gradually to the straight portion under the space between the two dorsal fins or under the anterior rays of the second dorsal fin. *Benbrops quadrisella* possesses four wide black dorsal saddles, located at the origin of the spinous dorsal fin, under rays 2–6 of the second dorsal fin, under rays 10–13 of the second dorsal fin, and on the posterior part of the caudal peduncle at the start of the secondary caudal fin rays, sharing this character with *B. raneyi.*

Description.—*Bembrops quadrisella* is most similar to *B. gobioides*, *B. ocellatus*, and *B. raneyi*, having high scale, fin-ray, and vertebral counts (Tables 1–4). *Bembrops quadrisella* lacks the intensive black ‘x’ and ‘v’ secondary scale pigment that characterizes *B. gobioides.* Male *B. quadrisella* have the distal ½ to ⅔ of the anal fin black, similar to *B. anatirostris*, *B. heterurus*, and *B. macromma*; other Atlantic *Bembrops*, *B. greyi*, *B. gobioides*, *B. magnisquamis*, *B. ocellatus*, and *B. raneyi* have clear or slightly dusky fins, without broad black bands in either sex. *Bembrops quadrisella* is the only Atlantic species in the genus possessing white pigment in the spinous and second dorsal, anal, and pectoral fins. Female *B. quadrisella* possess a black "ocellus" spot at the dorsal base of the caudal fin, differing from *B. anatirostris*, *B. heterurus*, *B. macromma*, and *B. magnisquamis* that lack ocelli in both sexes, but is similar to *B. greyi* and *B. gobioides*, where females also possess an ocellus, but differing from *B. ocellatus* and *B. raneyi* that have a basicaudal spot in both sexes. *Bembrops quadrisella* lacks black bands in the second dorsal fin, having small intense black marks only at the base of several anterior rays. This species lacks the elongate spine found on male *B. anatirostris* and scaled eyes, unique to *B. macromma*. *Bembrops quadrisella* never possesses vertically-oriented lateral blotches, sometimes found in *B. greyi*, *B. heterurus*, and *B. macromma.*

The first dorsal fin pigmentation of female *B. quadrisella* is distinct (Fig. 1H). There is a small spot of black at base of first membrane and a black, submarginal band, broader on first two membranes and then a narrowed band extending across third, fourth, fifth, and sixth membranes. The greater part of the fin is either clear or lightly sprinkled with melanaphores. Male *B. quadrisella* usually have a first dorsal fin pattern similar to the female, but some specimens lack this distinctive pattern, pos-

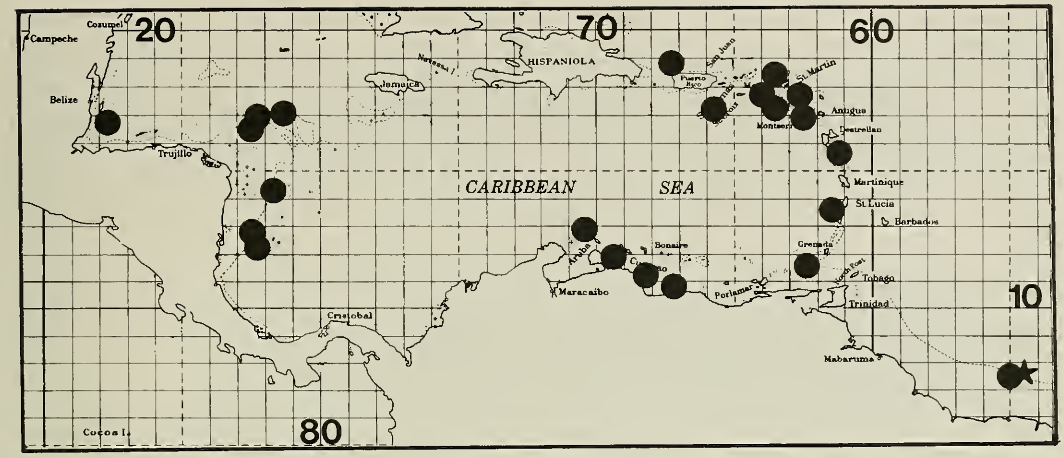

Fig. 10. Distribution of *Bembrops quadrisella* (●) based on specimens examined in this study. Type locality (★).

sessing only a light wash of melanophores over the entire fin.

Distribution/Depth.—Atlantic Ocean off Suriname (type locality; second site near type locality; widely distributed in the Caribbean Sea: along the coast of Venezuela; off Costa Rica, Nicaragua, and Honduras; S of Jamaica; near Puerto Rico and along length of Lesser Antilles (Fig. 10). We examined seven collections where *Bembrops quadrisella* was taken with *B. ocellatus* and one collection taken with *B. anatirostris. Bembrops quadrisella* is found from 347 to 914 m, usually between 400 and 600 m.

Etymology.—The species name *quadrisella* is from the Latin "quadrus", meaning fourfold or four, and "sella", a seat or saddle (Jaeger 1966) in reference to the four well-developed saddles on the dorsum of the body.

Bembrops raneyi, new species
Bahama duckbill
Fig. 11

Material.—Twenty nine specimens (69.0–176.0 mm SL) from ten localities. Holotype.—TU 180135, a male 136 mm SL, Atlantic Ocean, just east of Cay Sal Bank, 23°59′N, 79°43′W, 640 m, 24 Jul 1957; Combat Sta. 450; 10′ beam trawl.

Paratypes.—CU 77467 (1): 110 mm SL, TU 16849 (6): 69.0–145.0 mm SL; same data as holotype. TU 180260 (4): 107.0–164.0 mm SL; Atlantic Ocean, E of Vero Beach, Florida and north of Matanilla Shoal light; 27°53′N, 79°09′W; 686–759 m; 9 Jun 1958; Silver Bay Sta. 442; 40′ flat trawl. UF 212111 (1): 137.4 mm SL; Atlantic Ocean, Bahama Islands, Elbow Bank, W of Cat Cay, 26°27′N, 79°21′W–26°36′N, 79°24′W; 531–540 m; 25 Jun 1963; Gerda Sta. 158; otter trawl. UF 217644 (1): 125.1 mm SL; Atlantic Ocean, Bahama Islands, Elbow Bank, W of Alice Town, Bimini Island, 25°49′N, 79°21′W–25°53′N, 79°22′W; 284–293 m; 1 Jul 1965; Gerda Sta. 646. UF 220553 (1): 167.3 mm SL; Atlantic Ocean, Grand Bahama Island, S of Freeport, 26°26′N, 78°39′W–26°27′N, 78°41′W; 724 m; 22 Jul 1965; Gerda Sta. 709. UF 220554 (1): 109.9 mm SL, Atlantic Ocean, Bahama Islands, NW of Berry Islands, 25°56′N, 78°09′ to 05′W; 595–711 m; 20 Jul 1965; Gerda Sta. 679. USNM 269552 (4): 93.0–146.8 mm SL and one cleared and stained, 115.0 mm SL; Atlantic Ocean, off Nassau, exact locality uncertain, probably 26 Oct 1961; Silver Bay Sta. 3479. USNM 347223 (5): 82.9–151.7 mm SL; Atlantic Ocean in Straits of Florida, 23°09′N, 80°08′W; 466

Fig. 11. *Bembrops raneyi*, paratype, USNM 347223, 141.7 mm SL, male.

m; 16 Dec 1969; Oregon-II Sta. 10863. USNM 347252 (3): 104.4–176.0 mm SL; Atlantic Ocean in Straits of Florida; 23°59′N, 79°17′W; 530–549 m; 17 Nov 1960; Silver Bay Sta. 2469. USNM 347253 (1): 117.0 mm SL; Atlantic Ocean in Straits of Florida, 23°40′N, 79°18′W; 530 m; 5 Nov 1960; Silver Bay Sta. 2458.

Diagnosis.—Dorsal fin usually VI-16 (VI-15 in three, VI-17 in one). Anal fin usually 18 (17 in nine). Pectoral fin 25–29, usually 27. Lateral-line scales 56–61, $\bar{X}$ = 59.0. Gill rakers usually 5 on upper limb, 14 on lower limb, and total number usually 19. Vertebral number usually 30 (29 in two). Maxillary tentacle a long triangle, averaging 4.1% SL. Head very broad, width averages 1.5 times its depth. Snout short, slightly longer or shorter than orbit. Upper, lower jaws and postorbital lengths moderately short. The lateral-line has a relatively gentle slope reaching its lowest point between the two dorsal fins. Body pale. First dorsal fin with two black blotches, the smaller, a narrow submarginal bar spanning the first two membranes, the larger extending along base of fin, crossing the first to fourth membranes. The interspace between the distal and basal blotches is clear (Fig. 11). *Bembrops raneyi* possesses four wide dark dorsal saddles, located at the origin of the spinous dorsal fin, under rays 2–6 of the second dorsal fin, under rays 10–13 of second dorsal fin, and on the posterior part of the caudal peduncle at the start of the secondary caudal fin rays, sharing this character with only *B. quadrisella.*

Description.—Bembrops raneyi is most similar to *B. gobioides*, *B. ocellatus*, and *B. quadrisella*, having high scale, fin-ray, and vertebral counts (Tables 1–4). *Bembrops raneyi* lacks the dark black 'x' and 'v' secondary scale pigment that characterizes *B. gobioides* and *B. greyi. Bembrops raneyi* lacks both scaled eyes as found in *B. macromma* and elongate second dorsal spine of *B. anatirostris. B. raneyi* lacks black bands in the anal fin, distinguishing it from *B. anatirostris*, *B. heterurus*, *B. macromma*, and *B. quadrisella* whose males possess black in the anal fin. Both sexes of *B. raneyi* have a dorsally-placed, basicaudal spot; the only other Atlantic *Bembrops* sharing this character is *B. ocellatus. Bembrops raneyi* never possesses vertically-ori-

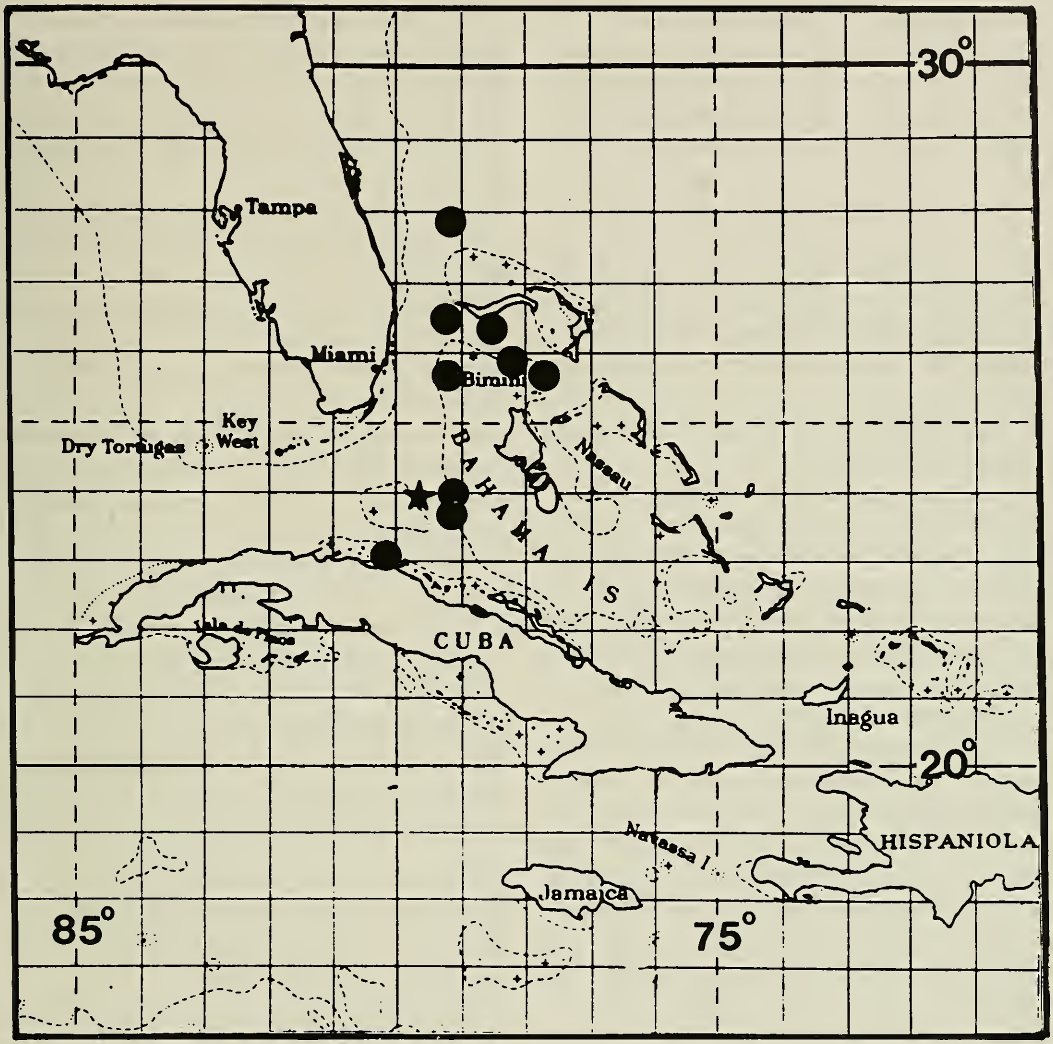

Fig. 12. Distribution of *Bembrops raneyi* (●) based on specimens examined in this study. Type locality (★).

ented lateral markings as sometimes found in *B. greyi*, *B. heterurus*, and *B. macromma*.

Bembrops raneyi has three very short pyloric caeca, 2.6, 3.9, and 3.4 (left to right) % of SL, across the stomach. These are the shortest caeca of any Atlantic species examined in the genus *Bembrops*. *Bembrops raneyi* has the longest tentacle for any Atlantic species of *Bembrops* except for *B. anatirostris* (Table 10).

Distribution/Depth.—Atlantic Ocean in western, southwestern and northwestern Bahamas Islands; (Fig. 12), three species of *Bembrops: B. anatirostris*, *B. macromma*, and *B. gobioides* have been taken in area near records of *B. raneyi*. *Bembrops raneyi* is one of the deeper dwelling species in the genus, being found from 284 to 759 m, with most specimens taken below 500 m.

Etymology.—We take great pleasure in naming this species after the late Dr. Edward C. Raney, former Professor of Ichthyology at Cornell University and teacher to many of North America's ichthyologists, our mentor, friend, and professional colleague, who had a long-standing interest in percophids and organized much of the study materials we have used in the present research. We made use of his notes, and an early draft of a manuscript describing the species that now bears his name.

Discussion

Our counts and measurements agreed, for the most part, with those of Ginsburg (1955). Our interpretation of the structural bases of the fin rays was verified by numerous x-rays. Our counts of 113 *B. anatirostris* resulted in eight with 14 dorsal rays and 105 with 15 dorsal rays.

Bembrops anatirostris and *B. gobioides* have the highest lateral-line scale counts of the nine species of *Bembrops* from the Atlantic Ocean. Both males and females display a silvery sheen on the prepectoral area and for a varying distance forward on side of isthmus. None of the other seven species was observed to have such coloration. *Bembrops anatirostris* and *B. gobioides* differ, however, in several characteristics. Previous studies have noted the elongate dorsal spine of *B. anatirostris.* Ginsburg (1955) and Grey (1959) stated that the second dorsal spine of male was prolonged, however Das & Nelson (1996) stated that the second or third spine of the male was produced. We found no male *B. anatirostris* with prolonged third dorsal spine, all were second dorsal spines. *Bembrops anatirostris* usually has 15 dorsal rays whereas *B. gobioides* usually has 17 dorsal rays; *B. anatirostris* invariably has 28 vertebrae whereas *B. gobioides* usually has 30. *Bembrops anatirostris* has a greater head, and caudal peduncle depth than *B. gobioides. Bembrops anatirostris* has a greater head length, head width, snout length, jaw length, and postorbital length than *B. gobioides. Bembrops anatirostris* has a smaller orbit relative to snout length and a very long attenuate maxillary tentacle in comparison to *B. gobioides* which has a larger orbit that is sometimes equal to snout length, especially in small juveniles and has a maxillary tentacle of moderate length. In addition to these differences, there are a number of differences in pigmentation of fins and body that are described above in the species accounts.

Bembrops macromma and *B. magnisquamis* were the only two previously known western north Atlantic forms possessing medium to large scales. These two forms differ markedly in a number of ways. Unfortunately, we have only eight specimens of *B. magnisquamis* to compare with *B. macromma. Bembrops macromma* invariably has 14 dorsal rays, usually 18 anal rays, and usually 25 pectoral rays, whereas *B. magnisquamis* has usually 15, occasionally 16 dorsal rays, 17 anal rays and either 23 or 24 pectoral rays. The number of lateral-line scales range from 53 to 61 in *B. macromma* vs. 44 to 47 in *B. magnisquamis. Bembrops macromma* usually has 28 vertebrae, occasionally 27 whereas *B. magnisquamis* has 29. *Bembrops macromma* has a greater head and body depth, but a similar caudal peduncle depth as *B. magnisquamis. Bembrops macromma* has the shortest maxillary tentacle of the nine species of *Bembrops* included in this study in contrast to *B. magnisquamis* which has a moderately long maxillary tentacle. Pigmentation differences are described in detail in the species accounts.

Bembrops ocellatus, *B. quadrisella*, and *B. raneyi* are quite similar in most meristics and morphometrics. These three new species typically have 16 dorsal rays and 18 anal rays, but occasionally have 15 of the former and 17 of the latter. *Bembrops ocellatus* and *B. quadrisella* typically have 26 pectoral rays whereas *B. raneyi* usually has 27 pectoral rays. *Bembrops ocellatus* and *B. quadrisella* have more lateral-line scales, 60 to 63 in former and 59 to 64 in the latter; *B. raneyi* with a lower count, 56 to 61. All three species usually have five gill rakers on upper limb, but *B. ocellatus* and *B. quadrisella* usually have 15 rakers on lower limb and *B. raneyi* usually has 14 rakers on lower limb, so total gill raker counts usually are 20 for *B. ocellatus* and *B. quadrisella* but 19 for *B. raneyi. Bembrops raneyi* has slightly greater body depth, less head depth, greater head width, and greater orbit length relative to snout length than the other two species. *Bembrops quadrisella* has a greater head length, greater head depth, greater snout length, greater upper jaw, lower jaw, and postorbital lengths than either *B. ocellatus* or *B. raneyi. Bembrops raneyi* has the longest maxillary tentacle, *B. ocellatus* the next longest, and *B. quadrisella* the shortest maxillary tentacle of the three new species. The maxillary tentacle of *B. raneyi* is slightly shorter than that of *B. anatirostris*, and the tentacle of *B. quadrisella* is only slightly longer than that of *B. macromma*. There are some distinct pigmentation patterns of fins and body but these are described above in detail.

We discuss *B. greyi* and *B. heterurus* together because our samples of both species are from the eastern Atlantic and both species have a general appearance distinct from the seven western north Atlantic species. These two species are quite easily separated: *Bembrops greyi* usually has 16 dorsal rays, *B. heterurus* usually has 15; *B. greyi* usually has either 17 or 18 anal rays, *B. heterurus* typically has 18. *Bembrops greyi* usually has 26 pectoral rays, whereas *B. heterurus* usually has 27. *Bembrops greyi* has a range in lateral-line scale counts from 45 to 52, whereas *B. heterurus* ranges from 55 to 60. There are fewer gill rakers in *B. greyi* than in *B. heterurus. Bembrops greyi* typically has 30 vertebrae whereas *B. heterurus* usually has 28. Das & Nelson (1996) reported *B. heterurus* from the western Atlantic with 17 anal rays (84% of specimens), differing from our findings from eastern Atlantic specimens with specimens having 18 anal rays (92% of specimens). Das & Nelson's (1996) analysis of western south Atlantic *Bembrops heterurus* shows that nearly all proportions of this species differed from our observations on the eastern Atlantic populations (considered *B. heterurus* by Poll (1959)), suggesting that the eastern Atlantic form is an undescribed species.

Bembrops heterurus has a greater body depth, greater head depth, greater head width, greater interorbital width, and greater snout length than *B. greyi. Bembrops greyi* has a greater head length and greater orbit length than *B. heterurus*. The relative length of snout versus length of orbit reveals that the orbital horizontal distance is usually greater than the snout length in *B. greyi* but never greater than or equal to snout length in *B. heterurus*. The maxillary tentacle is of moderate size in both *B. greyi* and *heterurus*.

There has been little discussion concerning sexual dimorphism in the Atlantic members of the genus *Bembrops*. Ginsburg (1955) noted the prolongation of the second dorsal spine in "larger males" of *B. anatirostris*. Grey (1959) also noted this sexual dimorphism in *B. anatirostris* and suggested "it is possible that other species may also exhibit sexual dimorphism", but provided no further observations. Ginsburg (1955:631) noted "the smaller specimens (referring to the genus *Bembrops*) having a spot on the caudal near its base, nearer to upper than lower margin, disappearing with growth . . .". Our observations on series of the Atlantic species of *Bembrops* shows this statement to be partially correct. All small specimens of *B. gobioides* and *B. greyi* possess an ocellus as described by Ginsburg (1955), however this mark is retained in adult females, but faded or completely lost in adult males. *Bembrops quadrisella* is also sexually dimorphic in females having a caudal spot that the males lack. Masuda et al. (1984) reported similar sexual dimorphism with the Pacific species, *B. caudimacula* and *B. filifera*. Two Atlantic species, *B. ocellatus* and *B. raneyi* and one Pacific species, *B. curvatura* have both sexes possessing a caudal spot. We find *Bembrops anatirostris*, *B. heterurus*, *B. macromma*, and *B. magnisquamis* lack a caudal spot for all life history stages. Das & Nelson (1996) reported that certain specimens of *Bem-*

brops species possess a caudal spot, but did not relate it to the sex of the specimen.

Bembrops anatirostris, *B. macromma*, and *B. quadrisella* are sexually dimorphic in anal fin pigment, with males having black in the fin that is lacking in females.

All species of *Bembrops* examined in this study are sexually dimorphic in genital papilla size; males having a longer and more robust, papilla, females having a much smaller papilla. This dimorphism in papilla sizes reaches an extreme in the Pacific species, *Bembrops curvatura*, whose males possess an elongate, club-shaped papilla, 2–3 times the length of the papilla of the female.

Most Atlantic *Bembrops* have a gentle slope to the lateral-line, descending to its lowest point on the body between the two dorsal fins. Interspecific variation of this character ranges from *B. heterurus* and *B. macromma* where the slope is so gradual that the straight section of the lateral-line starts under the anterior part of the second dorsal fin to *B. gobioides* that possesses an abrupt slope where the lateral-line descends to the straight section under the first dorsal fin. Among the new species, *Bembrops ocellatus* and *B. raneyi* have slightly steeper slopes to the lateral-line than *B. quadrisella.*

The nine species of Atlantic *Bembrops* have 27 to 30 vertebrae. Miller & Jurgenson (1973) listed precaudal, caudal and total counts for these species, but their values for *B. macromma* are partially in error. They report *Bembrops* normally having nine precaudal vertebrae, agreeing with our findings (except for an infrequent count of ten in *B. anatirostris*). Vertebral number seems to be a conservative character with little variation within most species (Table 4). What variation in vertebral number, within and between species, that does exist, results from differences in caudal vertebrae. This differs from *Chrionema*, the sister group to *Bembrops* (sensu Nelson 1994) since Iwamoto & Steiger (1976) report 19 caudal vertebrae in *Chrionema* and either 8 or 9 precaudal vertebrae for a total of 27 or 28.

We cannot agree with Das & Nelson's (1996) statement in the description of the genus that species of *Bembrops* possess "two small spinous processes on the posterior tip of posttemporal". In five species examined (Fig. 3) there is only a single prominent spine projecting dorso-posteriorly from the rear of the posttemporal bone. Just posterior and lateral to the posttemporal spine, a protuberance on the supracleithrum frequently projects through the epidermis suggesting the presence of a second spine near the anterior keeled lateral-line scale. Shape, size, and degree of curvature appears to vary among the species.

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A new species of cardinalfish (Apogonidae) from the Philippines, with comments on species of *Apogon* with six first dorsal spines

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Abstract.—A new species of *Apogon* (*A. bryx*) from deep water is described from the Philippines. It is the sixth species with six first dorsal spines, a completely serrated preopercular edge, black stomach and intestine, pored lateral line scales from the posttemporal bone to the caudal fin and eight anal fin-rays. The new species is compared with other six-spined (first dorsal) species with these characters and a key is provided. One rare, deep-dwelling *Apogon* from the Philippines and two undescribed species from the Indian Ocean and West Pacific Ocean are briefly discussed in relation to the new species. Two species have identifiable synonyms: *Apogon gularis* (*Apogon smithvanizi*) and *Apogon thermalis* (*Apogon sangiensis*). *Apogon unicolor* is removed from the subgenus *Pristicon.*

A new species of *Apogon* from deep water is described from the Philippines. It is the sixth known six-spined species in *Apogon* with a completely serrated preopercular margin, pored lateral-line scales from posttemporal to base of caudal fin, black stomach and intestine, and eight anal fin-rays. This description, based on one specimen, is being provided because the unusual depth of the trawl collection makes it unlikely that more material will be available soon.

Six spines in the first dorsal fin and a completely serrated preopercular margin are found in relatively few species of the genus *Apogon.* The pan-tropical subgenus *Apogon*, with about 35 species, has the ventral portion of the preopercle unossified, as a thin fleshly flap, the vertical edge of the preopercle serrated, two supraneural bones, no free uroneurals, ctenoid scales, pored scales forming a complete lateral line, eight anal fin-rays, and the stomach and intestine pale. An apparently related pan-tropical subgenus, *Zapogon*, with two species, has a free pair of uroneurals, a black pigmented stomach and intestine, and is otherwise similar to the subgenus *Apogon.* Fraser (1972) included *Apogon trimaculatus* Cuvier *in* Cuvier & Valenciennes, 1828 and *Apogon unicolor* Döderlein *in* Jordan & Snyder, 1901 in the subgenus *Pristicon* based on three supraneural bones, a free pair of uroneurals, strongly serrated infraorbitals and preopercular ridge. *Apogon unicolor* is removed from *Pristicon* based on the presence of a ventral fleshy, unossified flap of the preopercle, small body scales and a black stomach and intestine. This species may represent another line within *Apogon.* The Atlantic Ocean subgenus *Paroncheilus*, with one species, has a partially ossified ventral preopercular edge, nine anal rays, some canine teeth, cycloid scales, and is otherwise similar to the subgenus *Apogon.*

The remaining species of *Apogon* with six first dorsal spines, have an ossified, serrated ventral preopercular edge. These species have been placed in various subgenera. The subgenera *Pristicon* (2 species), *Yarica* (1 species), and a few species of *Ostorhinchus* (those with six first dorsal spines at least 3 species: *Apogon nigripes, Apogon amboinensis* and *Apogon lateralis*) have pale stomachs and intestines. This small group of *Ostorhinchus* is under review by

Fig. 1. The holotype of *Apogon bryx*, 42.5 mm standard length, from the Philippines, Luzon Island, Batangas Province, Balayan Bay.

me. Other species of *Ostorhinchus* (at least 107 species) may either have stomachs and intestines pale, speckled or black pigmented. The subgenera *Brephamia* (2–3 species), and *Zoramia* (4 species) have a black pigmented stomachs and intestines. *Apogon nanus*, provisionally allocated by Allen et al. (1994) in *Brephamia* has pored lateral line scales extending from the posttemporal bone to the caudal fin unlike the other two species. The subgenus *Ostorhinchus* has species with six (about 10) or seven (at least 107) visible first dorsal spines.

Methods

Methods of taking and recording meristic data and measurements are given in Fraser & Lachner (1985). All measurements are in millimeters to the nearest 0.1 mm. All proportions are based on standard length and all material is reported by standard length rounded to the nearest millimeter, except for the primary type material. All x-ray photographs are in data files maintained by the author. The following acronyms are used to designate institutions and collections cited: BMNH Natural History Museum, London; BPBM Bernice P. Bishop Museum, Honolulu; CAS California Academy of Sciences, San Francisco; (SU) Stanford University (collections now housed at CAS); MNHN Museum National d'Histoire Naturelle, Paris; RMNH Nationaal Natuurhistorisch Museum, Leiden; RUSI J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa; USNM collections of the former United States National Museum, deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Apogon bryx, new species
Fig. 1

Material examined.—Holotype: *Apogon bryx* CAS 34408; (42.5); Philippines, Luzon Island, Batangus Province, Balayan Bay, south of Barrio Nonong Casto, in 146-155 m. J. E. Norton. 25 Jun 1966. x-rayed.

Comparative material.—*Apogon atrogaster* Holotype USNM 70249; (46.8); Philippine Is., Western Luzon; x-rayed. Paratypes USNM 163227; 7(35–48); same data as holotype; x-rayed. *Apogon gularis* Holotype USNM 225672; (36.1); Red Sea; x-rayed. *Apogon kiensis* Holotype SU 6514; (56.9); Japan, Wakanoura Kii; x-rayed. Paratypes SU 6739; 21(47–59) same data as holotype. USNM 71232; 13(30–60); Japan, Shimizu; x-rayed. *Apogon* sp., cf. *kiensis* RUSI 3075; (39–43); Mozambique; x-rayed. RUSI 3074; (31); Mozamibque; x-rayed. RUSI 3073; (44–46); Mozambique, x-rayed. *Apogon nanus* Paratype USNM 328635; (28); Malaysia, Sabah. *Apogon nigripes* Syntypes BMNH 1864. 11.15.72-74; (37.3), 1865.2.2.23; (42.3); Zanzibar. *Apogon sangiensis* Holotype RMNH 5577; (63.7); Indonesia, Sangi I. *Apogon smithvanizi* Paratypes USNM 331174; (46); Bahrain. BPBM 36421; (49); Bahrain. *Apogon thermalis* Holotype MNHN 8686; (54.7); Sri Lanka, Trincomalee. *Apogon unicolor* Holotype USNM 49708; (59.6); x-rayed. Japan, Yokohama. USNM 173833; (85); Australia, NW Cape Arnhem. *Apogon* sp. USNM 349036; (42); Philippines, Palawan, Puerto Princesa. USNM 260920; (71); Fiji, Lau Group, Matuku Island (19°9′38″S, 179°45′23″E). USNM 260921; 2(49–72); Fiji, Charybdis Reef (17°12′S, 178°0′E).

Diagnosis.—An *Apogon* in the subgenus *Ostorhinchus* with six first dorsal spines, a completely serrated preopercular edge, black stomach and intestine, eight anal fin-rays, 14–15 pectoral fin-rays, 22 gill rakers (including rudiments) on first arch, no dark stripes or spots on the head, body or fins.

Description.—For general body shape see Fig. 1. Proportional measurements (as percentages of standard length, 42.5): body depth 34.6; head length 40.7; eye diameter 10.8; snout length 9.6; bony interorbital width 8.2; upper jaw length 19.8; caudal peduncle depth unknown; caudal peduncle length 27.5; first dorsal-fin spine length 10.6; second dorsal-fin spine length 17.4; third dorsal-fin spine length 15.3; fourth dorsal-fin spine length 12.5; spine in second dorsal fin 12.5; first anal-fin spine length 2.8; second anal-fin spine length 12.0; pectoral fin length 22.8; pelvic fin length 22.1.

Dorsal fin VI-I,9; anal fin II,8; pectoral fin-rays 14 (right), 15 (left); pelvic fin I,5; principal caudal fin-rays 9+8; pored lateral line scales 24; transverse scale rows above lateral line 2; transverse scale rows below lateral line 5; median predorsal scales unknown; circumpeduncular scale rows unknown; gill rakers 22 on first arch, well developed gill rakers 21, (1+4 upper, 17+0 lower).

Villiform teeth in many rows on the premaxilla; one to two rows of villiform teeth on the sides of the dentary; two to three teeth on the palatine and one row on the vomer; none on ectopterygoid, endopteygoid or basihyal.

Supramaxilla absent. Posttemporal smooth to crenulate on posterior margin. Preopercle serrate on vertical and horizontal margins. Infraorbitals smooth. Scales ctenoid on body. Pored lateral-line scales extend from posttemporal to caudal fin. Vertebrate 10+14. Three supraneural bones, a single supranumerary spine on the first pterygiophore. Three epurals, 5 hypurals and one pair of uroneurals.

Anal opening close to the origin of the anal fin. Caudal fin-rays broken.

Life colors.—Unknown.

Preserved color pattern.—Body, head and fins generally uniform light grayish with no indication of any dark melanophore patterns. Stomach and intestine black, peritoneum speckled with melanophores. Anal area pale, speckled with a few melanophores.

Distribution.—Known from Batangas Province, Balayan Bay, south of Barrio Nonong Casto, in 146–155 meters by trawl.

Etymology.—The Greek noun bryx, in apposition, meaning depth of the sea in reference to the relatively deep water from which this cardinalfish was collected.

Remarks.—Apogon bryx has six first dorsal spines, an uncommon number for nominal species of *Apogon* with a completely serrated preopercle edge, eight anal rays, pored lateral-line scales from the posttemporal to caudal fin, and a black stomach and/or intestine. *Apogon thermalis* Cuvier, 1829, *Apogon sangiensis* Bleeker, 1857, *Apogon kiensis* Jordan & Snyder, 1901b, a new species related to *Apogon kiensis*, *Apogon gularis* Fraser & Lachner, 1984, *Apogon smithvanizi* Allen & Randall, 1994, *Apogon nanus* Allen et al., 1994, and another new species have this combination of characteristics.

Apogon thermalis differs from *Apogon bryx* in having a dark head stripe and basicaudal spot and a deeper body depth (36–39%). The type specimens of *Apogon thermalis* from Sri Lanka and *Apogon sangiensis* from Indonesia have in common six first dorsal spines, serrated preopercular margins, 14 pectoral fin-rays, smooth posttemporal edges and similar gill raker counts (2+4–16+0 for *A. thermalis* and 2+4–15+3 for *A. sangiensis*). The type of *Apogon thermalis* has a dark snout mark continuing behind the eye, ending at the posterior edge of the opercle and a small, centered on the lateral line, basicaudal spot. The type of *Apogon sangiensis* has no remaining color pattern, however Bleeker (1857) provided a good color description of the type and a follow up color figure in the Atlas (Bleeker, 1873–76: pl. XLI, fig. 4). The color pattern appears very similar to *Apogon thermalis.* Both types are soft with poor body shapes and the type of *Apogon sangiensis* lack the premaxilla, so body proportions are of limited use for type comparisons. Based on the above information and examination of other material from the Indian Ocean and West Pacific Ocean, *Apogon sangiensis* is considered a synonym of *Apogon thermalis.*

Apogon kiensis has two stripes on the body, a snout mark, usually 15 pectoral fin-rays and 19–22 (16–18 well developed) gill rakers. The material from Mozambique identified by Smith (1961) as *Apogon kiensis* is an undescribed species having a third, shorter, stripe between the two stripes, usually 14 pectoral fin-rays and 22–25 (21–22 well developed) gill rakers. Both species differ from *Apogon bryx* in preserved color pattern. The undescribed African species has similar pectoral fin-ray and gill raker counts with the new species.

Apogon gularis has the anus near the pelvic fins unlike any other known species of *Apogon.* In the original description, *Apogon smithvanizi* was compared with *Apogon kiensis* but not with *Apogon gularis.* In addition to having similar preserved color patterns (a dark snout mark, a small spots behind the eye, generally pale body and fins) and body proportions, *Apogon gularis* and *Apogon smithvanizi* have in common: the anus in a forward position near the pelvic fin, black stomach and intestine, usually 14 pectoral fin-rays, six first dorsal spines, a serrated preopercular margin, and 23–26 (20–24 well developed) gill rakers. Both nominal species have been taken only from trawls in deeper waters, 30–40 m for *Apogon smithvanizi* and 60–290 m for *Apogon gularis.* No differences of substance were found. *Apogon smithvanizi* is treated here as a synonym of *Apogon gularis.*

Apogon nanus is a small, slender species with more gill-rakers on the first arch (28–29) than *Apogon bryx*, a dark spot on the tip of the lower jaw, a narrow dark band along the base of the anal fin and 13 pectoral fin-rays.

Apogon sp. has basicaudal and opercular spots, dark bars or saddles under each dorsal fin and 15–16 pectoral fin-rays, clearly different from *Apogon bryx. Apogon* sp. will be described by J. E. Randall and this author as part of their review of *Apogon trimaculatus* and *Apogon rhodopterus.*

Artificial key for preserved material of *Apogon* from the Indo-West Pacific region with six first dorsal spines, black stomach and intestine

1. Pored lateral-line scales from posttemporal to caudal fin 3

1′. Pored lateral-line scales incomplete, ending before origin of second dorsal fin, remaining scales of lateral line with pits. (*Brephamia*) (West Pacific Ocean) 2

2. Dark basicaudal spot present; no stripes on body. (West Pacific Ocean) . . . . *Apogon neotes* Allen et al., 1994

2′. No dark basicaudal spot; stripes on body. (West Pacific Ocean) . . . . *Apogon parvulus* . . (Smith & Radcliffe *in* Radcliffe, 1912)

3. Anal opening near origin of anal fin . . 4
3′. Anal opening near posterior base of pelvic fins. (Indo-West Pacific Ocean) . . . *Apogon gularis* Fraser & Lachner, 1984
4. Ventral part of preopercle an unossified moveable flap 5
4′. Ventral part of preopercle ossified and edge serrate 7
5. Preopercular ridge smooth (*Zapogon*) 6
5′. Preopercular ridge serrate. (West Pacific Ocean) . . . . *Apogon unicolor* Döderlein in Jordan & Snyder, 1901
6. Scales above and below lateral-line scales about the same size. (Red Sea) . . . *Apogon isus* Randall & Böhlke, 1981
6′. Scales in rows above lateral-line scales much smaller, more than 35. (Atlantic, Indian and Pacific Oceans) . . . . *Apogon evermanni* Jordan & Snyder, 1904
7. Nine anal fin-rays 8
7′. Eight anal fin-rays 12
8. Dark stripes on sides of body. (West Pacific Ocean). . . . . . *Apogon compressus* (Smith & Radcliffe *in* Radcliffe, 1911)
8′. No dark stripes on sides of body (*Zoramia*). (Indo-West Pacific Ocean) . . . 9
9. Dark line on dorsum from origin of first dorsal fin onto caudal peduncle; ventral margin of caudal peduncle with dark line. (Indo-West Pacific Ocean) . . . . . *Apogon leptacanthus* Bleeker, 1856
9′. No dark line on dorsum or on dorsal and ventral surfaces of the caudal peduncle 10
10. Gular area dark; vertical short dark lines just above insertion of some anal rays. (West Pacific Ocean) . . . . *Apogon perlitus* Fraser & Lachner, 1985
10′. Gular area pale; no vertical lines above anal rays 11
11. Opercular flap with prominent to diffuse dark spot; caudal spot small with many diffuse melanophores on caudal peduncle. (West Pacific Ocean) . . . . *Apogon gilberti* (Jordan & Seale, 1905)
11′. No spot on opercular flap; caudal spot small, without diffuse melanophores on caudal peduncle. (Indo-West Pacific Ocean) . . . . *Apogon fragilis* Smith, 1961
12. Gill-rakers 19–25; 14–16 pectoral rays 13
12′. Gill-rakers 28–29; 13 pectoral fin rays. (West Pacific Ocean) . . . . *Apogon nanus* Allen et al., 1994
13. Body and/or head with dark marks or stripes 14
13′. Body and head without dark marks or stripes. (West Pacific Ocean) . . . . *Apogon bryx*, new species
14. Body with dark stripes; no dark basicaudal spot 16
14′. No dark body stripes; dark basicaudal spot 15
15. Dark opercular spot; dark saddle under each dorsal fin; 15–16 pectoral rays. (West Pacific) . . . . *Apogon* sp.
15′. No dark opercle spot; dark stripe from snout ending on opercle; 14 pectoral rays. (Indo-West Pacific Ocean) . . . . *Apogon thermalis* Cuvier *in* Cuvier & Valenciennes, 1829
16. Two stripes, one over the eye to posterior base of second dorsal fin, second from snout to end of caudal fin; 16–18 well developed gill rakers; usually 15 pectoral fin rays. (Indo-West Pacific Ocean) . . . . *Apogon kiensis* Jordan & Snyder, 1901
16′. Three stripes, one over the eye reaching on to caudal peduncle, a second from over the eye just above the broader, mid-lateral stripe from snout to tip of caudal fin; 21–22 well developed gill rakers; usually 14 pectoral fin rays. (West Indian Ocean) . . . *Apogon* sp.

There is no obvious evidence, in the form of external damage, to suggest that an additional small first dorsal spine was present in the material of *Apogon bryx.* The x-rays provided no internal evidence of an articulation or support zone for an additional small first dorsal spine (two supranumerary spines instead of one). All of the other species with six first dorsal spines discussed here have only one supranumerary spine on the first pterygiophore. The only deep water (from 83 meters), seven-spined species from the Philippines with gill raker counts greater than 20 is *Apogon atrogaster* (Smith & Radcliffe *in* Radcliffe 1912) with 26–27 (24 well developed) gillrakers. It has a dark snout mark. Several of the paratypes appear to have six first dorsal spines (Fraser & Lachner 1984). At least one of these paratypes (41.0 mm SL) has a lower gill raker count (2+5–17+0 = 24) within an expected possible range of variation for *Apogon bryx.* Three other specimens are too badly damaged to obtain counts. None of this paratypic material can be identified with any certainty by me.

Apogon bryx may be more similar to the undescribed western Indian Ocean species than any of the other species mentioned, based on body shape, pectoral fin-ray and gill raker counts. These two species and *Apogon kiensis* need to be examined for possible relationships with the *Apogon quadrifasicatus* complex, all species with seven first dorsal spines.

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The Neotropical catfish genus *Epapterus* Cope (Siluriformes: Auchenipteridae): a reappraisal

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Abstract.—The Neotropical auchenipterid catfish genus *Epapterus* Cope is reviewed. *Epapterus* was found to share synapomorphies with *Auchenipterus* Valenciennes and *Pseudepapterus* Steindachner and within that clade it is the sister-group to *Pseudepapterus. Epapterus* lacks an adipose dorsal fin, a derived reductive feature unique to the genus within the clade consisting of *Epapterus*, *Auchenipterus*, and *Pseudepapterus* and which is hypothesized to be a synapomorphy for the genus. The extension of the interradial membrane to join the contralateral pelvic fins is identified as an additional possible synapomorphy for *Epapterus.* Contrary to recent practice, *Epapterus* is considered to consist of only two species, *E. dispilurus* Cope (1878) and *E. blohmi* Vari et al. (1984). Examination of *Epapterus* samples from a number of localities in the Rio Amazonas and Río Paraguay basins failed to reveal differences between the populations of the genus in those drainage systems. As a consequence *Epapterus chaquensis* Risso & Risso (1962), described from the Río Paraguay system, is placed as a synonym of *E. dispilurus* originally described from the western portion of the Amazon basin. *Euanemus longipinnis* Steindachner (1881) is retained as a synonym of *Epapterus dispilurus* as proposed by Steindachner (1882) and Eigenmann & Eigenmann (1888). *Epapterus dispilurus* is found to have a broad distribution in the central and western portions of the Rio Amazonas system and the Río Paraguay basin. The distribution of *E. blohmi* is extended from the state of Guarico, Venezuela to include other portions of the Río Orinoco basin and the Río Tuy of the Caribbean coast of Venezuela.

Resumo.—O gênero de bagres neotropicais *Epapterus* Cope é revisado. *Epapterus* compartilha várias sinapomorfias com *Auchenipterus* Valenciennes e *Pseudepapterus* Steindachner, e dentro deste grupo é o grupo irmão de *Pseudepapterus. Epapterus* não possui nadadeira adiposa, uma característica redutiva derivada única para o gênero dentro do grupo composto por *Epapterus*, *Auchenipterus* e *Pseudepapterus*, e proposta como sinapomórfica para o gênero. A extensão da membrana inter-radial que une as duas nadadeiras pélvicas é uma outra possível sinapomorfia para *Epapterus.* Contrariamente à opiniao corrente, *Epapterus* é composto de apenas duas espécies, *E. dispilurus* Cope (1878) e *E. blohmi* Vari et al. (1984). O exame de amostras de *Epapterus* provenientes de várias localidades no rio Amazonas e Río Paraguay não revelou nenhuma diferença entre as populações daquelas duas drenagens. Conseqüentemente, *E. chaquensis* Risso & Risso (1962), descrito da bacia do Río Paraguay, é colocado como sinônimo de *E. dispilurus*, originalmente descrito da porção ocidental da bacia amazônica. *Euanemus longipinnis* Steindachner (1881) é mantido como sinônimo de *E. dispilurus* conforme proposto por Steindachner (1882) e Eigenmann & Eigenmann (1888). *Epapterus dispilurus* possui ampla distribuição nas porções central e ocidental do sistema do rio Amazonas, assim como na bacia do Río Paraguay. A distribuição geográfica de *E. blohmi* é ampliada do estado de Guarico, Venezuela, para outras porções da bacia do río Orinoco e ao norte para o Río Tuy na costa caribenha de Venezuela.

In his original description of the auchenipterid catfish genus *Epapterus* from the Peruvian Amazon, Cope (1878:677) distinguished the genus and its single species from the other then-known genera now assigned to the Auchenipteridae by a combination of characters, most notably the lack of the adipose fin, the reduced dorsal fin, and the absence of jaw teeth. Soon thereafter Steindachner (1881) described another auchenipterid, *Euanemus longipinnis*, from specimens collected in the western Amazon along the present Peru-Brazil border. Steindachner (1882:31) noted that the two nominal species were apparently identical and Eigenmann & Eigenmann (1888:152) formally proposed that *Euanemus longipinnis* was a synonym of *Epapterus dispilurus*. Soon thereafter Eigenmann & Eigenmann (1890) redescribed *E. dispilurus* on the basis of specimens that they considered to be syntypes of *Euanemus longipinnis* (see, however, under "Remarks" for *Epapterus dispilurus*). The seven decades following this series of publications saw only one citation of *Epapterus* based on additional material, that of Fowler (1940) of a single specimen of *E. dispilurus* collected in the Río Ucayali in Amazonian Peru. This hiatus ended when Risso & Risso (1962) described *E. chaquensis* from five specimens collected in the Río Paraguay basin of Argentina. Risso & Risso distinguished their nominal species from *E. dispilurus* on the basis of purported differences in the number of pectoral- and anal-fin rays, relative eye size, and details of body and fin pigmentation. In the absence of available samples of *E. dispilurus*, Risso & Risso compared *E. chaquensis* to data in the original description of *E. dispilurus* by Cope (1878) and a relatively simple drawing of the lectotype of the latter species published twice by Fowler (1941:468, fig. 26; 1945:66, fig. 26).

Vari et al. (1984) described another species, *E. blohmi*, from samples originating in the central portions of the Río Orinoco system. *Epapterus blohmi* is readily differentiated from nominal congeners by its distinct caudal-fin pigmentation pattern, a difference supplemented by other features. In their discussion of *E. blohmi* Vari et al. (1984) also commented on the pronounced sexual dimorphism in the species of *Epapterus* and noted a series of characters potentially informative as to the phylogenetic position of the genus within the Auchenipteridae. Those authors noted, however, that definitive statements on the questions of the monophyly and relationships of *Epapterus* necessitated an encompassing phylogenetic analysis of the Auchenipteridae, an effort which was beyond the scope of their study. Vari et al. (1984) also briefly reported on new locality records for the two other *Epapterus* species (*E. dispilurus* and *E. chaquensis*) generally recognized as valid at that time, but lacked the population samples necessary to address the utility of the purported distinguishing features of those species.

In the course of our ongoing studies within the Auchenipterinae (Ferraris & Vari 1999) we have been able to examine numerous specimens of *Epapterus* in addition to those available to previous authors. This additional material led to a reappraisal of the distinctiveness of *E. dispilurus* and *E. chaquensis*. We address that problem herein, discuss the phylogenetic information pertinent to the monophyly of *Epapterus*, note broader meristic variation within *E. blohmi* revealed by the examination of additional specimens, and report extensions of the known distribution of *E. blohmi.*

Materials and Methods

Materials are listed alphabetically by country and within country by district, state, or province, and then repository abbreviation. Specimen sizes are reported in standard length (SL). Localities of specimens, other than type-localities, are translated into English when listed originally in another language. Coordinates are either taken from labels associated with specimens, or from publications, information provided by collectors, or from gazetteers when the locality is sufficiently precise.

Institutional abbreviations used are as follows: ANSP, Academy of Natural Sciences of Philadelphia; MCNG, Museu de Ciencias Naturales, Guanare; MCZ, Museum of Comparative Zoology, Cambridge; MHNG, Muséum d'Histoire naturelle, Geneva; MLP, Museo de La Plata; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museu de Zoologia, Universidade de São Paulo; NMW, Naturhistorisches Museum Wien, Vienna; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Vertebrae and unpaired fin rays were counted, when possible, from radiographs. Comparative counts made directly from specimens often failed to discern the anterior most anal-fin ray(s) and the posterior most dorsal- and anal-fin rays in small specimens. Vertebral counts were separated into precaudal and caudal elements. The anterior most caudal vertebra is the element possessing an elongate hemal spine that extended just anterior to the first basal radial of the anal fin. Usually, the last precaudal vertebra possesses a markedly shorter hemal spine than does the first caudal vertebra, and is the anterior most vertebra with a closed hemal arch. The ural complex is counted as one element. Precaudal and total vertebral counts assume that the Weberian complex is composed of four centra. The fifth centrum is suturally united to the complex and lacks articulated ribs. The first rib-bearing centrum is the sixth vertebra.

Fin-ray counts include all elements and treat the two posterior most dorsal- and anal-fin rays that articulate on the last distal radial as separate rays. The last pelvic-fin ray is often branched at its base, which is hidden beneath thick skin. Dissection was sometimes performed to verify the pelvic-fin ray count. Caudal-fin ray counts include only the branched principal rays. Anal-fin ray counts from sexually mature, transformed males assume that the gonopodium consists of one unbranched and one branched ray in the few instances in which separate elements could not be discerned from radiographs. The posterior most anal-fin rays are recorded as branched, although many were too small and/or fine to discern whether they actually branch. Rudimentary anal-fin rays occur irregularly. Rudiments that appear to possess a base that articulates with a basal radial element were included in counts, even if the rays do not extend distally to the fin margin. The first two rays posterior to the gonopodium in males often exhibit this rudimentary development. Rudiments suspended in the fin margin and fully formed rays that do not appear to articulate with a radial element were not counted.

Gill rakers were counted on the first gill bar on the right side of the specimen. Counts included all rakers, including anterior rudiments.

Measurements were made with digital calipers and were point-to-point, as follows: body depth was taken at the anal-fin origin; head length was measured parallel to the body axis, from the posterior tip of the bony operculum to the snout tip; length of anal-fin base was measured from the posterior edge of the anus to the insertion of the last anal-fin ray; orbital width was taken as the horizontal measure across the middle of the eye, bounded by the infraorbital bones; pelvic-fin length represents the distance from the attachment of the first branched ray to the fin tip; pectoral-fin spine length is from the anterior (or lateral) spine base to the tip of the bony spine not including the fleshy or flexible bony terminal parts; snout length is from the snout tip to the anterior margin of the eye.

Proportional measurements are presented as percentages of standard length (SL) or head length (HL). Values for the lectotype of *Epapterus dispilurus* are indicated in brackets in the description.

Nuptial males are those individuals demonstrating the transitory sexually dimorphic features of the maxillary barbels and dorsal-fin spine.

Epapterus Cope

Epapterus Cope, 1878:677 (type species: *Epapterus dispilurus* Cope, 1878, by monotypy).—Eigenmann & Eigenmann, 1888:152 [citation].—Eigenmann & Eigenmann, 1890:292 [citation].—Eigenmann, 1910:396 [citation].—Fowler 1951:465 [citation].—Vari et al., 1984: 468 [discussion of relationships and potential synapomorphies].

Diagnosis.—Epapaterus along with *Auchenipterus* Valenciennes, in Cuvier and Valenciennes (1840) and *Pseudepapterus* Steindachner (1915) form a monophyletic assemblage within the Auchenipteridae defined by various synapomorphies (Ferraris 1988, Ferraris & Vari 1999). The combination of the absence of jaw teeth and the possession of a reduced dorsal fin with only two to four short rays and a poorly developed spine (other than in nuptial males) delimits a clade formed by *Epapterus* and *Pseudepapterus* within the Auchenipteridae. The lack of an adipose fin is a synapomorphy for the species of *Epapterus* within that lineage. *Epapterus* species also have the pelvic fins joined to each other across the ventral midline by extensions of the interradial membrane; an additional potential synapomorphy for the members of the genus (see comments under "Phylogenetic relationships and monophyly of *Epapterus*" below).

Phylogenetic relationships and monophyly of Epapterus.—In his original description of *Epapterus*, Cope (1878:677) listed a series of "Char. Gen.", presumably the diagnostic features for the genus. These features largely consisted of what would now be regarded as various plesiomorphic characters, at least at the level of the Auchenipteridae. Nonetheless, three features cited by Cope as distinguishing *Epapterus* from *Euanemus* (=*Auchenipterus*), the lack of an adipose fin, the reduced number of dorsal-fin rays, and the absence of teeth on the jaw and palate, are considered derived within the Auchenipteridae under the context of an encompassing phylogenetic analysis (Ferraris 1988). Steindachner (1915) subsequently described *Pseudepapterus* as a subgenus of *Auchenipterus. Pseudepapaterus* shares with *Epapterus* a lack of jaw dentition and a reduced dorsal fin but was distinguished from the latter genus on the basis of the possession of an adipose fin. Mees (1974:112) commented briefly on the similarities between *Auchenipterus*, *Epapaterus*, and *Pseudepapterus*. Vari et al. (1984:467–468) identified a number of features in *Epapterus* of potential phylogenetic importance. Those authors were unable to make definitive statements on these questions in the absence of comparative specimens of *Pseudepapterus*, and as a consequence of the lack, at that time, of a rigorous hypotheses of higher level groupings within the Auchenipteridae.

Auchenipterus, *Epapterus*, and *Pseudepapterus* comprise a monophyletic group within the Auchenipteridae united by various characters summarized by Ferraris (1988) and Ferraris & Vari (1999). The reduced dorsal fin with only two to four short rays and a poorly-developed spine other than in nuptial males, along with the lack of dentition on both the jaws and palate, are derived features within the Auchenipteridae uniting *Pseudepapterus* and *Epapterus* as sister-taxa. *Epapterus* has been traditionally distinguished by its lack of an adipose dorsal fin. An adipose fin is also absent elsewhere in the Auchenipteridae in *Trachelyopterus* Valenciennes, *Trachelyopterichthys* Bleeker, and *Trachelyichthys* Mees (the reported absence of the fin in *Ceratocheilus* by Miranda-Ribeiro (1918) was in error; see comments in Ferraris & Vari (1999). The lack of an adipose fin is considered synapomorphic for the species of *Epapterus* in the clade consisting of *Auchenipterus*, *Epapterus*, and *Pseudepapterus* under the overall most parsimonious hypothesis of intrafamilial relationships for the Auchenipteridae (Ferraris 1988).

Epapterus species also have the pelvic fins joined to each other across the ventral midline by extensions of the interradial membrane. Such continuity of the contralateral pelvic fins is hypothesized as derived within the Auchenipteridae given the absence of a comparable union of the fins in most auchenipterids and in proximate outgroups to the family. A continuity between the contralateral pelvic fins also occurs elsewhere within the clade consisting of *Auchenipterus*, *Epapterus*, and *Pseudepapterus* in *Auchenipterus fordicei* Eigenmann & Eigenmann (Ferraris & Vari 1999). *Auchenipterus fordicei*, a poorly known species, shares with its congeners the presence of grooves on the ventral surface of the head that accommodate adducted mental barbels, a synapomorphy for the species of *Auchenipterus* (Ferraris & Vari 1999). Nuptial males of *A. fordicei* are unknown and it is uncertain whether *A. fordicei* has the second potential synapomorphy for *Auchenipterus*, the presence of papillae on the dorsal and medial surfaces of the ossified maxillary barbel of nuptial males (Ferraris & Vari 1999). *Auchenipterus fordicei*, nonetheless, lacks the derived features considered synapomorphic for *Epapterus* and *Pseudepapterus* and retains a relatively large dorsal fin and an adipose fin, contrary to the derived reduction and absence, respectively, of those structures in *Epapterus*. Thus, the common possession of pelvic fins joined to each other across the ventral midline by extensions of the interradial membrane in *Auchenipterus fordicei* and *Epapterus* is most parsimoniously considered a result of convergence.

Key to the species of *Epapterus*

1. Dorsal lobe of caudal fin with irregularly rounded patch of dark pigmentation in central portion of lobe, pigmentation not forming distinct transverse bar; ventral lobe of caudal fin with distinct patch of dark pigmentation in middle of lobe; pectoral-fin rays 11 to 13, typically 12 or 13 .... *E. dispilurus*

– Dorsal lobe of caudal fin with a dark transverse bar extending from upper anterodorsal margin to posterior margin of middle rays of dorsal lobe; ventral lobe of caudal fin without a distinct patch of dark pigmentation; pectoral-fin rays 9 to 11 .... *E. blohmi*

Epapterus dispilurus Cope, 1878

Figs. 1–3, Table 1

Epapterus dispilurus Cope, 1878:677 (type locality: Peruvian Amazon).—Steindachner, 1882:31 [*Euanemus longipinnis* Steindachner, 1881:17 equated with *Epapterus dispilurus*].—Eigenmann & Eigenmann, 1888:152 [citation].—Eigenmann & Eigenmann, 1890:292 [redescription based on specimens erroneously thought to be syntypes of *Euanemus longipinnis*].—Eigenmann, 1910:397 [citation].—Fowler, 1915:222 [citation; original Cope specimens cited as cotypes].—Fowler, 1940:231 [Peru, Río Ucayali].—Fowler, 1941:468, fig. 26 [lectotype designation].—Fowler, 1945:66, fig. 26 [reproduction of Fowler, 1941].—Fowler, 1951:465 [citation].—Böhlke, 1984:24 [type holdings at ANSP].—Vari et al., 1984:470, fig. 2 [Brazil, Ihla da Marchantaria; Peru, Río Ucayali basin; comparison with *Epapterus blohmi*].—Ortega & Vari, 1986:14 [as component of Peruvian freshwater fish fauna].

Fig. 1. *Epapterus dispilurus*, nuptial male, USNM 273591, 106 mm SL; showing pronounced development of dorsal-fin spine and maxillary barbel.

Euanemus longipinnis Steindachner, 1881: 17 (type locality: Hyavary [=Brazil, Amazonas, Rio Javari]).—Steindachner, 1882:31 [equated with *Epapterus dispilurus*].—Eigenmann & Eigenmann, 1888:152 [citation, as synonym of *Epapterus dispilurus*].—Eigenmann & Eigenmann, 1890:292 [citation, as synonym of *Epapterus dispilurus*].—Eigenmann, 1910:397 [citation, as synonym of *Epapterus dispilurus*].—Fowler, 1951:466 [citation, as synonym of *Epapterus dispilurus*].

Epapterus chaquensis Risso & Risso, 1962: 5, figs. 1–3 (type locality: Argentina, Chaco, Resistencia).—Risso & Risso, 1964:5 [citation].—Vari et al., 1984:470, fig. 3 [Paraguay, Río Negro of Río Paraguay].—[not Burgess, 1989, pl. 113, unnumbered figure].

Auchenipterus nuchalis, Sands, 1984:24, unnumbered photo.—Burgess, 1989; pl. 13.

Auchenipterus demerarae, Sands, 1986:43, unnumbered photos.

Diagnosis.—*Epapterus dispilurus* is diagnosed by, and is readily distinguished from its single congener, *E. blohmi*, by having a distinct, irregularly-shaped, patch of dark pigmentation on each caudal-fin lobe which contrasts with the dark transverse bar extending from the upper anterodorsal margin of the dorsal lobe of the caudal fin to the posterior margin of the middle rays of the dorsal lobe, and by the lack of a distinct patch of dark pigmentation on the ventral lobe of the caudal fin in *E. blohmi*. The two species also differ in the number of pectoral-fin rays (11 to 13, typically 12 or 13, in *E. dispilurus* versus 9 to 11 in *E. blohmi*), and in differences, other than for nuptial males of *E. dispilurus*, in the relative length of the maxillary barbel (166–194% of HL in *E. blohmi* versus 122–163% of HL in *E. dispilurus*). *Epapterus dispilurus* nuptial males also have a highly developed dorsal spine with well developed basal and distal anterior projections, modifications which are unknown in *E. blohmi*.

Description.—Body elongate, distinctly compressed, head depressed (Figs. 1, 2). Dorsal profile of head flat or barely convex. Dorsal profile of body from rear of head to end of caudal peduncle slightly to distinctly convex. Ventral profile of head slightly convex. Ventral profile of body gently curved to anal-fin origin. Intromittent organ of males extending along entire anterior margin of third anal-fin ray. Anal-fin base gently convex to caudal peduncle.

Greatest body depth 19.3–25.6 [19.6] of SL; snout tip to dorsal-fin origin 19.3–22.5 [19.7] of SL; snout tip to pelvic-fin origin 33.2–37.1 [34.0] of SL; snout tip to anal-fin origin 39.0–45.6 [39.6] of SL.

Head depressed. Snout viewed from dorsal view somewhat more truncate in mature males than in females in which snout mar-

Fig. 2. *Epapterus dispilurus*, female, USNM 305651, 102 mm SL; showing form of dorsal-fin spine and maxillary barbel in females and immature individuals.

gin distinctly rounded from that view. Head length 18.3–21.6 [18.9] of SL. Lower jaw slightly shorter than upper jaw in females and immature specimens, difference in jaw lengths slightly more pronounced in mature males; no teeth present on premaxillae, dentaries, vomer, and palatines. Lower pharyngeal tooth plates large and round with short conical teeth; convex fourth upper pharyngeal tooth plate with short conical teeth. Snout length 36.2–40.9 [40.7] of HL. Orbital margin not free, horizontal width of orbit 26.7–30.2 [29.2] of HL. Length of postorbital portion of head 41.5–46.7 [41.5] of HL. Interorbital region gently convex. Nares of each side of head separated by distance approximately equal to 4.5–5.0 times diameter of posterior nostril; anterior nostril somewhat tubular, located on anterodorsal surface of snout, above lip; posterior nostril larger, oval.

Gill rakers on first arch 33 to 42. Branchiostegal rays 6. Gill membranes broadly attached to isthmus. Maxillary barbels rounded in cross section, elongate, length 122–163% of HL in females, immature specimens, and males without fully developed ossification of barbel; barbel length 191% of HL in single available nuptial male; tip of barbel reaching posteriorly to, nearly or to, end of pectoral fin in females, immature specimens, and males without fully developed ossification of the barbel, extending distinctly beyond tip of pectoral fin in fully nuptial male; degree of ossification of barbel highly sexually dimorphic (see "Sexual dimorphism" below). Mental barbels four, transversely rounded, arranged in arc along ventral surface of jaw, barbels reaching posteriorly approximately to line through middle of pectoral fin.

Lateral line complete, dendritic, with short side branches at irregular intervals, divided on caudal fin into 2 or 3 branches that run in some individuals through slightly ossified tubes.

Dorsal fin greatly reduced, with 1 spine and 2 or 3 rays (2 rays present in 1 of 43 specimens examined for this feature). Dorsal-fin spine non-serrate and sexually dimorphic, relatively short and slender, length 2.8–3.6 of SL in females, immatures, and males not in reproductive condition. Dorsal fin proportionally much thicker and distinctly elongate in one available nuptial male, length 16.4 of SL (see "Sexual dimorphism" below for detailed description of spine). First dorsal-fin ray typically slightly longer than dorsal-fin spine in females and immature specimens. Single available nuptial male with first dorsal-fin ray distinctly longer proportional to SL than in females, immature specimens, and males not in reproductive condition, but with lengthened ray extending only about three-quarters of length of greatly enlarged dorsal-fin spine. Adipose dorsal fin absent.

Pectoral fin with 1 spine and 11 to 13, most often 12 [12], rays; pectoral-spine length 12.3–14.0 [13.0] of SL; medial margin of pectoral spine with series of serrations, serrations absent basally and sometimes along distal one-fifth of spine; rayed portion of fin pointed, longest pectoral-fin rays ranging from approximately same length as, to somewhat longer than, pectoral spine; length of longest pectoral-fin rays 12.3–14.4 of SL; tip of pectoral fin not reaching to pelvic-fin origin.

Pelvic-fin margin pointed, fin with 14 to 16 rays [15], lateral most rays longest, length of longest pelvic-fin rays 16.0–19.3 of SL; pelvic fin with broad, posteroventrally sloping base with interradial membrane continuing across midline of body to join interradial membrane of contralateral pelvic fin; insertion of pelvic fin situated distinctly dorsal of ventral margin of body.

Anal-fin margin in females smoothly convex anteriorly, straight for much of its length and convex posteriorly; last unbranched and first branched anal-fin rays in males greatly developed and conjoined for support of intromittent organ (see "Sexual dimorphism" below for details); remainder of anal fin of males as in females; length of anal-fin base 51.4–56.0 [55.5] of SL. Anal-fin rays 54 to 61 [59]. Caudal fin distinctly emarginate.

Precaudal vertebrae 14 to 16, typically 15 [15], caudal vertebrae 33 to 36 [35], total vertebrae 48 to 50 [50].

Color in life.—Sands (1986:43, unnumbered photos) published two photographs of what is apparently the same individual of *Epapterus dispilurus* (identified by that author as *Auchenipterus demerarae*). These illustrations were later reproduced by Burgess (1989, pl. 113, unnumbered photographs) who identified the species as *Auchenipterus nuchalis*. Overall dark pigmentation on the head and body in specimen in the photos is as described below for preserved specimens, but with more lightly pigmented portions of body having a silvery sheen which also extends onto the basal portions of the caudal and anal fins. The anterior margin of the pectoral fin white. Barbels with white tips. Neither the silvery pigmentation nor the white margin to the pectoral fin is apparent in the aquarium specimen of *E. dispilurus* published by Sands (1984:24, photo; identified therein as *Auchenipterus nuchalis*).

Color in alcohol.—Overall ground coloration ranging from tan to light purplish brown, overall pigmentation tending to increase with increasing body size, but with population samples of similar size individuals from different sites in the Río Ucayali basin showing notable difference in overall intensity of pigmentation.

Dorsal surface of head in lighter colored specimens with scattered chromatophores more concentrated lateral to, and particularly posterior to, fronto-parietal fontanel. Margin of upper lip in region anterior to orbit with distinct patch of dark pigmentation. With increasing intensity of overall head and body pigmentation, chromatophore field on dorsal surface of head expands laterally and anteriorly to contact orbit laterally and patch of pigmentation on upper lip anteriorly. In very dark individuals entire dorsal portion of head dark, other than for light anterior margin of upper lip. Lateral surface of head with scattered dark chromatophores in light specimens; darker specimens with patches of dark pigmentation anterior and posterior to orbit continuous dorsally with dark pigmentation on dorsal portion of head.

Dorsal portion of body with scattered dark chromatophores in lighter specimens, but with nearly solid purplish pigmentation in darker individuals. Distinct, dark humeral spot present in all individuals; spot slightly horizontally elongate in some smaller, lighter-colored specimens, more rounded in larger specimens, with posterior portion of spot continuous in some individuals with variably developed zigzag pattern of dark chromatophores overlying lateral line. Darker individuals with ventral and sometimes midlateral portions of body with dusky purplish pigmentation.

Caudal fin with irregular patch of dark pigmentation on dorsal lobe; vertical extent of patch usually greater than its horizontal length. Ventral lobe of caudal fin with irregular patch of dark pigmentation on center of lobe; shape of patch ranging from somewhat rotund to vertically elongate. Caudal pigmentation more intense in specimens with overall darker coloration. Anal fin nearly unpigmented in some specimens, with distal margin darker in most examined specimens. Dark pigmentation on distal portions of fin limited to anterior one-half to two-thirds of fin in some specimens whereas other individuals have field of pigmentation along distal region of fin more elongate, occasionally with fin margin quite dark along its entire length. Basal portions of anal fin purplish in very dark individuals. Extent of dark pelvic fin pigmentation variable among specimens with differences in degree of development correlated with overall intensity of dark pigmentation of specimen. Distal margin of pelvic fin dusky in all specimens, more so in dark individuals. Lateral margin and basal portions of pelvic fin in less intensely pigmented individuals with scattered dark chromatophores. Pelvic fin with dark patch of pigmentation in more intensely pigmented specimens. Pectoral fin with scattered dark chromatophores more concentrated along distal margin; more intensely pigmented individuals with varyingly developed basal patch of dark pigmentation.

Sexual dimorphism.—Females attain a greater maximum size than do males. The largest specimen examined by us was a 124 mm female and a number of females exceeded 110 mm. The largest identifiable male was 107 mm and the smallest was 97 mm. The snout in nuptial males is somewhat more truncate when viewed from a dorsal view than that in females in which the snout margin is distinctly rounded. Females have the bony core of the maxillary barbel relatively short with the remainder of the barbel flexible, thin, and extending posteriorly to the middle of, or to the posterior margin of, the pectoral fin. In the single examined nuptial male the barbel is greatly thickened, distinctly curved (Fig. 1), and somewhat lengthened relative to the condition in females. When adducted the barbel of the nuptial male reaches distinctly beyond the posterior tip of the pectoral fin.

The dorsal-fin spine in the single available nuptial male is distinctly thicker and more notably is distinctly longer than the spines of immature individuals, females, and males not in reproductive condition (compare Figs. 1 and 2). The spine in nuptial males is somewhat sinusoidal in lateral view, with a distinct anterior process toward its base and a well developed anterior process toward its tip which gives the distal portion of the spine a harpoon-like shape in lateral view (Fig. 1). The first dorsal-fin ray is also distinctly longer in the nuptial male than in immature specimens, females, and males not in reproductive condition. The dorsal-fin spine of males can be hyperextended anteriorly to an approximately 75° angle relative to the predorsal profile, instead of the vertical or slightly posterodorsal fully adducted position of the spine in females and juveniles. Mature males have an anal fin with the last unbranched and the first branched anal-fin rays distinctly thickened and more elongate than those in females and conjoined to form the structural support of an intromittent organ. The genital pore of males is at the end of an elongate tube that extends along, and is bound to, the anterior margin of the anal fin. The tube terminates slightly beyond the end of the tip of the conjoined last unbranched and first branched anal-fin rays.

Distribution.—Central and western portions of the Amazon basin along and south of the main channel of the Rio Amazonas, and the Río Paraguay system in Paraguay, northern Argentina, and southern Brazil (Fig. 3).

Remarks.—Epapterus dispilurus Cope (1878) was described on the basis of two specimens which originated in the upper Amazon basin of Peru. These specimens were cited as "cotypes" by Fowler (1915: 222). Some years later, and without any dis-

Fig. 3. Map of central portions of South America showing known distribution of *Epapterus dispilurus* (type locality of *E. dispilurus* inexact = Peruvian Amazon; 1 = type locality of *Euanemus longipinnis*; 2 = type locality of *Epapterus chaquensis*; some symbols represent more than one locality or lot of specimens).

cussion, that author (Fowler 1941:468, fig. 26 repeated in Fowler 1945:66, fig. 26) provided a cryptic, but valid, lectotype designation by the statement "tipo, largo 125 mm" which accompanied his line drawing of the species. The cited length corresponds with the total length of the larger of the two syntypes of *E. dispilurus* which we consequently consider to be the lectotype (ANSP 21353). This obscure lectotype designation was overlooked in Böhlke (1984).

The name *Euanemus longipinnis* is generally cited as being published in 1882 with the author credited as being Agassiz in a Steindachner paper. Both this date and author are questionable. The name was published as the first article of the Denkschntten der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse for 1882, but Troschel (1882) listed the paper as having been published in 1881. Barbara Hertzig (NMW, in litt.) indicated that separates of the publication were available, and probably distributed, in 1881, which would account for the date cited in Troschel's account. On the basis of this evidence, we use the year 1881 as the date of description of *E. longipinnis*.

Steindachner (1881:17) indicated that the specimens on which he based his description of the species were sent to him by Agassiz with the name "*Euanemus longipinnis* Agass." Agassiz's contribution appears to be limited to the creation of the name and sending the specimens to Steindachner given that the format of the species description is typical for Steindachner's other publications of the period. As such, we consider Steindachner as the author of the name and only the specimens examined by Steindachner can be considered as constituting the type series. Steindachner (1881:18) noted in the original description of the species that he examined four specimens, a number matching the identified syntypes in the NMW holdings (NMW 46682:1–4). We have examined two of the four syntypes catalogued as NMW 46682:1–4 and select the larger of those specimens (NMW 46682:1, 93 mm SL) as the lectotype of *Euanemus longipinnis.*

Four specimens deposited in MCZ (originally MCZ 9834 (4 specimens), now divided between MCZ 9834 (3 specimens) and MCZ 33450 (1 specimen)) were identified as syntypes of *Euanemus longipinnis* by Eigenmann & Eigenmann (1890:292) in their redescription of *Epapterus dispilurus.* However, given that all specimens cited as syntypes in the original description of *Euanemus longipinnis* are accounted for in the NMW holdings, we do not consider the MCZ material to be part of the type series.

Status of *Epapterus chaquensis*

In the abstract of their original description of *Epapterus chaquensis*, Risso & Risso (1962:4) noted that their nominal species differed from *E. dispilurus* in the form of the dark humeral spot and in the presence of dark pigmentation of the ventral (=pelvic) fin. Within the main body of the text Risso & Risso (1962:6) cited, however, a more extensive series of characters discriminating the two species, proposing that *E. chaquensis* differed from *E. dispilurus* "principally in the dark coloration of the anal fin and basal and distal regions of the ventrals [=pelvic fins]. The humeral mark is not rounded but obliquely lengthened. Lesser number of rays in the anal and pectoral. Head and eyes smaller, etc." (our translation).

Risso & Risso gave no indication that they examined comparative specimens of *E. dispilurus*, rather their literature cited and introductory remarks indicate that their comparisons were based on literature information, in particular the original description of *E. dispilurus* (Cope, 1878:677) and the line drawing of the lectotype of that species included in Fowler's listing of the fishes of Peru (1941, 1945). Cope (1878), in his original description of *E. dispilurus* (1878), commented neither on the form of the humeral spot nor made mention of any pigmentation of the pectoral, pelvic, and anal fins. Fowler's relatively simple line drawing (1941:468, fig. 26; 1945:66, fig. 26) was based on the lectotype of *E. dispilurus*, a specimen which is now in very poor condition and which may not have been in a much better state at the time that Fowler prepared the figure. Specimens of other species cited by Cope (1878) were already in poor condition less than two decades later when reported on in 1906 by Fowler (Vari 1992:117–118). More recently collected specimens of *E. dispilurus* from the Peruvian Amazon, the type region of that species, have a humeral spot which is much more horizontally elongate than that shown in Fowler's figure of the species. The humeral pigmentation pattern in *E. dispilurus* specimens from the Peruvian Amazon is comparable to that in population samples of *Epapterus* from the Río Paraguay, the type-region for *E. chaquensis.* Similarly, Fowler's drawing (1941, 1945) does not include the dark anal-, pelvic-, and pectoral-fin pigmentation which is typical for Amazonian *Epapterus* populations samples and which also occurs in population samples of the genus from the Río Paraguay basin as noted by Risso & Risso. The incomplete representation of the dark body and fin pigmentation in Fowler's figures (1941, 1945) presumably lead Risso & Risso to erroneously propose that the Amazonian and Paraguayan populations differed in details of dark pigmentation. Our comparisons of population samples from the two basins have, in contrast, failed to reveal any consistent dif-

Table 1.—Ranges in population samples of *Epapterus* from the Río Paraguay and Rio Amazonas basins for meristic and morphometric features cited by Risso & Risso (1962) as distinguishing *E. dispilurus* (Rio Amazonas) from *E. chaquensis* (Río Paraguay).

Feature	Basin	
	Rio Amazonas	Río Paraguay
Anal-fin rays	52–62	53–61
Pectoral fin rays	11–13	12–13
Head length in SL	18.3–21.9	18.5–20.9
Eye diameter in HL	25.0–33.1	26.7–29.8

ference in these or any other pigmentation patterns.

Risso & Risso (1962:6) also cited purported differences in the numbers of anal- and pectoral-fin rays and relative sizes of the head and eye as distinguishing *Epapterus chaquensis* from *E. dispilurus.* Presumably their comparative data for the latter species was taken from the original description by Cope (1878) which was based on only two specimens. Similarly, Risso & Risso had only five specimens of *E. chaquensis* available for their analysis. A comparison of larger population samples from the Amazon and Paraguay basins (see "Material Examined") has shown that the degree of variation in the number of anal- and pectoral-fin rays and in the range in the relative size of the head and eyes in the population samples from the Amazon and Paraguay basis is significantly greater than indicated by the limited type-series of *E. dispilurus* and *E. chaquensis.* As a consequence there is broad, or complete, overlap between the samples from the two basins in all features proposed by Risso & Risso (1962:6) to distinguish the nominal species (Table 1). We have been unable to identify any meristic, morphometric, or color pattern differences that would justify the continued recognition of *E. chaquensis* and we consequently place that species into the synonymy of *E. dispilurus.*

Material examined.—Total specimens: 75. Specimens from which counts and measurements were taken: 50, 59–123 mm SL.

Argentina: Chaco: Resistencia, Laguna along side of the Río Salado (27°27'S, 58°59'W), MLP 8017, 1 (124). Rio Negro, Resistencia (27°27'S, 58°59'W), MZUSP 10252–53, 2 (88–93).

Bolivia: El Beni: Canal San Gregório, Trinidad (14°47'S, 64°47'W), MZUSP 27816, 2 (63–72). Trinidad (14°47'S, 64°47'W), USNM 278586, 3 (59–92). Río ltenez, Londra, USNM 278563, 2 (78–100). Río Matos, 48 km E San Borja, below road crossing (14°55'S, 66°17'W), USNM 305651, 2 (79–102).

Brazil: Amazonas: Rio Javari of Rio Solimões (4°21'S, 70°02'W), MCZ 9834, 3 (75–107; erroneously identified as syntypes of *Euanemus longipinnis* by Eigenmann & Eigenmann 1888:292); MCZ 33450, 1 (78; erroneously identified as syntype of *Euanemus longipinnis* by Eigenmann & Eigenmann 1888:292). Humaitá, Igarapé Joari (7°31'S, 63°02'W), MZUSP 27912, 2 (88–95). Rio Aripuaná, Igarapé on Ilha do Castanhal (~5°07'S, 60°24'W), MZUSP 48866, 1 (73). Hyavary [=Rio Javari] (4°21'S, 70°02'W), NMW 46682:1, 1 (93, lectotype of *Euanemus longipinnis*); NMW 46682:2 (79, paralectotype of *Euanemus longipinnis*). Lago Terra Preta, Januari (3°12'S, 60°05'W), USNM 261422, 2 (73–86). Mato Grosso: Lagoa on Fazenda Onça Magra, Municipio de Cáceres (~16°04'S, 57°41'W), MZUSP 38172, 1 (90). Mato Grosso do Sul: Rio Aquidauana, Baia da Onça or Jatobá, Fazenda Alegrete (~19°44'S, 56°50'W), MZUSP 40084, 4 (98–122).

Paraguay: Cordillera: Río Piribebuy, 5 km N of Emboscada (~25°29'S, 57°03'W), MHNG 2212.27, 1 (123). Presidente Hayes: Río Negro, 6 km S of Chaco-I (~25°15'S, 57°38'W), MHNG 2212.30, 1 (116). Río Paraguay at San Antonio, MHNG 2213.25, 1 (119). Río Aguaray-guazu, at km 117 of Transchaco Road (24°47'S, 57°19'W), MHNG 2213.26, 1 (123). Río Negro at Trans-Chaco Highway crossing (~25°10'S, 58°30'W), USNM 232304, 1 (87).

Peru: Peruvian Amazon, ANSP 21353, 1

(107; lectotype of *Epapterus dispilurus*), ANSP 21354, 1 (96, paralectotype of *Epapterus dispilurus*). Loreto: Río Ucayali basin, Contamana (7°20′S, 75°01′W), ANSP 103412, 1. Reserva Natural Pacaya-Samiria, Caño Ungurahue of Río Pacaya (4°13′S, 74°24′W), MUSM 2524, 1 (66). Ucayali: Río Ucayali, Provincia Coronel Portillo, Bagazan, MZUSP 26183, 4 (96–110). Provincia Coronel Portillo, Pucallpa, Cashibococha (7°33′S, 74°53′W), MZUSP 26318, 6 (100–109). Provincia Coronel Portillo, Pucallpa, Río Ucayali (8°23′S, 74°32′W), MZUSP 26410, 7 (51–63). Provincia Coronel Portillo, Río Aguaytia, Nueva Requena (8°20′S, 74°34′W), USNM 261388, 6 (59–106). Provincia Coronel Portillo, Río Ucayali at Pucallpa (8°23′S, 74°32′W), USNM 263114, 1 (59). Provincia Coronel Portillo, Río Ucayali, Utuquinia (8°15′S, 74°33′W), USNM 263115, 4 (83–89); USNM 273591, 5 (103–115); USNM 273615, 4 (115–128).

Epapterus blohmi Vari et al., 1984

Epapterus blohmi Vari et al., 1984:463, fig. 1 (type locality: Venezuela, Guarico State, Fundo Pecuario Masagural, Laguna Los Guácimos).—Machado-Allison & Moreno, 1993:87 (Venezuela, Guarico State, Río Orituco).—Machado-Allison et al., 1993:130 (Venezuela, lower llanos).—Lasso et al., 1995:4, 7, 8 (Venezuela, flooded llanos; ecology).—Taphorn et al., 1997:83 (Venezuela).

Publications dealing with aspects of the distribution and ecology of *Epapterus blohmi* which appeared subsequent to its original description are cited in the synonymy for the species.

Remarks.—Vari et al. (1984) provide a detailed description of *Epapterus blohmi* and there is no need to repeat that account in its entirety. Nonetheless, in the course of this study we had the opportunity to examine a greater number of specimens of *E. blohmi* from a wider geographic range (see "Distribution" below) than were available to Vari et al. (1984). This increased sample, not unexpectedly, revealed that the following meristic values were found to demonstrate a broader range in this study than reported in the original description of *E. blohmi:* dorsal-fin rays 2 or 3; pectoral-fin rays 9 to 11; pelvic-fin rays 13 to 16; anal-fin rays 49 to 61; gill-rakers 29 to 40; precaudal vertebrae 14 or 15; caudal vertebrae 34 to 36; total vertebrae 49 to 51 (note: vertebral counts presented in original account did not include consolidated elements in Weberian apparatus). Vari et al. (1984) reported that teeth were absent on the lower pharyngeal tooth-plate of *E. blohmi.* Examination of additional cleared and stained specimens has revealed that the cited absence was an individual variant in a smaller specimen and that dentition on the lower pharyngeal tooth-plate is typically present in the species.

Distribution.—Vari et al. (1984) described *Epapterus blohmi* on the basis of a series of specimens collected from Guarico State, Venezuela, in the central portions of the Río Orinoco basin. Subsequent collecting efforts elsewhere in that river system have shown that the species is widespread in Apure State and occurs in the Portuguesa State, both of which are located to the west of the type-locality. These efforts have also revealed that the range of the species extends east into the Anzoategui State. More unexpected was the discovery of *E. blohmi* in the Río Tuy system, a Caribbean versant basin along the northern coast of Venezuela, a distinct range extension to the north of the type locality of the species and the first reported occurrence of *E. blohmi* outside of the Río Orinoco basin. A single lot of *E. blohmi* examined during this study originated in Quebrada Caraballo within the Río Tuy system, Miranda state.

The fishes of the Río Tuy basin are still poorly known, a problem exacerbated by the large scale pollution of the main channel of the river. Nonetheless, a pattern has become apparent in recently revised groups in which species are found to be common to the Río Tuy and Río Orinoco basins. In addition to *Epapterus blohmi*, these include the characiform species *Creagrutus melasma* (Vari et al. 1994:95) and *Steindachnerina argentea* (Vari 1991:41). Although the phylogenetic relationships of most species endemic to the Río Tuy basin remain uncertain, there is some indication of sister-group relationships between species in that basin and those of the Río Orinoco system (e.g., *Serrasalmus neveriensis* Machado-Allison et al., 1993:53; Machado-Allison & Fink, 1996:113). The distribution data from *Epapterus blohmi* is congruent with the hypothesis of a once continuous ichthyofauna between the Río Tuy and Río Orinoco basins which was disrupted by the uprise of the Serrania de la Costa as proposed by Machado-Allison et al. (1993:53).

Material examined (in addition to that cited in Vari et al. 1984).—Venezuela: Anzoategui. Río Zuata, near Zuata (8°22′N, 65°22′W), USNM 316822, 4. Apure. Modulo UNELLEZ, near Caño Caicara, MCNG 3599, 8. Modulo UNELLEZ, east dyke, MCNG 2435 1; MCNG 3932, 1. Modulo de Mantecal, MCNG 19593, 1. Hato El Frio (7°49′N, 68°54′W), MCNG 5963, 1; MCNG 9914, 1; MCNG 9668, 10. Laguna El Pozon, MCNG 24075, 1. Miranda. Quebrada Caraballo, along highway between Caracas and Caucagua, parcela Yaguara (Río Tuy basin), MCNG 27358, 7 (of 44). Portuguesa. Caño Maraca (8°47′N, 69°05′W), MCNG 8637, 1. Districto Turen, Caño Salado ~5 km S of Nueva Florida (latter locality at 8°57′N, 69°01′W), MCNG 12679, 1.

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Two new subspecies of *Cinnycerthia fulva* (Aves: Troglodytidae) from the southern Andes

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Abstract.—Analysis of geographic variation of plumage pattern and color within *Cinnycerthia fulva* (Troglodytidae) of the southern Andes revealed that this taxon, formerly treated as monotypic, consists of three discrete units. We describe two new subspecies; one (*C. f. fitzpatricki*) from the isolated Cordillera Vilcabamba, depto. Cuzco, Peru, and the other (*C. f. gravesi*) from depto Puno, Peru, south to depto. Cochabamba, Bolivia.

Our previous analysis of geographic variation in size and plumage color of *Cinnycerthia* wren populations of the Andes (Brumfield & Remsen 1996) suggested that the form previously treated as a single species, *Cinnycerthia peruana* (Sepia-brown Wren; Troglodytidae) consists of at least three biological species: *C. olivascens* of the northern Andes south to northern Peru, *C. peruana* of the Andes of Peru from depto. Amazonas south to the Río Apurímac canyon, and *C. fulva*, from depto. Cuzco, Peru, to the Andes of Bolivia. We also noted that *C. fulva* contains at least three distinctive populations, only one of which is named: a dark-crowned population restricted to the isolated Cordillera Vilcabamba, depto. Cuzco, Peru; a population in the main Andes of southern depto. Cuzco, including the type locality of *fulva*; and a small-sized, pale population in the main Andes from southern depto. Puno to depto. Cochabamba, Bolivia. We herein formally name the two undescribed populations.

The Cordillera Vilcabamba, depto. Cuzco, Peru, is a mountain range isolated from the main chain of the Andes by deep river valleys with tropical, non-montane habitats (Terborgh 1971, Haffer 1974). Although specimens of birds collected there by John Weske and John Terborgh have yet to be analyzed in a systematic manner, some endemic taxa have been described or are in the process of being described: *Schizoeaca vilcabambae* Vaurie et al., 1972 (see Remsen 1981), *Cranioleuca marcapatae weskei* Remsen, 1984, *Atlapetes rufinucha terborghi* Remsen, 1993, and undescribed subspecies of *Ochthoeca fumicolor* and *Coeligena violifer*.

Our analysis of geographic variation in the *Cinnycerthia peruana* superspecies (Brumfield & Remsen 1996) revealed that the population from the Cordillera Vilcabamba has a highly distinctive head pattern (Fig. 1) approached by no other population in the complex. This population, which is part of the complex that Brumfield & Remsen (1996) treated as a separate species, *C. fulva*, may be known as:

Cinnycerthia fulva fitzpatricki,
new subspecies

Holotype.—American Museum of Natural History (AMNH) 820311; mist-netted by John S. Weske and John W. Terborgh on 11 Jul 1967 at Cordillera Vilcabamba, elev. 2090 m, depto. Cuzco, Peru, 12°38′S,

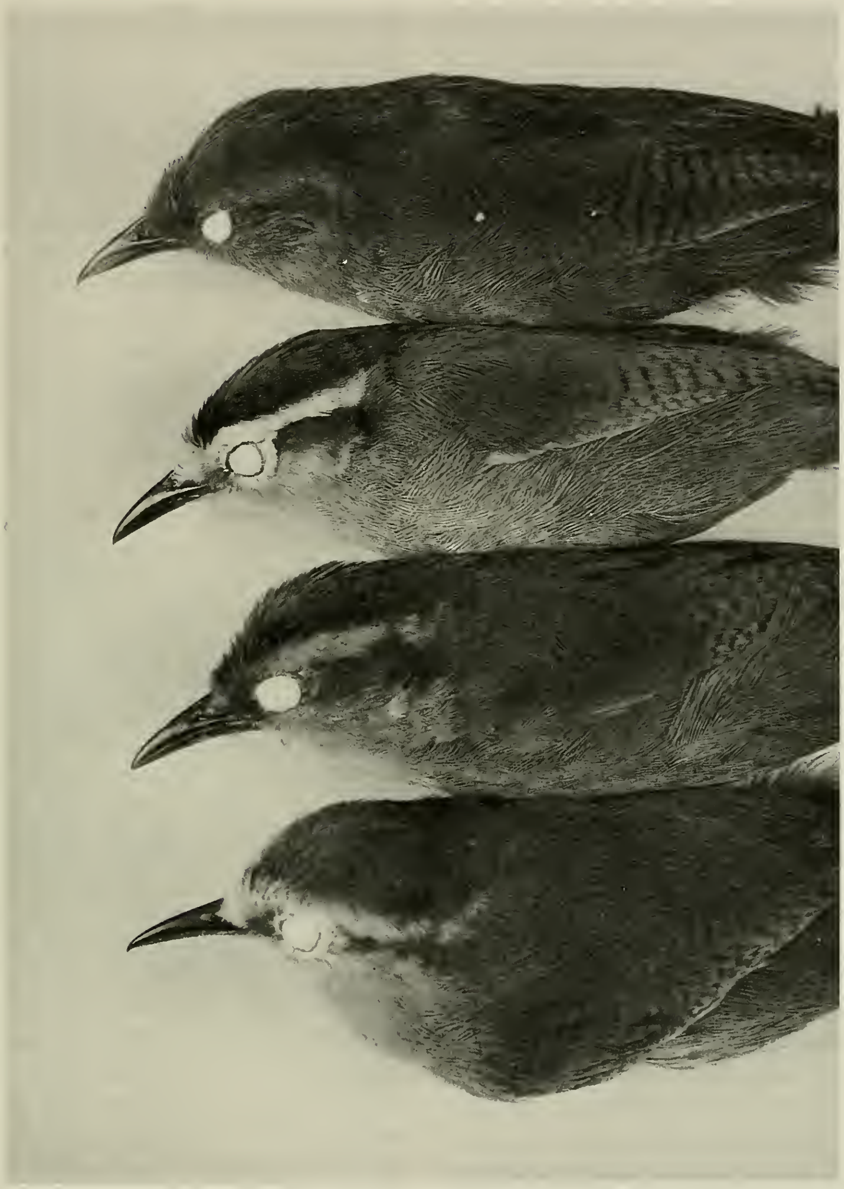

Fig. 1. Head patterns, from top to bottom, of *Cinnycerthia peruana, C. f. fitzpatricki, C. f. fulva.* and *C. f. gravesi.*

73°36′W. The specimen, prepared by Weske (#1285), is a male (largest testis 2 ½ mm diam) with a completely pneumatized skull and little fat.

Paratypes.—Six other specimens were also mist-netted in the Cordillera Vilcabamba by Weske and Terborgh and prepared by Weske: AMNH 820059, 14 km E. of Louisiana, 2050 m, 12°39′S, 73°34′W, ♂, 12 Aug 1966; AMNH 820210, 1740 m, 12°38′S, 73°38′W, ♀ (skull "scarcely pneumatized"), 12 Aug 1967; AMNH 820211, 1750 m, 12°38′S, 73°36′W, ♂ (skull completely pneumatized), 28 Jun 1968; AMNH 820309, 2160 m, 12°38′S, 73°36′W, ♀ (skull pneumatization incomplete), 29 Jun

1967; AMNH 820310, 2200 m, 12°38′S, 73°36′W, ♂ (skull pneumatization complete), 30 Jun 1967; and (6) AMNH 820507, 2830 m, 12°37′S, 73°32′W, ♂, 27 Jul 1967.

Diagnosis.—*Cinnycerthia f. fitzpatricki* can be distinguished at a glance from any other taxon in the genus by the narrow blackish border of the forecrown and the dark crown that contrasts with the back (Fig. 1). In *Cinnycerthia peruana*, the forecrown is slightly paler, not darker, than the rest of the crown and the crown and back are the same color. In *C. f. fulva*, the crown and back are concolorous. Otherwise, *fitzpatricki* is similar to *C. f. fulva* but has a whitish, not light brown, superciliary, and it is paler below (but sample sizes of both perhaps too small for confidence on this character). As noted by Brumfield & Remsen (1996), this subspecies may be larger in linear measurements than the other subspecies of *C. fulva*, but sample sizes are too small for statistical testing.

Description.—Capitalized color names are from Ridgway (1912). Forecrown narrowly Blackish Brown, blending to dark brown (near Raw Umber) crown, which then blends to a uniformly rich brown nape and back (Proutt's Brown). Uppertail coverts slightly more reddish than back. Outer webs of remiges (and both webs of inner secondaries) rich brown strikingly banded with narrow blackish bars; inner webs of most remiges dark fuscous. Upper wing coverts rich brown, faintly banded blackish; underwing coverts rich brown. Rectrices rich rufous brown strikingly banded with narrow blackish bars, slightly less conspicuously than remiges. Conspicuous buffy whitish superciliary from nares over eye to neck, sharply demarcated from the crown, which tends to be darkest at border of superciliary, and from broad, dark brown (Raw Umber) postocular stripe. Narrow whitish eyering. Lores brown, not distinctly separated from superciliary. Lower portion of auricular below postocular area dull light brownish (near Cinnamon), distinctly demarcated from postocular area. Malar region same color as lower auriculars. Chin and throat buffy whitish, noticeably paler than rest of underparts and malar area but not distinctly demarcated from them. Breast brown (Sayal Brown), blending to more rufous brown belly. Lower flanks, thighs, and undertail coverts darker (Proutt's Brown) than rest of underparts, as dark as back. Soft part colors recorded by Weske: iris brown; bill mainly black, shading to pale gray on gonys; legs brownish-gray. Measurements (mm): wing chord = 59.5; exposed culmen = 12.3; tail length = 55.8; tarsus length = 21.2.

Variation.—The seven specimens from the Vilcabamba show little individual variation except that one (AMNH 820211) has a slightly darker buffy chin, throat, and superciliary. One young bird (skull scarcely pneumatized; AMNH 820210) matches adult individuals closely in plumage, but its mandible is noticeably paler, a pale yellowish horn in the dried specimen (and described as "yellow-brown" by its preparator); those of the other birds are blackish. Measurements also show little variation (Table 1).

Natural history.—The only information available comes from the specimen labels. All specimens were mist-netted in humid, montane cloudforest and elfin forest, from 1740 to 2830 m, a considerable elevational range. Weske (1972) gave its elevational limits as 1710 to 2830 m. A male collected on 29 Jun had enlarged testes (left 6 mm, right 4.5 mm). A female collected on 12 Aug may have been in breeding condition (ovary 7 mm, largest ovum 1.2 mm). The other specimens did not have enlarged gonads.

Etymology.—It is a pleasure to name this distinctive taxon for John W. Fitzpatrick, whose fieldwork in depto. Cuzco and elsewhere in southern Peru has contributed greatly to knowledge of South American birds. His recent specimens from near the type locality of *C. fulva* (see below) were

Table 1.—Measurements (in mm) of *Cinnycerthia fulva fitzpatricki, C. f. fulva,* and *C. f. gravesi* southern Peru and northern Bolivia. The numbers in the columns are the means followed by the ranges in parentheses.

Population (*n*)	Wing chord	Exposed culmen	Tail length	Tarsus length
Males				
C. f. fitzpatricki (2)	60.8 (59.5–62.0)	12.6 (12.3–13.2)	55.6 (55.1–55.8)	21.5 (21.1–21.6)
C. f. fulva (2)	57.2 (56.7–58.6)	13.5 (13.4–13.5)	55.6 (54.2–57.0)	22.8 (21.1–24.4)
C. f. gravesi (depto. Puno; 2)	59.3 (57.8–60.7)	12.8 (12.4–13.1)	54.7 (53.5–55.8)	20.7 (20.4–21.0)
C. f. gravesi (depto. La Paz; 5)	57.2 (56.1–58.3)	12.9 (12.0–13.8)	54.6 (53.1–56.5)	22.0 (21.1–23.4)
C. f. gravesi (depto. Cochabamba; 3)	56.7 (54.8–58.8)	12.1 (11.2–13.6)	54.9 (53.0–56.7)	21.0 (20.9–21.0)
Females				
C. f. fitzpatricki (4)	55.7 (52.8–57.2)	12.8 (12.4–12.8)	54.1 (51.8–56.9)	20.7 (19.7–21.4)
C. f. fulva (0)	—	—	—	—
C. f. gravesi (depto. Puno; 5)	56.3 (54.1–58.8)	12.4 (11.2–13.1)	52.5 (50.3–55.4)	20.8 (19.9–21.7)
C. f. gravesi (depto. La Paz; 7)	55.0 (54.2–56.0)	12.9 (12.0–13.8)	54.6 (53.1–56.5)	22.0 (21.1–23.4)
C. f. gravesi (depto. Cochabamba; 2)	53.3 (52.1–54.4)	12.0 (12.0–12.0)	53.5 (53.1–53.9)	20.4 (19.8–21.0)

critical to the taxonomic conclusions of this paper.

Discussion.—Does the distinctive crown of *fitzpatricki* merit recognition as a species? Because its dark crown is a unique character within the genus *Cinnycerthia*, some might treat this taxon as a species. Because *fitzpatricki* is completely isolated from other populations of *Cinnycerthia*, direct assessment of reproductive isolation from other populations is not possible. However, we cannot find any comparable situation in the Troglodytidae in which two species-level taxa (e.g., in Hellmayr 1934, Ridgely & Tudor 1989, Fjeldså & Krabbe 1990) differ only in crown color and are otherwise extremely similar in plumage. Therefore, we recommend that *fitzpatricki* be treated as a subspecies of the biological species *C. fulva* in the absence of information on potential reproductive isolating mechanisms, particularly vocalizations. Although geographically closer to some populations of *C. peruana*, we place it within *C. fulva* because of the plumage similarities, particularly the prominent superciliary; also, most specimens of *fitzpatricki* clearly fit within *C. fulva* on the basis of measurements (Brumfield & Remsen 1996).

We previously proposed (Brumfield & Remsen 1996) that the remaining populations of *C. fulva* can be divided into two discrete units, the population in depto. Cuzco (where the type locality is) and the population from depto. Puno, Peru, south through depto. La Paz, Bolivia, to depto. Cochabamba. As discussed by Brumfield & Remsen (1996), few specimens exist from depto. Cuzco. The two that we examined, collected by J. Weske and J. Fitzpatrick at Pillahuata, were collected approximately 15 km north of the type locality of *C. fulva.* They match Sclater's type description ("brown, pale, but ill-defined superciliary mark") in the key feature that we propose distinguishes the Cuzco population from those to the south, namely that the superciliary is not dull white, but ochraceous brown. We have yet to find a specimen from farther south with a superciliary that is not at least partially whitish. Also, the auriculars of the specimens from Pillahuata are darker than those from farther south, thereby reducing the contrast between it and the dark brown postocular stripe.

Hellmayr (1934), who examined the unique type of *fulva* in the British Museum, stated that it "is more reddish, less olivaceous, throughout than a Bolivian series. The divergency requires confirmation by additional specimens." We are unable to see any such differences between the Pillahuata specimens and specimens from farther south. Curiously, Hellmayr did not remark upon the light brown superciliary of the type specimen, although he emphasized the "well-defined, large, buffy white superciliary streak" as a character for distinguishing *C. fulva* from *C. peruana*, which applies primarily to specimens that he also examined from Bolivia.

The Weske-Fitzpatrick specimens are the only two from depto. Cuzco, other than the type specimen, that we have been able to locate. Although a larger sample would be desirable, we believe that the distinctive features of these specimens signal that the Cuzco population is a separate taxonomic unit, and that they do not represent individual or clinal variation, especially given the relative uniformity (other than individual variation in number of white facial feathers) of the southern population over a range of at least 550 km. Therefore, we propose to name the southern population:

Cinnycerthia fulva gravesi, new subspecies

Holotype.—Academy of Natural Sciences of Philadelphia (ANSP) 138618; ♂ collected at Incachaca, 8000 ft, depto. Cochabamba, Bolivia, on 4 Jun 1937 by M. A. Carriker, Jr.

Paratypes.—Peru (depto, Puno): Santo Domingo, 6000 ft (AMNH 146335; ♂, 14 Sep 1916; H. Watkins); Santo Domingo, 4500 ft (AMNH 502123; ♂, 24 May 1901; G. Ockenden); Limbani, 9500 ft (AMNH 502122; ♀, 28 Feb 1904; G. Ockenden); Valcón, 5 km NNW Quiaca, 3000 m (Louisiana State University Museum of Natural Science [LSUMZ] 98604-607; 11–24 Oct 1980; L. C. Binford, M. Sánchez S., T. S. Schulenberg); Abra de Maruncunca, 10 km SW San Juan del Oro, 2000 m (LSUMZ 98608; 26 Nov 1980; T. S. Schulenberg). Bolivia (depto, La Paz): Río Zongo Valley, 1.9 road km downstream Saenaní, 2236 m (Delaware Museum of Natural History 67191; ♂, 15 Mar 1979; D. C. [Cole] Schmitt); Sandillani, 6800 ft (ANSP 121196-197; males, 13 and 19 Dec 1934; M. A. Carriker, Jr.); Sacramento Alto, 2575 m (LSUMZ 90885-890; 27–31 Jul 1979; L. S. Hale and J. V. Remsen); ca. 1 km S Chuspipata, 2725 and 3050 m (LSUMZ 102809-816; 30 Jul–5 Aug 1981; S. M. Lanyon, J. V. Remsen, T. S. Schulenberg, D. A. Wiedenfeld). Bolivia (depto, Cochabamba, prov. Chapare): Incachaca, 11000 ft (ANSP 138617; ♂, 10 Jun 1937; M. A. Carriker, Jr.); 10000 ft (ANSP 138616; ♀, 1 Jun 1937; M. A. Carriker, Jr.); 2600 m (Carnegie Museum of Natural History [CM] 85205, 85234; 25 Mar and 5 Apr 1921; J. Steinbach); 2500 m (CM 85176; 28 Feb 1921; J. Steinbach); 2200 m (LSUMZ 38048; 17 (?) Nov 1921; J. Steinbach); 2225 m (CM 120415; 7 Sep 1927; J. Steinbach); El Limbo, 2200 m (LSUMZ 36405; 14 Oct 1960; F. Steinbach).

Diagnosis.—*Cinnycerthia f. gravesi* can be distinguished from *C. f. fulva* by its whitish, rather than buffy brown (close to Clay Color), superciliary stripe and forecrown (Fig. 1). It also is paler below than *C. f. fulva* (but only two of the latter are available for comparison). In having a whitish superciliary that contrasts strongly with darker auriculars, the head pattern resembles that of distant *C. f. fitzpatricki* more so than adjacent *C. f. fulva.*

Description.—Forecrown mostly dull white, mixed with two or three brown feathers. Crown and rest of dorsum rich brown (near Proutt's Brown). Uppertail coverts slightly more reddish than back. Outer webs of remiges (and both webs of inner secondaries) rich brown strikingly banded with narrow blackish bars; inner webs of most remiges dark fuscous. Upper wing coverts rich brown, faintly banded blackish; under-wing coverts rich brown. Rectrices rich rufous brown strikingly banded with narrow blackish bars, slightly less conspicuously than remiges. Conspicuous buffy whitish superciliary extends from nares over eye to neck and becomes darker posteriorly; it is sharply demarcated from the crown, which tends to be slightly darker at border of superciliary, and from broad, rich brown (near Proutt's Brown) postocular stripe. Narrow whitish eyering. Lores brown mixed with white. Lower portion of auricular below postocular area is dull light brownish (near Cinnamon), distinctly demarcated from postocular area. Malar region same color as lower auriculars. Chin and throat buffy whitish, noticeably paler than rest of underparts and malar area but not distinctly demarcated from them. Breast brown (Sayal Brown), blending to more rufous brown belly. Lower flanks, thighs, and undertail coverts darker (Proutt's Brown) than rest of underparts, as dark as back. Soft part colors recorded by Carriker: iris gray; bill black, bluish black below; legs dark horn. Measurements (mm): wing chord = 57.0; exposed culmen = 11.6; tail length = 56.7; tarsus length = 20.9.

Variation.—As noted by Brumfield & Remsen (1996), about 30% of the individuals examined show "extra" white in the face, similar to but not nearly as extensive as variation in *C. peruana* (Graves 1980). Otherwise, the series is relatively uniform in plumage color and pattern, with individuals from depto. Puno virtually identical to individuals from depto. Cochabamba. Also, specimens taken in 1980 from depto. Puno are virtually identical in plumage to those taken there from 1904 to 1916, and so we see no evidence for "foxing." However, the recent specimens from July and August from Chuspipata and Sacramento Alto, depto. La Paz, are puzzling. These stand out strongly as being less reddish above and below, paler ventrally, and darker dorsally. Although we previously attributed this to seasonal wear, we now think that the differences are too great to be caused by wear, and we found no seasonal effects on plumage color in deptos. Puno or Cochabamba. Furthermore, the plumage of these puzzling specimens does not seem to be more abraded than specimens taken elsewhere at other times of the year. We would be tempted to describe the depto. La Paz population as a distinct subspecies, but two specimens from Sandillani, fewer than 10 km away and in the same drainage, are virtually identical to specimens from elsewhere in the range. The basis for this variation can only be resolved by further field-work in the area.

Natural history.—The scant information published concerning the natural history of *Cinnycerthia peruana* (e.g., Ridgely & Tudor 1989, Fjeldså & Krabbe 1990) probably applies in general to *C. f. gravesi.* The only published information that applies explicitly to *C. f. gravesi* comes from Remsen (1985), who classified it as a rare insectivore at a study site at 3050 m and as occurring primarily in single-species flocks. Here, we expand on Remsen's (1985) data on diet, breeding condition, and body weights by including specimens from other localities in Bolivia and Peru. Of 11 stomach contents recorded, all consisted of arthropods. Of six specimens collected in October, three were in breeding condition (males with testes 4 × 4 and 6 × 3 mm; female with brood patch); a female collected in March may have been breeding (ovary 5 × 5 mm, largest ovum 1 × 1 mm). Fjeldså & Krabbe (1990) collected a male with enlarged testes in January. Only one of the 13 specimens from July and August was possibly in breeding condition: a male with testes 3 × 2 mm. The body masses of five males with "no" or "light" fat were 14.5, 15, 16, 18, and 18 g; one with "moderate fat" weighed 22.5 g. The body masses of 12 females with "no" or "light" fat ranged from 12.4 to 19.2 g (mean 15.2); one with "moderate" fat weighed 16 g. Body or tail molt was recorded on the labels of 6 of 14 specimens collected in July and August, but none of the six specimens from October. Foraging observations of *C. f. gravesi* are difficult to obtain because this species is wary and remains on or near the ground in dense undergrowth.

Etymology.—It is a pleasure to name this distinctive taxon for Gary R. Graves. Not only has he studied plumage variation in the genus (Graves 1980), but his synthetic analyses of geographic variation of Andean birds, which have included *Cinnycerthia* wrens (Graves 1985), have contributed greatly to knowledge of Andean birds.

We previously proposed the English name "Superciliated Wren" for *C. fulva* (Brumfield & Remsen 1996), a slight modification of Hellmayr's (1934) English name for this taxon, "Superciliated Brown Wren." We overlooked, however, that Hellmayr and everyone since then used "Superciliated Wren" for *Thryothorus superciliaris.* Unfortunately, virtually all *Thryothorus* species have superciliaries, whereas the presence of a strong superciliary distinguishes *C. fulva* from other *Cinnycerthia.* Nevertheless, we do not wish to change a long-established English name. Therefore, we propose "Fulvous Wren" as the English name for *C. fulva.*

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