Lucius G. Eldredge III Memorial Volume: Tribute to a Polymath

Neal L. Evenhuis
James T. Carlton, co-editors

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PREFACE

The theme of this book is a return to complete and in-depth information. In the frenetic tempo of modern times, we often bypass this goal. In our multitasked lives, we tend to have a focused search for specific items of information we need at the moment, usually on Internet search engines such as Google or on electronic databases and digital libraries. After we are provided an array of sources, we grab the particular piece of information and move on. Perhaps the new culture of science of keeping focus in the specific objective at hand and not delving deeper is an adaptation to the speed at which changes are coming. A colleague recently confided that a genetics professor that has been around for decades has no advantage over a post-doc because the genetic techniques are changing so fast that both are challenged equally in keeping up. As the Red Queen (in *Through the Looking Glass*) said, "It takes all the running you can do, to keep in the same place." PhD candidates in genetics, when analyzing their data and writing their dissertations, are finding the techniques they used in obtaining their data are becoming out of date during the four or five years they were in graduate school and so they need to publish each individual chapter before they finish their dissertation.

Lu Eldredge always had been different. Lu may have started after particular facts, but he always wanted to learn the whole story and would keep digging deeper even when most others would have considered they had enough. At the University of Guam, the University of Hawaiʻi and the Bishop Museum, Lu mentored young scientists and students and was an encyclopedic source of information for the tropical Pacific. When a student or colleague asked for information on a little-known creature or location for which there seemed to be almost no information, he would always find in his files important articles from obscure sources. This book is dedicated to the memory of Lucius G. Eldredge (1938–2013).

Lu was renowned for compiling files of every publication, including technical reports, grey literature, and even newspaper and magazine articles, in existence on the marine fauna of Pacific islands, both by animal group and by island. The records of quantitative coral-reef surveys and monitoring programs in the middle of the past century are especially valuable, but these were done before data were recorded electronically and have the potential to be lost. Lu compiled a number of bibliographies, one of which was a collection of all survey reports, technical reports and publications of all the Pacific Island coral-reef sites that had been surveyed or monitored. It is especially valuable for people who are about to do a survey of a coral-reef site to determine if there is a quantitative record for the same site decades previous.

Hawaiʻi is the only state for which there exists a complete listing of all described species. This results from Lu's rigorous and relentless scouring of the literature. The annual *Records of the Hawaii Biological Survey* is a registry of all native and introduced species of plants and animals in the Hawaiian Islands. Lu coedited the *Records of the Hawaii Biological Survey* since 1999 and was working towards publishing an update of this summary list of Hawaiian species when he passed away. Lu also coedited with the late Dennis Devaney two important volumes from the *Reef and Shore Fauna* series published by the Bishop Museum that covered 17 phyla of Hawaiian invertebrates.

Hawaiʻi is almost certainly the tropical geographic region for which the information on introduced marine animals and algae is most complete. Starting in the 1980s, Lu and James Carlton worked together to document and validate the sites of origin, the dates of introduction, and present day status of introduced marine and brackish water animals and algae. In 2009, they published this comprehensive inventory through the Bishop Museum entitled *Marine Bioinvasions of Hawaiʻi*. As Lu diligently produced this project, he mentored students and colleagues in designing and acquiring funds for major research endeavors towards discerning previously undetected introduced marine species and determining their effects on native communities.

— *Charles Birkeland*

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(taken on his 50th wedding anniversary)

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Lucius G. Eldredge (1938–2013): the man and his work

Neal L. Evenhuis
Bishop Museum, 1525 Bernice Street, Honolulu Hawaii 96817-2704, USA; email: neale@bishopmuseum.org

& James T. Carlton
Williams College, Mystic Seaport, P.O. Box 6000, Mystic, Connecticut 06355, USA

In May 2013 we lost a valued colleague and close friend. Lucius G. Eldredge ("Lu" to everyone he met) had lost his battle with a bad heart. Those who came from throughout the Pacific to attend his memorial service in Honolulu are a testament to the many friends and colleagues he had during his life and career. He touched the lives of many and was selfless in his frequently helping others with their needs, both academically and personally. His expertise was in his knowledge of all things Pacific, but primarily in marine biology and the history of virtually all islands in the Pacific.

Early Years and Education

Lucius Gilbert Eldredge III was born in East Greenwich, Rhode Island, on 1 March 1938, to Lucius Gilbert Eldredge, Jr. and Harriet (née House) Eldredge. He was the youngest of three children (his two older sisters are Charlotte and Harriet). Genealogy was one of Lu's interests and the Eldredge clan could trace their ancestry in New England back to the *Mayflower*. Lu told many that Pocahontas was a relation of the Eldredge family; a large lithograph done in the 1880s of the marriage of Pocahontas and John Rolfe was proudly displayed in the hallway of the Eldredge home in Hawai‘i.

Fig. 1. A young Lu Eldredge (center) with his sisters Charlotte (left) and Harriet (right).

Lu grew up on the family farm in East Greenwich tending to various animals including having a pet goat and mule. He was a 4-H member during his secondary school years and his capstone project was carefully describing four years of maturation in the personal garden he tended to. The project included growing new plants, experimenting with different fertilizers, and cutting down trees to provide more sunlight, all written in his characteristically beautiful longhand script. He attended Rocky Hill School, a private school in East Greenwich, which started in 1935 backed with funding from Lu's grandfather, Garry C. House. It initially held classes in the living room of his parent's home on Division Street until the school was built in 1937.

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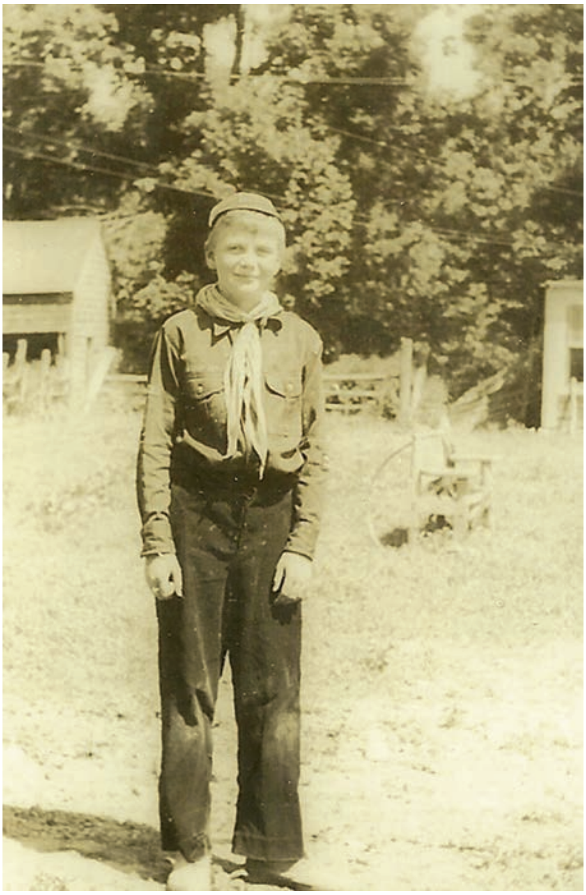

Fig. 2. Lu at 10 years of age in his 4-H outfit.

His first job was in 1950 advertising the movie *Francis the Talking Mule* by walking his mule up and down the streets of East Greenwich while wearing a sandwich board. He also worked in a florist shop, which gave him a special interest in flowers. The Eldredge home in Hawai‘i was never without a display of fresh flowers that he would bring home after work.

In 1956 Lu matriculated at the University of Rhode Island. One year after beginning his college studies, Lu met Joanne (“Jo”) Travell (who coincidentally could also trace her lineage back to the *Mayflower*) and the two were married the following year. After Lu received his BS in zoology from the University of Rhode Island in 1959, he and Jo set off to Hawai‘i where he joined the Ph.D. program at the University of Hawai‘i Mānoa campus in Honolulu. His doctoral dissertation was on the systematics of the ascidian (sea squirt) family Didemnidae; in that study he described 6 new species, including one named after his and Jo’s favorite beverage, *Didemnum gintonicum*. He completed his thesis in 1965 and published the results of his dissertation in 1967.

During his studies at the University of Hawai‘i, Lu spent time at the nearby Bernice Pauahi Bishop Museum, where he examined the invertebrate collection for his dissertation. Two things happened at the Bishop Museum that were to be a great influence on Lu for the rest of his life. It was at the Museum that he met Edwin H. Bryan, then the head of the Pacific Science Information Center located there. Ed was the center of knowledge of all things Pacific (having begun his gathering of such information soon after arriving in Hawai‘i in 1916) and maintained numerous files on every island in the Pacific Ocean, with publications, notes, and newspaper clippings sorted both to island and also to subject. One of Lu’s first scientific contributions was published by the Pacific Science Information Center: a *Catalog of the invertebrate type specimens in the Bishop Museum*. (Eldredge, 1967). Ed showed Lu the value of collecting all of this information and publishing bibliographies and checklists on them and Lu was hooked. From then on, one of Lu’s specialties would be continuing Ed’s passion for gathering information on all aspects of Pacific Islands, while specializing on marine invertebrates.

A result of this highly sought expertise was that many of Lu’s colleagues would have Lu provide the bibliography of all the literature pertaining to their various surveys, and his own literature studies resulted in synthesized bibliographies of a number of various subjects. Lu’s passion for bibliographical research was strong enough for him to take classes in Library Studies at the University of Hawai‘i in 1981–1982 during a sabbatical and obtain the Master of Library Science degree in 1987. In what is doubtless one of the more unusual theses in Library Science, Lu produced a detailed catalog of all of the described species of the tropical intertidal snails known as nerites.

Fig. 3. Lu’s wedding with Jo Eldredge in 1958.

The other transformative event that happened to Lu at the Bishop Museum was his introduction to the Pacific Science Association, which had its Secretariat offices at the Museum. Lu’s work in marine biology for his PhD was deeply Pacific-related and the Pacific Science Association was to be central to many of Lu’s science activities for decades to come. He attended his first Pacific Science Congress in Honolulu in 1961 as a student, and in Tokyo as an official delegate in 1966, eventually becoming its Executive Secretary in 1989, as we describe below.

Life in Guam

After obtaining his PhD in 1965, Lu and his family left Hawai‘i and arrived in Guam to begin his position as Associate Professor teaching biology at the University of Guam (UOG). Lu quickly ascended from a professorship to chairman of the Division of Biosciences and Marine Studies and then to Director of the Marine Laboratory (then operating out of the UOG Science building). Soon after Lu’s arrival, Benjamin Stone, a botanist at UOG, and Lu envisioned a new laboratory building devoted to biology and began plans to see it to fruition. Stone left Guam in 1967 and plans focused more on the laboratory specializing in marine biology. Lu spearheaded the efforts to get the Guam legislature and governor to support the plan and to eventually obtain matching funds from Washington, D.C. Ground was broken in early 1970 on the new lab and it officially opened on December 17, 1970. Ichthyologist Robert S. Jones was selected by Lu and UOG President Antonio C. Yamashita as its new director, allowing Lu the time to continue with curriculum development and building the research staff there.

The Marine Lab was the center of Lu’s life for 20 years. An incredibly active research facility, resident and visiting investigators conducted numerous surveys and research expeditions throughout western Pacific Islands. Surveys and scientific expeditions were made to virtually every one of the

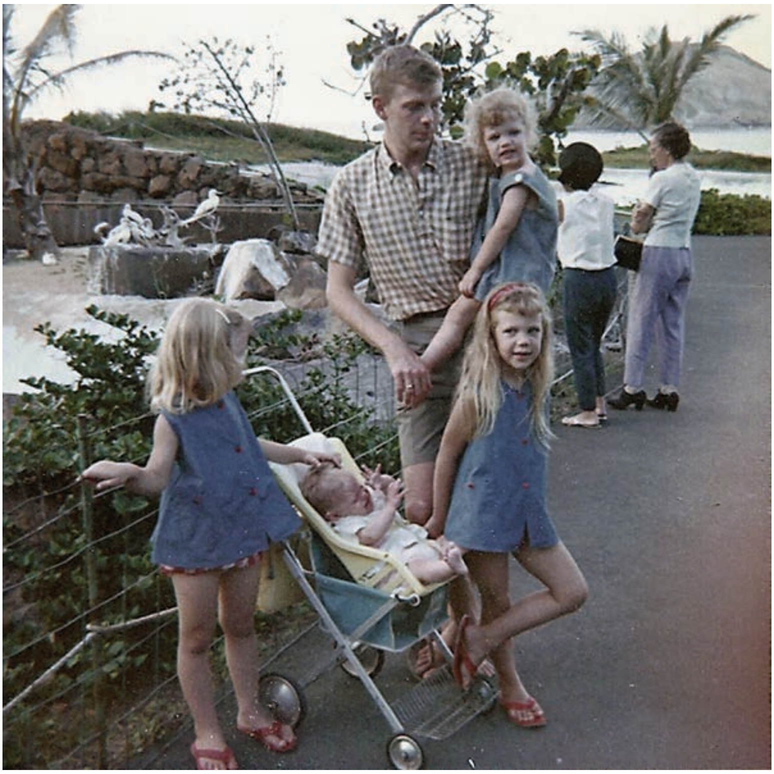

Fig. 5. Lu with his daughters at Sea Life Park, Hawai‘i (1965).

Northern Mariana Islands, as well as to the Marshalls, and Caroline Islands. A large number of publications resulted from all of this activity, with many of these having a detailed bibliography printed at the end, synthesized and completed by Lu. In addition to these surveys, Lu also conducted his own scientific research and conducted fieldwork in Fiji, Indonesia, Taiwan, Samoa, Fiji and a number of smaller Pacific islands. Not surprisingly, as a result of Lu's extensive work through the Pacific, and related to a special affinity he had for decapods, three crab species and a crab genus were named for him (*Pseudomiccipe eldredgei* Griffin & Tranter, 1986, *Petrolisthes eldredgei* Haig & Kropp, 1987, *Homola eldredgei* Guinot & Richer de Forges, 1995) and *Luciades* Kropp & Manning, 1996). In addition, 5 additional new taxa: a coral (*Psammocora eldredgei* Randall), an isopod (*Avada eldredgei* Boyko) and 3 crabs and hermit crabs [*Forestiana lucius* Ng, *Leptomithrax eldredgei* Richer de Forges & Ng, and *Porcellanopagurus eldredgei* Kropp) are named after Lu in the present volume.

Work was not the only activity for Lu. He was a devoted family man as well. The Eldredges had four daughters [Sarah, Deborah, Emelyn, and Rebecca] and, since marine biology was pervasive in the household, it was not unusual for the daughters to quip that they learned to swim before they could walk. The girls would often accompany their dad and his visitors on beach collecting trips.

During their stay in Guam, the Eldredges generously opened their home to numerous visiting researchers from all over the world. If someone was going to visit Guam to conduct research, a stay at the Eldredge residence was essential. Word passed quickly to the scientific community that if you needed a place to stay, just call the Eldredges. In one case, that advice was taken to heart by a person who had no idea of who Lu Eldredge was—or vice versa. One day, Jo Eldredge answered the telephone and on the other end was a scientist who said. “Hi there, I just arrived at the Guam airport and I was told to call you if I needed a place to stay.” The Eldredges proceeded to take him in despite not having any idea of who this person might be. Such was typical of the generous nature of Lu Eldredge.

In 1987, Lu finished his library degree at the University of Hawai‘i. Almost immediately after that, he took a short-term position in Rome working in the Regional Seas Directories and Bibliographies section of the United Nations Food and Agriculture Organization. This work with FAO and some work for them conducted previous to his official employment there resulted in a directory of coral reef researchers, a bibliography of marine ecosystems, and a directory of coral reef research facilities.

Fig. 4. Lu in his office at the University of Guam (1976).

Pacific Science Association and Bishop Museum

In 1988, long-time Executive Secretary of the Pacific Science Association, Brenda Bishop, passed away. The vacancy for that position was filled by Lu, who took up residence once again in Hawai‘i in 1989 and remaining in the islands for the remainder of his life.

Back at the Bishop Museum, Lu had the best of both worlds. He could deliver the results of his passion on gathering information on Pacific Islands, and he could always be close to the marine invertebrate collections housed at the Museum. With Museum invertebrate zoologist Dennis Devaney having passed away in a diving accident in 1983, Lu also became the resident specialist in marine biology and marine invertebrate zoology at the Museum.

Aside from the normal Executive Secretary duties of organizing the Congresses and Inter-Congresses, publishing the *Pacific Science Association Information Bulletin*, and liaising with many scientists throughout the Pacific, Lu devised a way—in the pre-internet world—to locate and distribute up-to-date information on Pacific-based literature to researchers around the world. He started the *Recent Pacific Titles* series as a supplement to the *Pacific Science Information Bulletin* (1991–2000). Every Friday when new journals arrived on the display rack in the Bishop Museum Library, Lu would assiduously photocopy the tables of contents of all the journals relating to the Pacific and compile them into an issue that was sent to members of the Pacific Science Association twice per year. Characteristic of Lu’s careful scholarship and vast breadth of interests, he included journals from the humanities to biology to the physical sciences, and for many years his *Recent Pacific Titles* provided researchers the only way to learn of a vast amount of published work in journals that many never saw and, in not a few instances, did not even know existed.

Alien Species

In the 1980s, Lu’s research interests began to turn to the diversity and proliferation of non-native species in coral reef systems of the Pacific – in so doing, he became one of the first and earliest workers to address the extent and impact of alien invasions in tropical marine communities. Again Lu’s remarkable *forte* in ferreting out obscure information is reflected in much of this work, with a vast amount of the research requiring extrication of data from gray literature, internal memoranda, and the personal memories of those involved in intentionally moving marine invertebrates, algae, and fish around the Pacific. Years of meticulous Holmesian tracking, one clue leading to the next, resulted in a major synthesis in 1994 on the introductions and transplantations of commercially important species to and around the Pacific islands. In the 1990s Lu spear-headed, with Steve Coles, Ralph DeFelice, Ron Englund, Scott Godwin and others, a decade-long series of field and laboratory studies of marine, estuarine, and freshwater introduced species throughout the Hawaiian Archipelago, from Midway to the Big Island. Much of this work culminated in a 2009 monograph (with the junior author) that reviewed the history, distribution, biology of nearly 500 introduced and cryptogenic species in Hawaiʻi.

Lu had many other interests and paths that he had hoped to follow relative to alien species in the Pacific theater, not the least of which was one of his long abiding interests (with Bob Gillett) on the history of the introductions of the Indo-Pacific top shell *Trochus niloticus*. A *Trochus* manuscript remains amongst Lu's papers, awaiting the resumption of this important analysis. Lu was actively working on a 5-year update of the 2009 Hawaiian invasions book, and it is thus with no small pleasure that we are able to have one of Lu's final papers on alien species in this very volume.

Later Years

In 2012, Lu retired from paid work at the Museum, but this did not stop his coming in every day and continuing his searches—now both "hard" (the library) and "soft" (online) —for the latest literature on Pacific marine invertebrates, updating his checklist of Hawaiian invertebrates, and letting others know of recent literature he found that might be of interest to them and their specialty. As in the halcyon days before the web, he would still go down to the library every week to look at the actual hard copies of journals, often sending an email to the junior author with new references on Hawaiian marine invasions, opening with the line, "Just arrived in the Library …". He continually mentored staff and liaised with and met with task forces relating to alien species—in Hawaiʻi, and nationally, and throughout the Pacific. The junior author continued to visit Oʻahu to work with Lu on alien species, and here, as always, was the consummate host: attentive, concerned, making sure all resources were at hand, dropping whatever he had been working on to pursue a curious new lead, arranging visits with other Island colleagues. Every visit to the Islands was an occasion to gather all the old friends and colleagues on the windward shore on Milokai Street in Kailua for a dinner party, for an always elegant spread prepared by Jo and Lu, and hours of long conversations ranging across history, culture, and science.

Lu kept busy with his genetic passion of information gathering up to the end. A failing heart was to do him in, though. He battled it as best he could but after a month-long hospital stay, Lu passed away on 1 May 2013.

Epilogue

For the last 10 years or so, Lu would start his day virtually the same: up at 5am to get the newspaper, back to bed to read it, feed the dog, and off to work by 8 or 9am. Upon arriving at the Museum, he would head to the senior author's office for a fresh cup of coffee, sit and chat about his latest readings of great places that should be checked for lunch or dinner, chat about nomenclature or taxonomy and frequently remind the more terrestrial-minded senior author that "there's an ocean out there," or maybe talk about a recipe he tried the night before; then off to his office to get online, answer emails from correspondents around the world, and start searching the web. At 12 noon sharp, he would walk back into the senior author's office and complain that he had the "grumblies" [= he was hungry and wanted to go out to lunch ... and now!]. The lunch group would get into his car and head someplace off-campus for lunch [Lu never once in his life ever brought lunch to work]. Before leaving for lunch, he would always place his coffee cup in his mail slot to grab on his way back from lunch to have an afternoon cup of coffee.

With Lu gone, the chair in the senior author's office is empty and there is no more discussion of recipes, good food to eat, or where the lunch group should go that day. However, the coffee cup remains in his mail slot, reminding everyone who passes that he wants to return and get that afternoon cup of coffee.

Acknowledgments

Many thanks to the Eldredge daughters, especially Rebecca Eldredge, who read an early version of this biography, helped with information on Lu's early years and provided the images used here. Roy Kropp kindly supplied the list of new species described by Lu. Many thanks to Roy Tsuda for his review of the final draft.

Appendix I. Complete Bibliography of Lucius Gilbert Eldredge III

As complete as possible a listing of all reports and publications written by Lucius G. Eldredge is given. Full authorship listed in square brackets at the end of each citation. Pages in square brackets are unpaginated.

1965

The taxonomy of the Didemnidae (Ascidiacea) of the central Pacific including Indo-Pacific records. Unpublished Doctoral Dissertation, University of Hawaiʻi at Mānoa, Honolulu. 193 pp. [Eldredge, L.G.]

1967

Record of a lancelet from Hawaii. *Pacific Science* **21**: 564. [Eldredge, L.G.]

Catalog of the invertebrate type specimens in the Bishop Museum. Pacific Science Information Center, Honolulu. 21 pp. [Eldredge, L.G.]

A taxonomic review of the Indo-Pacific didemnid ascidians and descriptions of twenty-three central Pacific species. *Micronesica* **2**: 161–261. [Eldredge, L.G.]

1969

Notes on some marine invertebrates, p. 14. *In*: Tsuda, R.T. (ed.), Biological results of an expedition to Rota, Mariana Islands. Division of Biosciences, Marine Studies, University of Guam. 37 pp. [Eldredge, L.G.]

Notes on some terrestrial and freshwater invertebrates, p. 27. *In*: Tsuda, R.T. (ed.), Biological results of an expedition to Rota, Mariana Islands. Division of Biosciences, Marine Studies, University of Guam. 37 pp. [Eldredge, L.G.]

Birds, pp. 28–29. *In*: Tsuda, R.T. (ed.), Biological results of an expedition to Rota, Mariana Islands. Division of Biosciences, Marine Studies, University of Guam. 37 pp. [Eldredge, L.G.]

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1970

Acanthaster Newsletter No. 1. University of Guam Marine Laboratory. 6 pp. [Eldredge, L.G.]

Acanthaster Newsletter No. 2. University of Guam Marine Laboratory. 8 pp. [Eldredge, L.G.]

1971

Recent Pacific bibliographies. *Micronesica* **7**: 238–239. [Eldredge, L.G.]

1972

University of Guam Marine Laboratory. *Guam Recorder* **2**(1): 52–55. [Eldredge, L.G.]

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1974

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1975

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A *New World* adventure. *Glimpses of Guam* **15**(2): 36–45. [Eldredge, L.G.]

1976

The need for faunistic information on Pacific coral reefs: introductory remarks. *Micronesica* 12: 149. [Eldredge, L.G.]

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1977

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1978

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1979

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1980

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Appendix II. New Species Described by Lucius G. Eldredge

Tunicates (all Dideminidae)
Trididemnum banneri Eldredge, 1966
Didemnum edmondsoni Eldredge, 1966
Didemnum elikapekae Eldredge, 1966
Didemnum gintonicum Eldredge, 1966
Didemnum pele Eldredge, 1966 [currently treated as *Didemnum granulatum* Tokioka, 1954]
Diplosoma abbotti Eldredge, 1966
Diplosoma handi Eldredge, 1966
Diplosoma hitatti Eldredge, 1966

Crustaceans
Homola dickinsoni Eldredge, 1980 — Homolidae
Paralomis seagranti Eldredge 1976 — Lithodidae
Paralomis haigae Eldredge 1976 — Lithodidae
Yaldwynopsis hawaiiana Ng & Eldredge, 2012 — Homolidae
Rochinia decipiata Williams & Eldredge, 1994 — Epialtidae

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Update and Revisions of *The Marine Bioinvasions of Hawai'i: the Introduced and Cryptogenic Marine and Estuarine Animals and Plants of the Hawaiian Archipelago*

James T. Carlton
Williams College, Mystic Seaport, P.O. Box 6000, Mystic, Connecticut 06355, USA

& Lucius G. Eldredge†
Hawaii Biological Survey, Bishop Museum, 1525 Bernice Street, honolulu, Hawaii 96817-2704, USA

Abstract. This paper provides a revised and updated assessment of the non-native and cryptogenic marine and estuarine biota of the six largest Hawaiian islands from Kaua'i to Hawai'i. Carlton & Eldredge (2009) reported 301 introduced and 117 cryptogenic marine and estuarine species in the Hawaiian Islands. We report an additional 32 introduced and 25 cryptogenic species for the Hawaiian marine fauna and flora, along with a Caribbean box jellyfish, whose establishment is uncertain. Four species (the sponge *Tedania ignis*, the hydroid *Eudendrium capillare*, the nematode *Spirocamallanus istiblenni*, and the copepod Haplostomides hawaiiensis) previously regarded as cryptogenic are now treated as introduced, while two species (the sponge *Monanchora dianchora* and the copepod *Psammopsyllus* sp.), previously treated as introduced, are now considered cryptogenic One vector-intercepted species (the ascidian *Symplegma reptans*) incorrectly previously listed as introduced is deleted, and 11 species of green algae (10 cryptogenic and 1 introduced) are also deleted, unsupported by subsequent taxonomic analysis. The net change to the non-native and cryptogenic inventory is thus an additional 32 and 13 introduced and cryptogenic species, respectively, for a total of 463 species (333 introductions and 130 cryptogens) that are either non-native or candidates for such in the Hawaiian marine biota.

Introduction

Carlton & Eldredge (2009), in a study largely completed in 2008, reported 301 introduced and 117 cryptogenic marine and estuarine species in the Hawaiian Islands. We provide here an updated and revised picture of the non-native and cryptogenic marine and estuarine biota of the six largest islands from Kaua'i to Hawai'i. Newly added introduced and cryptogenic species are based on published literature, either previously overlooked or published since Carlton & Eldredge (2009). The locations of voucher (museum) material of these additional species are provided in the papers cited. In addition, we clarify, update, or correct some earlier records, and delete from the Hawaiian biota certain species mistakenly interpreted either by us or in the literature as established invasions. We further consider name changes and additional locations as these have come to our attention.

We use the notation "Introduced (addition)" and "Cryptogenic (addition)" to indicate taxa that we now add to the register of non-indigenous and cryptogenic salt-water or maritime species in the Hawaiian Islands. Most of the introduced species were first collected before 2008. Some species were first collected between 2008 and 2010, but were almost certainly present earlier and overlooked. We know of no species that have newly invaded Hawaiian marine ecosystems in the past 5 to 6 years, a phenomenon we comment on in the Discussion.

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Systematic Account of Introduced and Cryptogenic Species

FUNGI

A number of species of marine fungi, particularly lignicolous taxa found in the Hawaiian Islands and recorded elsewhere (Gareth-Jones *et al.* 1976), remain to be evaluated for their geographic origin. We add one species to the two mangrove-associated fungi treated by Carlton & Eldredge (2009), but predict that additional species will be found to have been introduced.

Xylomyces rhizophorae Kohlmeyer & Volkmann-Kohlmeyer, 1998 **Introduced (addition)**

Kohlmeyer and Volkmann-Kohlmeyer (1998) first collected this Western Atlantic species "between 1970 and 1992" in the Hawaiian Islands, and described it in part on the basis of material collected in 1992 from He‘eia State Park, Kāne‘ohe Bay, O‘ahu, from the intertidal roots of the red mangrove *Rhizophora mangle*, also introduced from the Atlantic.

CILIOPHORA
(ciliates)

Chonotrichida

Lobochona insularum Matsudo & Mohr, 1964 **Introduced (addition)**

This ectocommensal ciliate was described as a new species living on the pleopods of the introduced Indo-Pacific boring isopod *Paralimnoria andrewsi*. It was first reported from the Hawaiian Islands by Mohr *et al*. (1963) as *Lobochona prorates*, but recognized the next year as a distinct species. Collections were made by Bayard McConnaughey in 1940 in Waikīkī, O‘ahu. It is doubtless still present.

PORIFERA
(sponges)

Recognition of non-native sponges in the fouling communities of Hawaiian harbors and estuaries remains vexing (van Soest *et al.*, 2012), as the systematics and historical biogeography of many taxa throughout the Indo-West Pacific remain obscure. Genetic analyses will be required to resolve many identifications of species and species-groups. This said, it is critical to not default to the assumption that marine sponge distributions are natural throughout the Indian and Pacific Oceans, in the absence of clear evidence of introduction by human activities. Given the many centuries of ship traffic throughout the Indo-Pacific, many species must be viewed as cryptogenic, especially those clearly susceptible to transport by ship fouling, in aquaculture products, or by other vectors (Carlton 2009).

Recent published work has revealed a plethora of additional bay- and harbor-dwelling sponges in the Hawaiian Islands. Several of these have such remarkably disjunct distributions, and have not been reported from intervening locations across the Pacific, that we tentatively consider them as introductions, noting the *caveat* above. One species, the Caribbean *Tedania ignis*, moves from cryptogenic to introduced status as discussed below. All general distributions given below are from van Soest *et al.* (2014) unless otherwise indicated.

Class Demospongiae

Order Hadromerida

Suberitidae

***Protosuberites epiphytum* (Lamarck, 1815)** **Introduced (addition)**

Calcinai *et al.* (2013) reported this Australian species encrusting the introduced octocoral *Carijoa riisei* from shallow water on O‘ahu in 2003, 2006, and 2007 samples. Given how long this species has been recognized in the Australian fauna, and its absence in numerous surveys of sponge faunas across the Pacific, we regard this as an introduction.

Prosuberites oleteira de Laubenfels, 1957 **Cryptogenic (addition)**

Lim *et al*. (2009) reported *Prosuberites oleteira* in Singapore fouling communities. This suggests that this species, originally described from Pearl Harbor (1948, with an additional record of that date off Diamond Head), must be viewed as cryptogenic in the Islands.

Order Halichondrida

Halichondriidae

Topsentia halichondrioides (Dendy, 1905) **Cryptogenic (addition)**

Coles *et al.* (2009) reported this Indo-Pacific species from Pearl Harbor (2007) and Honolulu Harbor (2008).

Scopalinidae

Scopalina sp. **Cryptogenic (addition)**

Scopalina species occur in both the Atlantic and Pacific Oceans. This unidentified taxon was collected in Honolulu Harbor in 2008 (Coles *et al.* 2009)

Callyspongiidae

***Callyspongia* (*Callyspongia*)** sp. **Cryptogenic (addition)**

Calcinai *et al*. (2013) recorded this species from O‘ahu at 30 m collected in 2005 and 2007, growing on the octocoral *Carijoa riisei*. Carlton & Eldredge (2009) noted another callyspongiid, but in a different subgenus.

Chalinidae

Cladocroce burapha Putchakarn, de Weerdt, Sonchaeng & van Soest, 2004 **Cryptogenic (addition)**

This Gulf of Thailand species was collected in Pearl Harbor in 2007 (Coles *et al.* 2009) and in Kāne‘ohe Bay in 2006 (S. Coles, pers. comm. 2010).

Order Poecilosclerida

Chondropsidae

Batzella aurantiaca (Lévi, 1958) **Introduced (addition)**

A Red Sea (Calcinai *et al*. 2013) and Madagascar (Vacelet & Vasseur 1971) species, this sponge was first collected in the Islands in 2007 in Shark's Cove on the north shore of O‘ahu in shallow water (Calcinai *et al.* 2013). We tentatively consider it introduced, based on this vast disjunct distribution.

Coelosphaeridae

Lissodendoryx similis Thiele, 1899 **Cryptogenic (addition)**

A widespread Indo-Pacific sponge first collected in Pearl Harbor in 2008 (Coles *et al.* 2009).

Desmacellidae

Biemna fistulosa (Topsent, 1897) **Cryptogenic (species resolution)**

Beginning in 1996, a *Biemna* sp. was reported from a number of locations around O‘ahu. Although originally identified as *B. fistulosa*, this identification was subsequently questioned (Carlton & Eldredge 2009). Calcinai *et al*. (2013) restored this identification for O‘ahu material of this widespread Indo-Pacific species.

Iotrochotidae

Iotrochota purpurea (Bowerbank, 1875) **Cryptogenic (addition)**

Iotrochota baculifera Ridley, 1884 **Cryptogenic (addition)**

These Indo-Pacific species were first collected in 2008 in Pearl Harbor (*I. purpurea*) and Honolulu Harbors (both species) (Coles *et al*. 2009).

Mycalidae

Mycale (Carmia) phyllophila Hentschel, 1911 **Cryptogenic (addition)**

A widespread Indo-Pacific species collected in 2008 in Pearl Harbor (Coles *et al.* 2009).

Mycale* (*Aegogropila*) *cf. M. lilianae Carballo & Hajdu, 1998 **Cryptogenic (addition)**

This Brazilian species was collected in 2003 and 2007 in shallow water on the octocoral *Carijoa riisei* (Calcinai *et al.*, 2013). Calcinai *et al.* (2013), while finding the Brazilian population (including paratypes) and Hawaiian material to be a close match, hesitated to confirm the identification, because of it being "unlikely that the Hawaiian and the Brazilian specimens are conspecific with such a disjunct distribution" (unless, of course, this species was introduced from Brazil).

Mycale (Carmia) cf. M. toxifera (Dendy, 1896) **Cryptogenic (addition)**

Another species epibiotic on *Carijoa riisei*, this Australian sponge was collected in 2005 and 2007 in shallow water in Shark's Cove, on the north shore of O'ahu (Calcinai *et al.* 2013). We demur from assigning this species an introduced status because of the tentative nature of the identification, based in part on the poor condition of the Hawaiian material examined by Calcinai *et al.* (2013).

Crambeidae

Monanchora clathrata Carter, 1883 **Cryptogenic (addition)**

This Indo-Pacific sponge was collected in Pearl Harbor in 2008 (Coles *et al.* 2009).

Monanchora dianchora de Laubenfels, 1935 **Cryptogenic (previously Introduced, and species resolution)**

Carlton & Eldredge (2009) noted a *Monanchora* sp. in Honolulu Harbor and Ke'ehi Lagoon (collected in 1997, and initially identified as *Neofolitispa unguiculata*). Coles *et al.* (2009) identified this as the Indo-Pacific *M. dianchora* based on 2008 collections.

Monanchora quadrangulata (Lévi, 1958) **Introduced (addition)**

A Red Sea species collected in 2005 at a popular dive site, a shipwreck (the fuel boat *Yo-257)* off Waikīkī in 30 meters, growing on *Carijoa riisei* (Calcinai *et al.*, 2013). The distribution appears to be too disjunct to be natural.

Tedaniidae

Tedania ignis (Duchassaing & Michelotti, 1864) **Introduced (previously Cryptogenic, and species resolution)**

Referred to as the Indo-Pacific species *Tedania reticulata* by Carlton & Eldredge (2009), Calcinai *et al.* (2013) returned the identification of this Hawaiian population to the Caribbean *Tedania ignis*, under which name it was earlier treated by de Laubenfels (1950) and Bergquist (1967). It is thus a member of the introduced Caribbean element in the Hawaiian fauna.

Raspailiidae

Raspailia* (*Clathriodendron*) *darwinensis Hooper, 1991 **Introduced (addition)**

An Australian species collected in 2008 in Pearl and Honolulu Harbors (Coles *et al.* 2009). As with the Australian *Protosuberites epiphytum* (above), the lack of reports of this species in intervening localities suggests an introduced status.

CNIDARIA
Class Hydrozoa
(hydroids)

Oceaniidae

Corydendrium parasiticum (Linnaeus, 1767) **Introduced (addition)**
Coles *et al.* (2009) discovered this species, of unknown origin but now circumglobal in warm waters, in Pearl Harbor fouling communities in 2008. Independently, Calder (2010) reported it from Pearl Harbor based on Bishop Museum collections from a "boat in drydock, 5.iv.1950." The location, position (drydock) and date (5 April 1950) identify the vessel as the *YON-146*, a fuel barge towed to Pearl Harbor in 1950 from Guam, where *C. parasiticum* is established (Kirkendale & Calder 2003). The first record of this species as present and established in the Hawaiian Islands should thus be 2008.

Turritopsis sp. **Introduced (name change)**
Calder (2010) noted that the specific name of the *Turritopsis* populations in the Hawaiian Islands [referred to as *T. nutricula* by Carlton & Eldredge (2009)] remains to be determined, although he provisionally retained the name as "*cf. nutricula*." We revert here to *Turritopsis* sp., given that populations in the Islands differ from those from the type locality of *T. nutricula* in Charleston, South Carolina (Calder 2010). Nevertheless, we still regard it as introduced. Calder (2010) further noted that Miglietta *et al.* (2007) referred Cooke's first record of *T. nutricula* from Ala Wai Yacht Harbor to the offshore Hawaiian species *T. minor* Nutting, 1905, but argued for direct comparison of the two species "before it can be determined whether or not they are conspecific." We concur that the habitats of the harbor-dwelling fouling populations and offshore populations are sufficiently distinct that they are unlikely to be the same species.

Bougainvilliidae

Bimeria vestita Wright, 1859 **Introduced (addition)**
It is surprising that this common fouling hydroid was not recorded earlier from the Islands. Calder (2010) collected it in 2009 on bridge pilings in Hawai‘i Kai on O‘ahu. Its type locality in Scotland suggests that more than one species has been captured in the species concept, especially for populations in warmer waters. While described from Europe long ago, it may have been introduced there, and its origin remains unknown.

Bougainvillia muscus (Allman, 1863) **Introduced (Change of Record [earlier date])**
Many species in Hawaiian fouling communities were doubtless present much earlier than first recorded in the literature, and museum collections can assist in resolving past records. The first record of this species recognized by Carlton & Eldredge (2009) was from 1967 in Kāne‘ohe Bay, its only known location in the Islands. Calder (2010) reported Bishop Museum collections from Honolulu Harbor (1945) and Pearl Harbor (1948), with additional collections (Calder 2010) from both stations in 2009 and 2007, respectively, indicating that it remains established in these harbors. *Bougainvillia muscus* may have been one of many World War II era arrivals.

Halopterididae

Halopteris plagiocampa (Pictet, 1893) **Introduced (addition)**
Cole *et al.* (2009) reported this species from Honolulu Harbor based on 2008 collections. Schuchert (2003) described a broad Indo-West Pacific distribution, including Japan and northern Australia. Kirkendale & Calder (2003) also recorded it from Guam.

Pandeidae

Amphinema sp. **Cryptogenic (addition)**
Calder (2010) reported a yet-to-be-identified species of this fouling hydroid from bridge pilings in Hawai‘i Kai, O‘ahu, collected in 2009.

Hydractiniidae

Stylactaria munita Calder, 2010 **Cryptogenic (addition)**

Described as a new species from bridge pilings in Hawai‘i Kai, O‘ahu, based on material collected on an oyster shell in 2009, *S. munita* is close to Mediterranean species and to a species of *Stylactaria* from Pacific Mexico (Calder *et al.* 2010), suggesting an allochthonous origin.

Eudendriidae

Eudendrium capillare Alder, 1856 **Introduced (previously Cryptogenic)**

Calder (2010) has assigned Cooke’s 1972 collections (Carlton & Eldredge 2009) of *Eudendrium* from Honolulu Harbor and Kāne‘ohe Bay to *E. capillare*. We treated it as *Eudendrium* sp. and as cryptogenic. Calder collected further material in 2009 in fouling communities on a bridge piling in Hawai‘i Kai. This species is thus known only from O‘ahu. As with *Bimeria vestita*, the origin of this species is unknown, and it may comprise a group of cryptic species.

Eudendrium carneum Clarke, 1882 **Introduced (addition)**

Reproductive material of this widespread fouling species collected in 1976 in Pearl Harbor and in 1997 in Honolulu Harbor (Calder 2010) indicate that this hydroid is established in the Islands. While Calder (2010) concluded that *“Eudendrium carneum* has been established in waters of the state for more than 50 years based on previously unidentified material,” these earliest specimens were collected (as with *Corydendrium parasiticum*, above) from a visiting fuel barge, the *YON-146*, brought to Pearl Harbor in 1950 from Guam. *Eudendrium carneum* may have occurred in Guam at that time, but was not present in collections there from 1997 to 2000 (Kirkendale & Calder 2003). This said, the *YON-146* may have picked up this hydroid somewhere else in the Pacific, prior to Guam.

Tubulariidae

Ectopleura sp. *cf.* ***E. viridis*** (Pictet, 1893) **Cryptogenic (addition)**

Material in the Bishop Museum collected in 1978 from anchor cables at 3 m depth in Kāne‘ohe Bay was provisionally assigned to this Indo-West Pacific species by Calder (2010), constituting the first report from the Islands.

Corynidae

Coryne sp. **Introduced (addition)**

[= *Syncoryne mirabilis* of Chu & Cutress (1955), *nec* L. Agassiz, 1849]

Carlton & Eldredge (2009) noted the report of *Syncoryne mirabilis* (Agassiz, 1862) by Chu & Cutress (1955) as found in 1954 in Hilo Harbor, Hawai‘i, but set it aside as a probable misidentification and because of the lack of any subsequent report of a similar corynid. Calder (2010) recovered colonies of this small and inconspicuous *Coryne* in 2009 on O‘ahu that he believed are conspecific with the species of Chu & Cutress’s (1955) report. *Coryne* sp. was found by Calder on algae in fouling communities on bridge pilings in Hawai‘i Kai. Despite the lack of species-level identification, we feel confident in assessing this species as introduced.

Class Anthozoa

(sea anemones)

Order Actiniaria

Haliplanellidae

Diadumene lineata (Verrill, 1869) **Introduced (Change of Record [earlier date])**

[= *Haliplanella luciae* (Verrill, 1898)]

Daphne Fautin collected *D. lineata* on Coconut Island in Kāne‘ohe Bay, Oahu, in November 1972 (California Academy of Sciences collections, CAS-IZ 9974.00, Accession Number 24280; record accessed August 2014; name shown as *Haliplanella luciae* and collector shown as D[aphne]. F. Dunn), extending the first record of this well-known Asian anemone to more than 40 years ago, rather than 1999 as reported by Zabin *et al.* (2004). It remains unreported from other Islands.

Class Scyphozoa

(jellyfish)

Magistiidae

Mastigias sp. **Introduced (addition)**

In October 1974, a *Mastigias* species was observed and photographed in Kāne‘ohe Bay, off the He‘eia pier (Devaney & Eldredge 1977). Tentatively identified by Devaney and Eldredge as the native species *Thysanostoma flagellatum* (Haeckel, 1880), Cooke (1984) recognized it as *Mastigias* near *M. papua* (Lesson, 1830), a non-native species. DeFelice *et al.* [2001; cited as “Eldredge and Smith, 2001” by Bayha & Graham (2011)] then noted it in passing with a brief entry (a “ … smaller species of jellyfish, *Mastigias* sp. … is also thought to be an alien”), accompanied by a photo by “T. Kelly” of two *Mastigias* of unknown provenance. The *Mastigias papua* reported and photographed by Reed (1971, p. 50, fig. 14) as “particularly abundant” in Kāne‘ohe Bay is, however, *Phyllorhiza punctata* (Cooke, 1984).

Bayha & Graham (2011), in reporting the jellyfish *Mastigias* from Florida, noted that the Hawaiian record constituted the first occurrence of this jellyfish outside its native western and central Indo-Pacific range. *Mastigias “papua”* consists of a complex of Indonesian species (Dawson 2005, Bayha & Graham 2011). It is not known to which member of this complex the Hawaiian population belongs. While apparently unreported since 1974, Hawaiian jellyfish are poorly studied, and *Mastigias* may well still be present, mistaken for *Phyllorhiza punctata*, another introduced jellyfish in the Islands.

Class Cubozoa

(cubomedusae, box jellyfish)

Tripedaliidae

Copula sivickisi (Stiasny, 1926) **Introduced (name change)**

[= *Carybdea sivickisi*]

Bentlage *et al.* (2010) transferred this species to the new genus *Copula*. Crow *et al.* (2015, this volume) review the occurrence of *C. sivickisi* in the Islands.

Tripedalia cystophora Conant, 1897 **Introduced (Establishment Unknown)**

Crow *et al.* (2015, this volume) report the discovery of a single specimen (a mature ovigerous female) of this Caribbean species in August 2011 “at a boat dock near mangroves in the Ka‘elepulu Canal, Enchanted Lakes, O‘ahu.” The location (near Kailua, on the windward coast) is distant from O‘ahu’s major ports, and would suggest that a population had become established and dispersed around the island. That said, we await further records to confirm its continued presence. *Tripedalia cystophora* was described from Jamaica and subsequently reported from Florida to Brazil, with further isolated records from Indonesia and the Seychelles (Crow *et al.* 2015). We suggest that the tropical western Atlantic Ocean is its native region, and that transport of polyps or medusae by ships have introduced it to the Indo-Pacific theater. It would not be surprising to find that it is much more widespread than now reported.

NEMATODA

(nematodes)

Order Secernentea

Camallanidae

Spirocamallanus istiblenni Noble, 1966 **Introduced (previously Cryptogenic)**

Regarded as possibly native by previous workers, and first described from native fish in the Islands, Gaither *et al.* (2013) have shown that this parasitic nematode was introduced with the bluestriped snapper, *Lutjanus kasmira*, from French Polynesia (Marquesas and Society Islands) between 1958 and 1961. Native host acquisition was rapid: by 1962 it had been found in the endemic *Istiblennius zebra* (zebra blennies; *pao‘o*) (Noble 1966). Historical, biogeographic, molecular, and ecological evidence confirm that this parasite is non-native.

PLATYHELMINTHES

(flat worms)

Class Monogenea

(flukes)

Euryhaliotrema anguiforme (Zhang, 2001) Kritsky, 2012	**Introduced (addition)**
Euryhaliotrema chrysotaeniae (Young, 1968) Kritsky & Boeger, 2002	**Introduced (addition)**
Euryhaliotrema spirotubiforum (Zhang, 2001) Wu, Zhu, Xie & Li, 2006	**Introduced (addition)**
Haliotrematoides patellacirrus (Bychowsky & Nagibina, 1971) Kritsky, Yang & Sun, 2009	**Introduced (addition)**
[= *Haliotrema patellacirrus*]	
Haliotrematoides longitubocirrus (Bychowsky & Nagibina, 1971) Kritsky, Yang & Sun, 2009	**Introduced (addition)**
[= *Haliotrema longitubocirrus*]	
Haliotrema sp. 1	**Introduced (addition)**
Haliotrema sp. 2	**Introduced (addition)**
Lutianicola sp.	**Cryptogenic (addition)**
Polylabris sp.	**Cryptogenic (addition)**

At least 7 monogene parasites of two introduced French Polynesian fish, the bluestriped snapper *Lutjanus kasmira* and the blacktail snapper *L. fulvus*, were imported to the Islands in the late 1950s and early 1960s, although not discovered until these fish were sampled in Oʻahu for parasites in 2006 and 2007 (Vignon *et al.* 2009). Vignon *et al.* (2009) noted that two additional monogenes, *Lutianicola* sp. and *Polylabris* sp., were "likely" non-indigenous, but preferred to assign these a cryptogenic status. Kritsky (2012) noted that Vignon *et al.*'s *E. spirotubiforum* may be *E. paululum* Kritsky & Justine *in* Kritsky, 2012. Kritsky further assigned Vignon *et al.*'s (2009) *Euryhaliotrema cf. E. anguiforme* to *E. anguiforme*.

ANNELIDA

Class Clitellata

(oligochaetes)

Marionina coatesae Erséus, 1990	**Introduced (addition)**

Demopoulos *et al.* (2007) and Demopoulos & Smith (2010) reported this marine oligochaete from Kāneʻohe Bay, Oʻahu, based on 2001 collections. Described from Hong Kong and China, it was subsequently reported from Bermuda (Healy & Coates 1999) and Australia and Japan (Torii 2012). Given its widespread distribution through the western North and South Pacific, we regard it as a probable introduction (perhaps by ballast water) to both the Hawaiian Islands and Bermuda.

Class Polychaeta

(polychaetes)

Capitellidae

Magalhães & Bailey-Brock (2012) revised the Hawaiian capitellid polychaetes, a notoriously difficult group, based on morphology. Molecular work may change the identification of some of the following species, but regardless it is probable that the species considered as introduced do indeed represent non-native taxa; several others are cryptogenic.

Capitella giardi (Mesnil, 1897) **Introduced (species resolution)**
Bailey-Brock (1990) reported "*Capitella capitata*" [quotation marks added] co-occurring with the introduced polychaete *Polydora nuchalis* in oyster aquaculture ponds on Oʻahu. This capitellid has now been identified (Magalhães & Bailey-Brock 2012) as the European species *Capitella giardi.* It has also been reported from Florida (Warren 1976), to where it would appear to be introduced if the identification is correct. Warren (1976) suggested that a record of *Capitella capitata* from Point Barrow, Alaska was "probably *C. giardi*," but she did not examine the material on which that record was based, and this record should be set aside. *Capitella giardi* was collected again in 1988 and 1989 at Kahuku, Oʻahu, in 1990 on the Kona coast of the Big Island in an oyster farm, and in 2004 in Waikoloa at the Anchialine Pond Preservation site.

Magalhães & Bailey-Brock (2012) noted that *C. giardi* "was collected from oyster farms and may have been introduced to the Hawaiian Islands together with *Polydora nuchalis* and *Boccardia proboscidea.*" However, the vector for bringing this European species to the Islands is unclear. The *Polydora* and *Boccardia* were introduced with commercial oysters from the Pacific coast of the United States, where *C. giardi* is unknown (but may have been overlooked, as capitellids are often misidentified or remain unidentified in collections). Shipping directly from Europe remains a possibility, although presumably this would involve transport of warmer-water stocks of *C. giardi*, such as from the Mediterranean.

Capitella jonesi (Hartman, 1959) **Introduced (addition)**
Magalhães & Bailey-Brock (2012) identified capitellid populations collected in 1992 from Maunalua Bay, Kawainui Beach Park near Niu Valley, Oʻahu as this Western Atlantic species, previously known from Massachusetts and Florida. Aquaculture products from the Atlantic coast or shipping may have brought this species to the Islands.

Mediomastus californiensis Hartman, 1944 **Introduced (addition)**
No *Mediomastus* species had been previously reported in Hawaiian waters until Magalhães & Bailey-Brock (2012) identified specimens from Oʻahu as this Eastern Pacific species, which ranges from Alaska to southern California. Locations include Paikō Lagoon, Maunalua Bay (1980), Honolulu Harbor (1997), Pearl Harbor and adjacent Mamala Bay (2002 and 2001 respectively) and Kāneʻohe Bay (1993). Magalhães & Bailey-Brock (2012) noted that *M. californiensis "*may have been introduced to Oʻahu, as it is found mainly at Honolulu and Pearl harbors." There are a number of undescribed species of *Mediomastus* in California (Leslie Harris, pers. comm. 2013), and the Hawaiian specimens are larger than Californian *M. californiensis*. We admit this species as an introduction to the Islands, while noting that it may prove to be a species other than *M. californiensis*. Ballast water appears to be the most likely mechanism of transport.

Capitella singularis (Fauvel, 1932) **Cryptogenic (addition)**
Previously known from the Indian Ocean and Indonesia, this species was first collected in the Hawaiian Islands in 2004 from Mamala Bay, Oʻahu, under threadfin mariculture cages at 40 m depth.

Capitella sp. **Cryptogenic (addition)**
An unidentified *Capitella*, part of the "*Capitella capitata"* complex, was collected in 2002 in Moanalua Stream on Oʻahu (Magalhães & Bailey-Brock 2012).

***Heteromastu*s** sp. **Cryptogenic (addition)**
Magalhães & Bailey-Brock (2012) noted that Hawaiian material resembles *H. filiformis* (Claparède, 1864), a name applied to what is almost certainly a number of similar-looking species from the Atlantic (including Mediterranean) and Pacific Oceans. Specimens were collected in 2010 in Maunalua Bay, Oʻahu, intertidally on the introduced alga *Avrainvillea amadelpha*.

Scyphoproctus edmondsoni Magalhães & Bailey-Brock, 2012 **Cryptogenic (addition)**

Described as a new species from Nuʻupia Pond, Oʻahu (where the introduced polychaete *Polydora websteri* was also recorded) based on 2002 material, this worm appears to be related to species from the Indian Ocean (Magalhães & Bailey-Brock 2012). Additional specimens were collected on the hull of the *USS Machinist* floating dry dock in 1996 in Pearl Harbor, the *Machinist* having been towed to Pearl Harbor from the Philippines in 1992 (whether the population on the drydock was reproducing, or the worms were four years old, is unknown, although the latter seems unlikely). Based on the habitat and locations, we regard this as a cryptogenic species.

Spirorbidae

Protolaeospira capensis (Day, 1961) **Cryptogenic**

[= *Protolaeospira* sp. A of Vine *et al.*, 1972]
[= *Protolaeospira translucens* (Bailey & Harris, 1968) *in* Bailey-Brock, 1976]

Vine *et al.* (1972) reported *Protolaeospira* sp. A, collected in 1970, from Coconut Island, Oʻahu, on a fouling settlement panel, noting that "It appears to be closely related to, or perhaps the same as, *S*[*pirorbis*] *translucens* … from the Galapagos Islands." Bailey-Brock (1976) recorded additional specimens from Oʻahu, Maui, and Hawaiʻi, and confirmed the identification as *P. translucens*, a species then synonymized with the South African *P. capensis* by Knight-Jones *et al.* (1979). This highly disjunct distribution suggests ship-mediated distribution from an unknown origin, and we thus consider it cryptogenic in the Islands.

Serpulidae

Pomatoleios kraussii (Baird, 1865) **Introduced (Retention of Status)**
Salmacina tribranchiata (Moore, 1923)
Serpula watsoni Wiley, 1905

Zabin *et al.* (2013), in a paper comparing intertidal species richness and composition between central California and Oʻahu, treated three species of Hawaiian serpulid polychaetes, *Salmacina tribranchiata* (as "*Salmacina dysteri*"), *Serpula watsoni* (as "*Serpula vermicularis*"), and *Pomatoleios kraussii* as cryptogenic, cryptogenic, and status unknown, respectively. These three species were treated as introductions by Carlton & Eldredge (2009). However, these re-assignments were in error (C. Zabin, pers. comm., 2013).

MOLLUSCA

Class Gastropoda
(snails)

Littorinidae

Littoraria scabra (Linnaeus, 1758) **Cryptogenic (addition)**

Reid (1986) commented that this Indo-West Pacific snail, largely restricted to mangrove communities, was "Rare in [the] Hawaiian Islands where mangroves were only established this century." Whether *L. scabra* was introduced inadvertently with mangroves imported from the Philippines in the early 20th century thus bears consideration.

The presence of *Littoraria scabra* in the Islands was overlooked by the long-term misidentification of the native periwinkle *Littoraria intermedia* (Philippi, 1846) as *L. scabra*. Thus, in the most widely used identification guide to Hawaiian mollusks (Kay 1979, page 72, fig. 24G) *L. intermedia* is mis-identified as *L. scabra* (Reid 1986, p. 125). Jeannette Whipple Struhsaker's work on *L. scabra* is also based on *L. intermedia* (Whipple 1965, Struhsaker 1966, Reid 1986), and *L. intermedia* is still omitted from monographic treatments of Hawaiian mollusks [e.g., Severns (2011)].

True *L. scabra* occur on at least three islands: Oʻahu, Molokaʻi, and Hawaiʻi (Table 1). One specimen was collected in 1916 on *hau* (*Hibiscus tiliaceus*) in Kāneʻohe Bay, but *L. scabra* was not found again in the Islands until the 1960s, when it was collected from mangroves, *hau*, *kiawe* (*Prosopis pallida*), and on mud near mangroves (Table 1). The Oʻahu population of *L. scabra* took a dip *circa*

Table 1. **Records of the gastropod *Littoraria scabra* in the Hawaiian Islands**

1916	O‘ahu	Kāne‘ohe Bay: Mokuolo‘e [= Coconut Island]	D.B. Langford	1 (mixed with *L. intermedia*, *fide* D. G. Reid)	“on branches of Hawtrees overhanging the shore + at high water dipping into the water. The 2 largest shells were a couple of feet above high water level.” (BPBM catalogue entry) [Hawtree = hautree or hau = *Hibiscus tiliacaeus*]	BPBM 228537	Reid, 1986, p. 103; D.G. Reid, pers. comm., February 2011
1961 (July)	Hawai‘i	Puakō	Carl C. Christensen	3		BPBM 205244	Reid, 1986, p. 103
1979	Hawai‘i	North end of Puakō Reef	M. Severns	2 (mixed with *L. intermedia*)	“From Keawe tree” [kiawe, *Prosopis pallida*]	E.A. Kay Collection	D.G. Reid, pers. comm., February 2011
1982 (May)	Moloka‘i	One Ali‘i Fishpond	Ann Fielding	1	“living in mud near mangroves”; 27 o/oo (BPBM catalogue entry)	BPBM 207349	Reid, 1986, p. 103
1982	O‘ahu	Kāne ‘ohe Bay: Coconut Island	D.G. Reid	—	On *Rhizophora* and *Hibiscus* trees	BM	D.G. Reid, pers. comm., February 2011
2004 (31 August)	O‘ahu	Kāne ‘ohe Bay: Coconut Island	Chela Zabin	—	From mangroves and on dead wood on shore, in 2003–2004.	BM (wet collection, unregistered)	Chela Zabin and D.G. Reid, pers. comms., May-June 2011
2006 (February)	O‘ahu	“channel to Pearl Harbor” at Hickam Air Force Base	David Lum	—	“ … collected some giants ([up to] 36.7mm) until about two years ago from mangroves lining the channel to Pearl Harbor. They were quite common up until that point in time, but they suddenly disappeared.”	Lum Collection	David Lum, pers. comm., February–March 2011
2006	O‘ahu	Hickam AFB (Ft Kam reef area)	John Jacobs	“a number of live specimens”	“In 2010, I couldn't find a single shell”	Jacobs Collection	John Jacobs, pers. comm., 15 March 2011
2000s	O‘ahu	Pearl Harbor	Chris Takahashi		“… from a mangrove tree in the middle of a sand bar off Pearl Harbor. They tend to be under leafs and in the center of the mangrove patches …… Recently they seem to have totally disappeared.”	Takahashi Collection	Chris Takahashi, pers. comm., 28 March 2011
2011 (June)	O‘ahu	Pearl Harbor	David Lum and J.T. Carlton	Common	On *Rhizophora mangle*	—	Herein

BPBM = Bernice P. Bishop Museum, Honolulu

BM = British Museum (Natural History), London

2009–2010 (Table 1), but the snail is now common on red mangroves (*Rhizophora mangle*) in Pearl Harbor at Hickam Air Force Base, O‘ahu (J.T. Carlton & D. Lum, field observations, June 2011).

The presence of *L. scabra* in 1916 in Kāne‘ohe Bay is difficult to explain. Oceanic rafting of mangrove-associated *Littoraria* species has been invoked (Reid 1986) but remains speculative, although it may explain this early record. More probable as a vector are unrecorded attempts to introduce mangroves from the Philippines to the Hawaiian Islands prior to the officially recognized records commencing in 1922 (reviewed by Carlton & Eldredge 2009). Cooke (in MacCaughey 1917) mentioned in passing, for example, an attempted introduction from the Philippines in 1908, and it is unlikely that this casual note records the sole such attempt. Exactly how mangrove seeds or seedlings were transported in these early years is not known and we have not found detailed descriptions of such shipments, so we cannot ascertain with certainty the potential for additional species to be carried with them. Nevertheless there seems to be significant potential for associated biota to be transported in crates containing plants, root masses, soil, leaves, and so forth. Regardless, it may be that the O‘ahu population (if there was a reproducing population prior to the 1920s) went extinct, given the lack of collections for much of the rest of the century in a region well-known for an intensive continuous history of shell collecting.

Alternatively, D.G. Reid (pers. comm. 2011) has suggested that *L. scabra* may have been naturally present prehistorically on the Islands, but maintained low-density populations in the absence of mangroves. As the mangrove populations grew in size, sparse populations of a species such as *L. scabra* that thrives best on mangroves may have increased. It would be interesting to learn if populations of other mangrove-obligate species, such as insects or other arthropods, thought to be native to the Islands, increased through the 20th century.

If, however, *L. scabra* successfully colonized the Islands in the last half of the 20th century, mechanisms of introduction also remain unclear. The gap between importations of mangroves in the 1920s and the 1960s collections of *L. scabra* suggests that mangrove introductions were not the vector. As noted above, rafting to the Islands remains speculative, the more so since mangroves themselves did not manage to colonize the Islands naturally.

Finally, we note that whether *Hibiscus tiliaceus* is native to the Islands remains uncertain (J. Price 2006, at HEAR: http://www.hear.org/species/hibiscus_tiliaceus; last accessed May 2014), leaving open the possibility of its introduction by the Polynesians. *L. scabra* does occur with *H. tiliaceus* (D.G. Reid, pers. comm. 2011, and Table 1) although not abundantly so, and may thus be transportable with *H. tiliaceus*. This said, *H. tiliaceus* does not appear to show a founder effect in the Islands (Takayama *et al.* 2006), which, however, could be the result of multiple synanthropic introductions over centuries. As *Prosopis pallida* is also introduced, it is thus possible that all the host plants that support *L. scabra* are themselves not native.

Phylogeographic studies of *Littoraria scabra* in the Hawaiian Islands and the Indo-Pacific would permit determining to which populations the Hawaiian *L. scabra* are most closely related.

Class Bivalvia

(mussels, oysters, clams, shipworms)

Mytilidae

Mytilus galloprovincialis Lamarck, 1819 **Deleted**

Severns (2011, p. 436 and facing pl. 199) reported this mussel from the Hawaiian Islands with the notation, “Intertidal. Between rocks in tidal areas with high water flow.” The provenance of the photographed specimen is not given, nor are any locations for this species in the Hawaiian Islands. Other than being intercepted in vessel fouling in Pearl Harbor in 1998 (Carlton & Eldredge 2009), we know of no populations of this cold- to warm-temperate species in the Islands, and do not treat it as a member of the non-indigenous fauna.

Ostreidae

Saccostrea sp. **Introduced (taxonomic status)**

Carlton & Eldredge (2009) treated the *Saccostrea* established on O‘ahu as a member of the species group *S. “cucullata,”* pending genetic analyses of the Hawaiian population. Severns (2011, p. 464, pl. 212) identified the Hawaiian *Saccostrea* as *S. scyphophilla*, a widespread Indo-West Pacific species (Huber 2010). We await genetic confirmation of the Oʻahu material of this difficult group for species-level identification, which work may also assist with resolving the origin of the Hawaiian *Saccostrea*. Severns attributed the source of his illustrated specimen to the collections of the Florida Museum of Natural History, but the specimens are at the Field Museum (Chicago) (Janeen Jones, pers. comm. June 2014). The illustrated specimens (FM 203516), originally identified as *Saccostrea glomerata*, are not from the Islands, but were collected in 1955 from New South Wales, Australia.

Anomiidae

Monia nobilis (Reeve, 1859) **Introduced (retention of status; name change)**

Huber (2010) argued for placing this species in the genus *Monia*, with which assignment we agree. Kay (1979) noted that this jingle shell was "widely distributed in the Indo-West Pacific," which distribution Huber (but repeating Kay's statement as "West Pacific") felt could not be verified; he therefore concluded that "*nobilis* is endemic Hawaiian." However, Huber (2010) also noted that *Anomia caelata* Reeve, 1859 (= *Monia caelata*) is a junior synonym of *Anomia nobilis* Reeve, and that the former occurs in the Red Sea. Tan & Woo (2010) further recorded the former (as *Pododesmus caelata*) from Singapore. Following Carlton & Eldredge (2009), we retain *Monia nobilis* as introduced to the Islands.

Chamidae

Chama pacifica Broderip, 1835 **Introduced (new location)**

Severns (2011, p. 466) illustrated a specimen of this species collected at 10 m depth attached to dead coral in Kihei, Maui. It was previously known only from 1996 collections in Pearl Harbor (Carlton & Eldredge, 2009).

Chama lazarus Linnaeus, 1758 **Introduced (new location)**

Severns (2011, p. 466, pl. 213 on facing page) illustrated a specimen of this species from 50 m depth, "growing within a wreck off Lahaina, Maui." It was previously known only from Pearl and Honolulu harbors, Oʻahu, based on 1996 collections (Carlton & Eldredge, 2009).

Teredinidae

Teredo parksi Bartsch, 1921 **Introduced (addition)**

Bartsch (1921) described the shipworm *Teredo parksi* from Pearl Harbor, based on specimens collected in 1920. Carlton & Eldredge (2009) remarked that Bartsch (1921) did not provide the date of collection, but we have since found that Walcott (1922) reported the date of Bartsch's activities and collections in the Islands. Turner (1966) considered *T. parksi* to be juvenile *Teredo furcifera* von Martens, 1894, and thus a junior synonym of that species, which is how Carlton & Eldredge (2009) treated it. However, we overlooked the fact that Turner (in Santhakumaran, 1986) resurrected *T. parksi* as a distinct species, based on its reproductive biology. *Teredo parksi* is widely distributed throughout the Indo-West Pacific, and we regard it as introduced to the Islands.

CRUSTACEA

Class Copepoda

Leptopontiidae

Psammopsyllus sp. **Cryptogenic (previously Introduced)**

Karaytug & Sak (2005) suggested that Kunz's (1993) report of the Atlantic interstitial sand-dwelling copepod *Psammopsyllus stri* Mielke, 1983 (from Kauaʻi and Oʻahu) be reconsidered, pending a redescription of the Hawaiian material. They noted that the Hawaiian population does not match Mielke's description in several regards. Although this copepod may have been introduced to the Islands in ships' sand ballast, and while it seems probable that it has strong affinities to Atlantic clades and is thus allochthonous, we revert to a cryptogenic status for it pending further study.

Botryllophilidae

Haplostomides hawaiiensis Ooishi, 1994 **Introduced (previously Cryptogenic)**

Carlton & Eldredge (2009) considered this species cryptogenic pending further data on its host ascidian specificity. The discovery of *H. hawaiiensis* with its host ascidian *Polyclinum constellatum* in Mazatlan harbor, southern Gulf of California, Mexico, in 2008 supports "the notion of a high host specificity of *H. hawaiiensis*" (Tovar-Hernández *et al.* 2010). We suggest that this copepod coevolved with *Polyclinum constellatum* in its native range, which is probably in the Indo-West Pacific or Australian theaters, the centers of diversity of the genus *Polyclinum*.

Class Ostracoda

We omitted ostracods from our previous work, lacking any clear evidence of either introduced or cryptogenic species. Kornicker *et al.* (2010) reported on collections of several species from ports and harbors on Kaua‘i, Moloka‘i, Maui, and Hawai‘i. The ostracod fauna of bays and estuaries in the Pacific theater is poorly known, and little attention has been paid to the question of which, if any, species may have been distributed anthropogenically. We here assess just one example.

Cypridinidae

Paravargula trifax Kornicker, 1991 **Cryptogenic (addition)**

Of the species treated by Kornicker *et al.* (2010), only one occurs elsewhere: *Paravargula trifax*, which was described from Enewetak Lagoon, and also occurs in American Samoa. It was collected in 1996 and 2003 in shallow water in boat harbors and around docks on Kaua‘i and Maui.

Class Isopoda

Philosciidae

Littorophiloscia culebrae (Moore, 1901) **Introduced (new location)**

Howarth *et al.* (2012) reported this maritime isopod on Maui, based on 2006 collections near Hobron Point on a rocky beach strand.

INSECTA

Class Diptera (flies)

Chironomidae

Kiefferulus longilobus (Kieffer, 1916) **Introduced (addition)**

[= *Chironomus* sp. near *C. hawaiiensis* of Howarth *et al.* (2012); nec Grimshaw, 1901]

This Indo-Pacific marine midge was first collected in 2006 on Maui in wetlands at the Kanahā Pond State Wildlife Sanctuary (Howarth *et al.* 2012), and again in 2012 on Sand Island, O‘ahu, where it was found to be "breeding in large numbers in [sea urchin] rearing tanks containing seawater" (Howarth & Oishi 2013). Howarth and Oishi speculated that adults could have arrived in the Islands as stowaways via airplanes or ships, or that larvae could be transported in ballast water or in crevices in ships' hulls.

BRYOZOA

(bryozoans)

Class Gymnolaemata

Schizoporellidae

Schizoporella errata (Waters, 1878) **Introduced (species resolution)**

Carlton & Eldredge (2009) noted that "one or more" species of *Schizoporella*, a genus of bryozoans well-known to include a number of species associated with ship fouling, were present in the Hawaiian Islands, with possible candidate taxa including *S. errata* and *S. japonica*. McCann *et al.* (2007) reported the Hawaiian populations under the Atlantic-based name *Schizoporella pungens* (Canu and Bassler, 1928), but this designation was meant to be preliminary (L. McCann, pers.comm.

May 2011). Collections made in Pearl Harbor in 1996 and 2011 have now been identified as *Schizoporella errata*, a warm-water Mediterranean species that has also been introduced to California (Ryland *et al*. 2014).

Lepraliellidae

Celleporaria brunnea (Hincks, 1884) **Deleted**

Koçak (2007) remarked that this Eastern Pacific species "was also recorded from Hawai'i, where it may have been transported via hull fouling," citing Godwin (2003). The record is based on finding this bryozoan on a barge towed from southern California to Pearl Harbor in 1999; it was not found in the wild. We do not consider it to be a member of the Hawaiian fauna.

Celleporaria pilaefera (Canu & Bassler, 1929) **Introduced (addition)**

The Indo-Pacific bryozoan *Celleporaria pilaefera* was first collected in 1997 on O'ahu (Honolulu Harbor and Ke'ehi Lagoon), and subsequently in Kāne'ohe Bay and Waikīkī (Coles *et al.* 1999, 2002a, 2002b), but inadvertently omitted by Carlton & Eldredge (2009). It was found in 2002 in Florida (McCann *et al.* 2007). It is probable that it has been introduced via ship fouling much more widely around the world than reported.

CHORDATA

Class Ascidiacea (sea squirts)

Didemnidae

Diplosoma sp. *cf.* ***D. spongiforme*** Giard, 1872 **Introduced (addition)**

A species similar to this European (Turon & Becerro 1992) ascidian has apparently been spreading in recent years, but the identification remains unresolved. In 2002 it was reported from Florida (McCann *et al.*, 2007, and NEMESIS data base: http://invasions.si.edu/nemesis/browseDB/SpeciesSummary.jsp?TSN=-457; last accessed May 2014), in 2002–2003 it was reported from Brazil (Rocha & Faria 2005), and in 2007 from Puerto Rico (NEMESIS data base, *op. cit.*). In 2008 Coles *et al.* (2009) collected it in Pearl Harbor and Ke'ehi Lagoon on O'ahu.

Ascidiidae

Phallusia philippinensis Millar, 1975 **Introduced (name correction)**

An introduced *Phallusia* present in the Islands since the 1930s was previously identified as the Indian Ocean–Red Sea species *P. nigra* (Carlton & Eldredge 2009). Based on genetic and morphological evidence, the Indo-Pacific fouling ascidian *P. philippinensis* and not *P. nigra* is present in the Hawaiian Islands (Vandepas *et al.* 2015).

Styelidae

Polycarpa cryptocarpa (Sluiter, 1885) **Introduced (addition)**

A new addition to the Hawaiian ascidian fouling fauna is *Polycarpa cryptocarpa*, previously known from the Western Pacific Ocean and the tropical Indian Ocean (Monniot & Monniot 2001). It was collected in 2008 in both Pearl Harbor and Honolulu Harbor (Coles *et al.* 2009).

Symplegma reptans (Oka, 1927) **Deleted (previously Introduced)**

We inadvertently included this species as an established introduction in our earlier work. However, specimens were collected in 1996 in O'ahu only on the *USS Machinist,* which had been towed from the Philippines to Pearl Harbor in 1992. While the ascidians may have been reproducing on the drydock (rather than being four years old), the *Machinist* was then towed to Guam in 1999. As *S. reptans* has not otherwise been reported from O'ahu (Coles *et al.* 2009), we delete it from the record.

Botryllus sp. and ***Botrylloides*** sp. **Introduced (Change of Record [earlier date])**

Carlton & Eldredge (2009) reported that the first record of botryllids in the genera *Botryllus* and *Botrylloides* was 1973. One of us (LGE) conducted fouling plate surveys on O'ahu between May

1961 and January 1962. The original laboratory analysis notes of these plate surveys have now been located, and we note that *Botryllus "schlosseri"* and *Botrylloides* sp. were present in 1961. As with many other fouling species, these common harbor and ship fouling taxa may have been introduced even earlier, perhaps associated with the extensive shipping traffic of World War II.

Symplegma brakenhielmi (Michaelsen, 1904) **Introduced (Change of Record [earlier date])**
We note an earlier record of this fouling ascidian than the one (1967) previously reported (Carlton & Eldredge 2009): in September 1961, the fouling community on the Hawaiian Marine Laboratory (now the Hawai'i Institute of Marine Biology) research vessel *Salpa* was sampled by one of us (LGE) and found to include this species (recorded as *S. connectans*).

Class Aves
(birds)

Anatidae
Anas platyrhynchos Linnaeus, 1758 **Introduced (addition)**
While occasional apparently migratory Northern Hemisphere mallards have long been recorded in the Hawaiian Islands, *Anas platyrhynchos* owes its modern-day established populations in the Islands to introductions that commenced in the 1800s (Pyle & Pyle 2009). Mallards are a member of the brackish-water fauna of the Islands, and, as such, function as consumers in these communities. Mallards can be observed, for example, feeding in the brackish water Manoa-Palolo Channel (a stream leading to the Ala Wai Canal) and at Ala Moana Park (JTC, field observations, June 2011).

ALGAE
(seaweeds)

Chlorophyta
(green algae)

Ulvaceae
Ulva spp. **Deleted (previously 10 Cryptogenic and 1 Introduced)**
Carlton & Eldredge (2009) treated 11 species of the sea lettuce *Ulva* as cryptogenic and one species, *Ulva expansa*, as introduced, based on older morphological concepts of species differentiation and biogeography, as reflected, for example, by Abbott & Huisman (2004). However, based on molecular re-assessments beginning in the 20th century, algal species concepts have changed dramatically. One result of this is the resolution (long known or suspected by many phycologists) that the application of species names based on cold-water European or American populations to tropical and subtropical seaweeds was not supportable.

O'Kelly *et al.* (2010), applying a molecular approach to the *Ulva* species in the Hawaiian Islands, found that only one of the previous 12 named species in the Islands, *Ulva fasciata*, was substantiated by molecular analysis. Rather, of 11 resolved OTUs, 6 were "not previously reported from anywhere in the world" (but could represent named species not yet characterized genetically), 3 matched named species (but 2 of these prove to be synonyms), and 2 others match "unnamed species from Japan and New Zealand." We thus delete from further consideration 10 species previously treated as cryptogenic (*Ulva clathrata, U. compressa, U. flexuosa, U. intestinalis, U. linza, U. paradoxa, U. prolifera, U. reticulata, U. rigida,* and *U. taeniata)* and 1 species previously treated as introduced (*Ulva expansa*). None of these taxa are now recognized by these names in the Hawaiian flora. We retain *Ulva fasciata* (now known by its senior synonym *Ulva lactuca*) as cryptogenic (see below), and newly recognize *Ulva ohnoi* as cryptogenic (see below).

Ulva "lactuca Linnaeus, 1753" **Cryptogenic (name change)**
[= *Ulva fasciata* Delile, 1813]
While this alga is traditionally considered native, ulvoid algae are one of the most common groups of plants on ships' hulls (e.g., Mineur *et al.* 2007, 2008), making it difficult to distinguish natural

occurrences from human-mediated transport and introduction. O'Kelly *et al.* (2010) noted that what was long treated in the Hawaiian literature as *Ulva fasciata* is now considered a synonym of *Ulva lactuca*, a species said to occur on almost every coast of the world from polar to tropical waters. Not surprisingly, the species concept *lactuca* remains unclear (Kirkendale *et al.* 2013), and we therefore place the name in quotation marks.

Ulva ohnoi Hiraoka & Shimada, 2004 **Cryptogenic (addition)**
The native range of this bloom-forming alga, recently described from Japan, is not known. It has been recognized from both the Hawaiian Islands (O'Kelly *et al.* 2010) and Australia (Kirkendale *et al.* 2013). There has been speculation that *U. ohnoi* was not native to Japan (Hiraoka *et al*. 2004). It has been found in ballast water samples intercepted in Italy (Flagella *et al*. 2010).

The material analyzed by O'Kelly *et al.* (2010) was collected in 2007 on both O'ahu and Maui (GenBank accession numbers 02907, 03282, and 03276, *fide* O'Kelly *et al.* 2010, fig. 3, p. 7, with locations and date from http://algae.manoa.hawaii.edu/hadb/database/index.php?action= search &srhm=gnus&q=Ulva+ohnoi&x=42&y=17; last accessed May 2014).

Udoteaceae
Udotea argentea Zanardini, 1858 **Introduced (addition)**
An unusual addition to the non-native marine flora of the Islands (a group of species which in general is characterized by shallow-water, hard-bottom species) is this deeper-water green alga, typically found growing in sand in 20 to 60 m depth (Bailey-Brock & Magalhães, 2010). Bailey-Brock & Magalhães (2010) reported it as discovered in 2007 in south-west O'ahu. Widely found throughout the Indo-Pacific, it appears to be a ballast-water introduction to the Hawaiian Islands.

Rhodophyta
(red algae)

Sherwood & Carlile (2012) reported that the Atlantic alga *Schimmelmania* sp., *cf. S. elegans* Baardseth, 1941, was found in 2010 in a closed tank in an abalone aquaculture facility on the Big Island; the tank and the algae were subsequently destroyed after this discovery. While the Islands appear to be too warm for this cool- to warm-temperate seaweed, its transportation with aquaculture products highlights concerns that these operations can serve as viable vectors for non-native species.

Spyrideae
Spyridia "filamentosa (Wulfen, 1803) Harvey, 1833" Clade A **Introduced (addition)**
Spyridia "filamentosa (Wulfen, 1803) Harvey, 1833" Clade B **Introduced (addition)**
Conklin & Sherwood (2012) demonstrated that this red seaweed consists of five distinct clades in the Hawaiian Islands. Whereas Clades A and B are of wide occurrence in the Pacific Ocean, they are restricted to around O'ahu (with the majority of samples collected on the south shore – that is, close to the two principal harbors), with additional samples from the Maui Nui complex (i.e., Moloka'i, Lāna'i, and Maui). The earliest sample of Clade A is from Moloka'i in 1991 and of Clade B is from Magic Island, O'ahu in 1978, but both clades were probably present in the Islands much earlier. Conklin & Sherwood (2012) suggested that these clades are possible introductions with shipping traffic.

Rhodomelaceae
Polysiphonia sp. **Introduced (addition)**
Hollenberg (1968) recorded a *Polysiphonia* from the Hawaiian Islands under the name *Polysiphonia tepida* Hollenberg, 1958, originally described from Beaufort, North Carolina. Locations and habitats included Kāne'ohe Bay (1952), on a boat hull in Ala Wai Yacht Harbor, Honolulu (1951), a fish rearing facility aquarium in Waikīkī (1962), and Keawanui Pond on Moloka'i (1944). Abbott (1999) repeated Hollenberg's record, but had no new collections. *Polysiphonia "tepida"* is now reported

from a broad suite of locations from the Atlantic Ocean and throughout the Indo-West Pacific (http://www.algaebase.org/search/species/detail/?species_id=11318; last accessed May 2014), and thus doubtless involves a number of similar-looking species. We thus demur from using a species name for this *Polysiphonia*, but predict that it will be found to be non-native once genetic studies are done.

Gracilariaceae

Hydropuntia perplexa (Byrne et Zuccarello, 2002) **Introduced (addition)**
Conklin, O'Doherty et A.R.Sherwood, 2014

Conklin *et al.* (2014) reported the cryptic invasion of the red alga *Hydropuntia perplexa*, possibly of Micronesian origin, which had been previously confused with the native alga *Gracilaria coronopifolia* (*limu manauea*). Populations are established on Maui, Kaua'i and O'ahu. Herbarium material dates from 2007 (Conklin *et al.* 2014), but the introduction may have occurred much earlier.

Phaeophyta
(brown algae)

Sargassaceae

Sargassum muticum (Yendo, 1907) Fensholt, 1955 **Deleted**

We re-emphasize that this Asian species is not established in the Hawaiian Islands. It was treated by Abbott & Huisman (2004) as a "new record" for the Islands, on which basis it has now appeared as a distributional record in Algae Base (http://www.algaebase.org/search/species/detail/?species_id=90; last accessed May 2014). This alga was collected as a fouling species from a barge towed to Pearl Harbor from California. We have no record of its establishment.

Results and Discussion

We report an additional 32 introduced and 25 cryptogenic species for the Hawaiian marine fauna and flora, along with one additional species, the Caribbean box jellyfish *Tripedalia cystophora*, whose establishment is uncertain. Four species previously regarded as cryptogenic (Carlton & Eldredge, 2009) are now treated as introduced (*Tedania ignis, Eudendrium capillare, Spirocamallanus istiblenni,* and *Haplostomides hawaiiensis*), while two species previously treated as introduced are now considered cryptogenic (*Monanchora dianchora* and *Psammopsyllus* sp.). One vector-intercepted species (*Symplegma reptans*) incorrectly listed as introduced is deleted, and 11 species of green algae (10 cryptogenic and 1 introduced) are also deleted, unsupported by subsequent taxonomic analysis. The net change to the non-native and cryptogenic inventory is thus an additional 32 and 13 introduced and cryptogenic species, respectively.

From our 2009 assessment of 301 introduced and 117 cryptogenic species, we thus now recognize 333 introductions and 130 cryptogens, for a total of 463 species that are either non-native or candidates for such in the Hawaiian marine biota. Given the limited understanding of the historical biogeography and systematics of a vast number of marine invertebrates and algae in the Hawaiian Islands – including protozoans, sponges, hydroids, flatworms, nemerteans, nematodes, gastrotrichs, kinorhynchs, gnathostomulids, rotifers, kamptozoans, tardigrades, oligochaetes, polychaetes, ostracodes, copepods, isopods, tanaids, amphipods, pycnogonids, mites, littoral insects, bryozoans, ascidians, and filamentous algae, among other groups—the actual number of non-native and cryptogenic marine species in the Archipelago is, without doubt, considerably greater.

We emphasize that collections of species associated only with transport vectors should not be recorded as new members of the Hawaiian flora or fauna. If there is no evidence that these species have escaped into the wild (from, for example, aquaculture facilities or ships' hulls) or are reproducing in the wild, then these species would not be considered as established and therefore not members of the Hawaiian biota. As noted above, then, the alga *Sargassum muticum* and the bryozoan *Celleporaria brunnea* (both found in 1999 on a barge towed from California), as well as the alga *Schimmelmania elegans* (found in 2010 in an aquaculture facility on the Big Island) are deleted from the Hawaiian inventory. Similarly, earlier interceptions, such as the hydroid *Corydendrium para-*

siticum (found in 1950 on a barge from Guam) would not constitute first records of the species in the Islands, although they provide robust evidence for (rather than speculation about) specific vector transport.

Finally, as we noted in the Introduction, no species are known to have arrived and become established in the Hawaiian Islands since 2009. While this may reflect the efficacy of increased control of certain vectors, such as ballast water or aquaculture imports, it is more likely that species have continued to arrive (such as in hull fouling) but remain undetected. Species arriving and becoming established may remain below the level of detection for some years due to lag times in building up populations that would be found in casual encounters, while at the same time systematic surveys of Hawaiian marine fouling communities in ports and harbors have not been conducted since the summary by Carlton & Eldredge (2009).

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The first author notes, with great sadness, that Lucius Eldredge, my co-author on this paper and our earlier monograph, is no longer with us to continue to explore and expand our understanding of the marine fauna and flora of the Hawaiian Archipelago. Introduced species were a deep and abiding interest of Lu, and he had a genetic ability to ferret out on the one hand the most obscure records in the grayest of literature, while, on the other, to spot a new mention of an alien marine species in the Hawaiian Islands buried in the midst of a 300-page taxonomic monograph dealing with some element of the Indo-West Pacific biota. This paper reflects Lu's extraordinary lifetime of meticulous and painstaking scholarship which, while it can be well-remembered, cannot be surpassed.

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Dating, publication, and authorship of Froriep's "*Wörterbuch der Naturgeschichte*" (1824–1837)

Neal L. Evenhuis
*J. Linsley Gressitt Center for Entomological Research, Bernice Pauahi Bishop Museum, 1525 Bernice Street,
Honolulu, Hawaii 96817-2704, USA; email: NealE@bishopmuseum.org*

Abstract. The dates of publication are given for all parts of Ludwig Friedrich von Froriep's never-completed 11-volume "*Wörterbuch der Naturgeschichte*" by the Weimar publisher Landes-Industrie-Comptoir. Because this little-known work published many new nomenclatural acts for both botany and zoology (especially some of the earliest type designations for many genera), specialists should examine it in order to analyze the nomenclatural and taxonomic information it contains.

Introduction

In my *Litteratura Taxonomica Dipterorum* (Evenhuis 1997) I listed an anonymous German natural history dictionary, the *Wörterbuch der Naturgeschichte* published by the Landes-Industrie-Comptoir in Weimar, and gave as good a breakdown of published volumes as I could at the time. The information presented there was extremely incomplete because at the time I had not personally seen a copy but had listed the contents and dates based on secondary sources. Since then, I have been able to examine all 11 volumes (published in 21 parts; the *Wörterbuch* was never completed) and have found accurate dates of publication for almost all the volumes. The accurate dates of 19 of the 21 parts published are given. Additionally, authorship of the *Wörterbuch* is shown to be its coordinator, Ludwig Friedrich von Froriep (1799–1847). Although not listed by name in any of the volumes of the *Wörterbuch*, external sources indicate that he was the one responsible for its coordination, printing, and publication.

Abbreviations used in this paper

The following abbreviations and shortened titles are used for book, journal and institutional titles throughout the paper:

ATGM =	*Allgemeines Teutsches Garten-Magazin*
ICZN =	International Commission on Zoological Nomenclature
IZEW =	*Intelligenzblatt der Zeitung für die Elegante Welt*
Notizen =	*Notizen aus dem Gebiete der Natur- und Heilkunde*
Wörterbuch =	*Wörterbuch der Naturgeschichte, dem gegenwärtigen Stande der Botanik, Mineralogie und Zoologie angemessen.*

Background

The publishing firm of the *Wörterbuch*, the Landes-Industrie-Comptoir in Weimar, was begun in 1791 by the publisher Friedrich Johan Justin Bertuch (1747–1822), who by then had been involved in many other publishing ventures including some books as well as the creation of periodicals such as the *Bilderbuch für Kinder*, the *Deutsche Merkur* [a German analog to the French *Mercure de France* published by Charles Panckoucke; see Evenhuis (2003) for more details on this recording journal], the *Journal des Luxus und der Moden*, and the *Allgemeine Literatur-Zeitung*, the last of which reviewed contemporary literature and scientific publications. By 1791, with business burgeoning, Bertuch realized that he needed to bring all his multifarious enterprises under one umbrella and on 26 March he applied to the Grand Duke for a privilege for his Landes-Industrie-Comptoir, roughly translatable as "Regional Repository of Industry". "I ask for no support, no monopoly, no limitation of any other trading enterprise" he wrote, asking only for the ducal seal of approval of it

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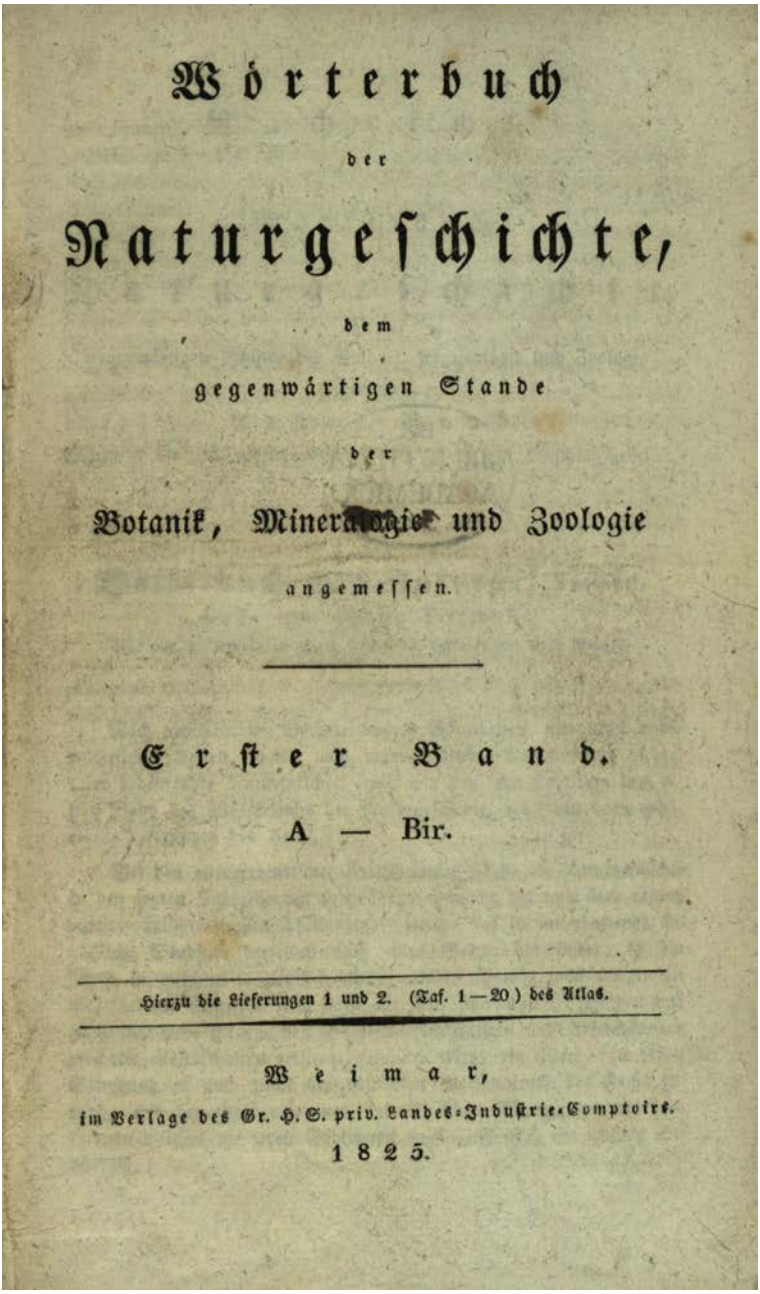
as an institution operating for the common good. “In order to forestall any doubts I declare furthermore that the business of my repository will mainly consist of my existing small publishing house and art business and that its overriding purpose will be to promote our active trade, to bring in money for goods sent out from this region, and not to allow more foreign goods to enter the retail markets here for ready money, thus increasing further our previous passive trade.” Bertuch obtained his “privilege” and the Repository was established on 19 April (Maxted 2011).



Wörterbuch
der
Naturgeſchichte,
dem
gegenwärtigen Stande
der
Botanik, Mineralogie und Zoologie
angemeſſen.

Erſter Band.
A — Bir.

Hierzu die Lieferungen 1 und 2. (Taf. 1—20) des Atlas.

Weimar,
im Verlage des Gr. H. S. priv. Landes-Induſtrie-Comptoirs.
1825.

Fig. 1. Title page of Volume 1 of the *Wörterbuch der Naturgeschichte* (1825).

The actual start of the publishing company under this business began in 1801 after he applied for a license to operate his own printing company. That same year his daughter married Ludwig Friedrich Froriep (1779–1847) [editor of the Weimar-published *Notizen aus dem Gebiete der Natur- und Heilkunde*; father of Robert Froriep who edited the Paris-published *Bulletin Universel des Sciences et de l'Industrie*]. Froriep specialized in medicine, was the personal physician to the King of Württemberg, and had a professorship at the University of Jena, which is where he was when Bertuch called him back to Weimar in 1815. Bertuch's wife died in 1810 and his son Carl had died in 1815. Bertuch had no successors to take over his publishing business. Froriep decided to help his father-in-law and moved his family to Weimar in the spring of 1816.

With the Landes-Industrie-Comptoir under severe financial duress due to the Napoleonic wars, Froriep wasted no time in bolstering revenues and acquiring printers to come to Weimar and help get the firm back on track. The firm had specialized for many years on geographical titles and maps and this continued under Froriep, but an increase in medical and in natural sciences works was seen under his direction. One of these natural history works was the *Wörterbuch der Naturgeschichte.*

In order to promote more natural history in the firm's repertoire of publications Froriep designed a plan to produce a natural history dictionary. The first volume of the *Wörterbuch der Naturgeschichte* [Dictionary of Natural History] appeared in 1824, but the hopes of establishing a completely new dictionary for German readers ultimately failed due to lack of subscribers. Lack of revenue forced the later volumes (the initial series was published only through the letter "O") to essentially to be reduced to just German translations of the same entries found in the contemporaneously published French *Dictionnaire Classique d'Histoire Naturelle*.

Despite falling on hard times and having to resort to publishing translations of previously published entries, the *Wörterbuch* still has much new nomenclatural and taxonomic information in it including type designations for genera and even full descriptions of obscure or forgotten genera [see Evenhuis (2012) for notice of the little-known Germar Diptera genus *Dicera*]. Despite the financial hardships of the publishing firm, Froriep was still working to produce novel and up-to-date information on natural history subjects.

Because of the new information contained therein, the taxonomic importance of this work needs to be further investigated by botanists and zoologists. The Diptera genera that were treated and the type designations found in this work will be treated in a separate work and include type designations for a number of genus-group names that are earlier than previously recorded. Numerous other nomenclatural acts exist in the work and specialists should examine it carefully to obtain all the novel nomenclatural acts that are there.

Unfortunately, Froriep's leadership of the company did not result in it faring well financially, which was no doubt a reason for not being able to complete the *Wörterbuch* (even an attempt to revise and reprint the first few volumes did not meet with success). He eventually sold the company in 1845.

Authorship of the *Wörterbuch*

Although it is clear from external evidence that Froriep was the person responsible for coordinating this project, none of the demi-volumes of the *Wörterbuch* issued has the name of anyone responsible for the specific entries contained therein. This was not uncommon for dictionaries of the time, which were usually coordinated by publishers who gathered specialists to write entries and the publisher was thus essentially the "author" or "editor" of the entire work.

However, a paragraph in the Nachricht of the first part of volume 1 states: "*Es haben Herr Prof. Bernhardi, Ober-Medicinalrath v. Froriep und Herr Hofrath Oken ihre regelmässige Teilnahme, zumal durch Revision zugesagt und betätig, und mehrere andere Naturforscher haben ihre Beirat und Hülfe versprochen*." [Herr Prof. Bernhardi, the Superior Medicine Councilor v. Froriep and Herr Councilor Oken have promised and put into effect their regular participation, especially by revision, and several other naturalists have promised their advisement and help.] This indicates that in addition to Froriep, others took part in many of the entries of the *Wörterbuch*. However, because there is no indication in the work as to who was responsible for what, their specific participation cannot be accurately ascertained. I thus treat Froriep as the inferred author of the entire work. Using

Recommendation 51D of the ICZN *Code* (ICZN 1999), Froriep can be considered the author of any novel nomenclatural acts contained in this *Wörterbuch*, and his name should be placed in square brackets, viz., "[Froriep]" to indicate authorship was ascertained through external evidence.

Sources Consulted for Dating

A number of contemporary periodicals listing new books published were consulted for dates of notice of the *Wörterbuch* during this study. Entries were often found in the section on books received, but sometimes advertisements on the wrappers of certain issues of periodicals provided earlier dating of the demi-volumes as they were issued.

The Landes-Industrie-Comptoir published their own periodicals and a check of these was sometimes, but not always, successful. Either an issue simply failed to list the latest issuance of the *Wörterbuch* or the copy consulted might have had this information printed on the wrapper and the wrapper was not bound with the copy seen.

Periodicals consulted during this study included the *Intelligenzblatt der Zeitung für die Elegante Welt* (IZWE) (which recorded issues as received but also sometimes had publisher's advertisements on the wrappers), Froriep's *Notizen* (published by the Landes-Industrie-Comptoir and which also had advertisements on the wrappers), *Allgemeine Teutsches Garten-Magazin* (also published by the Landes-Industrie-Comptoir), *Allgemeiner Typographischer Monats-Bericht für Teutschlands*, *Isis* (von Oken), *Annales der Physik*, *Augsberger Allgemeine Zeitung*, *Verzeichniss der Hinrichs Buchhandlung*, *Blätter für Literarische Unterhaltung*, the *Buchmesse* catalogs of the Leipzig Easter and Michaelismesse Book Fairs, and the *Literarische Zeitung.*

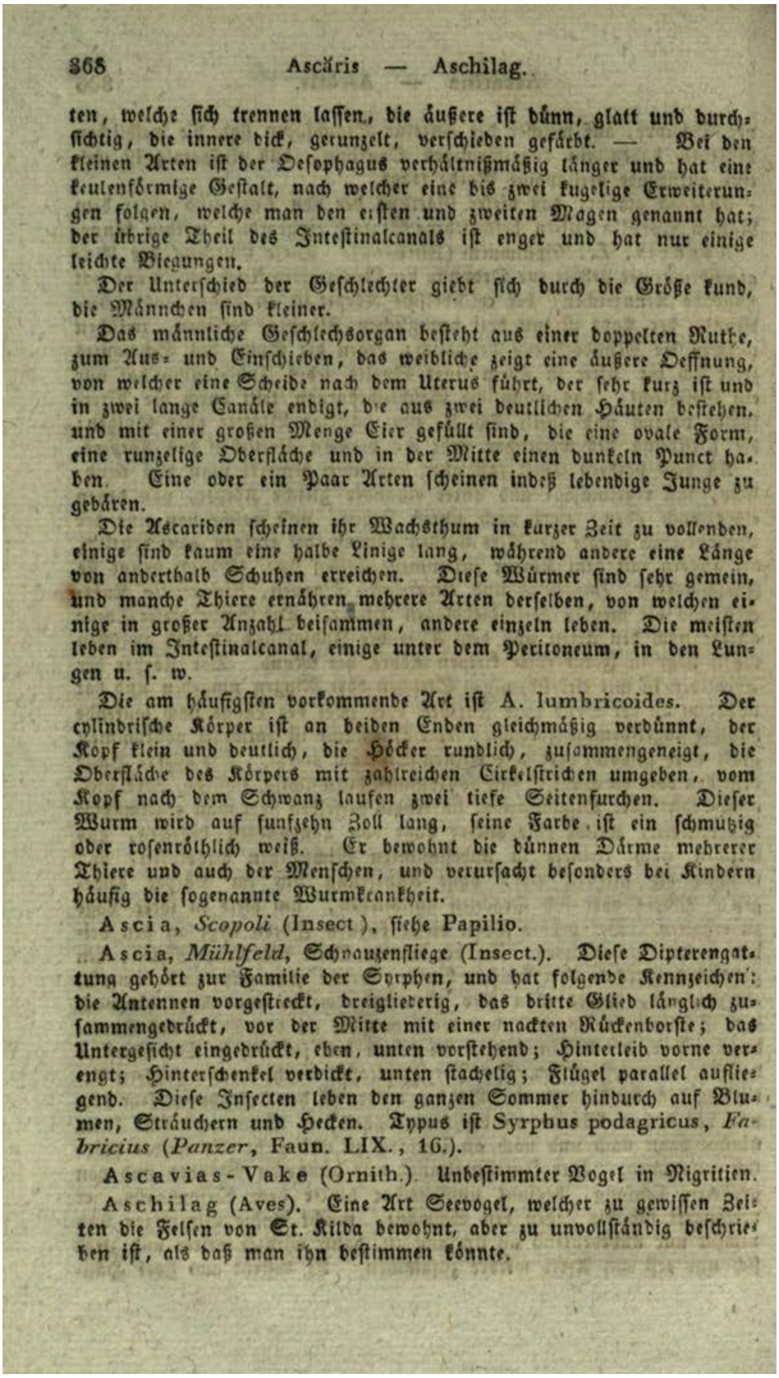
Dating and publication of the *Wörterbuch der Naturgeschichte*

The *Wörterbuch* was initially planned to be issued in a series of Lieferungen [= demi-volumes] comprising text and an atlas of 10 plates for each issue; plus a separately published index of species listed in the text also issued with the demi-volumes. A full description of the project was printed in the September 1824 issue of the *Allgemeiner typographischer Monats-Bericht für Teuchslands* (Anonymous 1824) [the same description also appeared on the back cover of the wrapper for Froriep's *Notizen* (vol. 7; for April–July of 1824); both descriptions are signed as "Weimar Juni 1824"]. According to these descriptions, initially 12 volumes were anticipated, issued in 24 demi-volumes and to take an estimated five to six years to complete. However, as with many natural history dictionaries of that time, printing expanded as more entries appeared than had been planned, or those that were printed were longer than had been anticipated. Subscribership also dwindled and no *Lieferungen* were listed for sale at the Leipzig Book fairs after 1833. Eventually, without funds to continue the project due to paltry subscribers, the project was abandoned in 1837 after the first demi-volume of the 11th volume appeared, some 13 years after the project started. A short notice dated October 1837 in the *Blätter für Literarische Unterhaltung* gives some hints at problems underlying the issuance of parts of the *Wörterbuch*:

> „*Der Druck der folgenden Lieferungen geht so lange in der seitherigen Weise fort, bis wir, aufgemuntert durch grössere Zahl von Subskribenten, eine grössere Beschleunigung eintreten lassen können*" [The publication of future parts will continue as in the previous manner until, encouraged by a greater number of subscribers, we are able to introduce a more rapid speed] (Anonymous, 1837)

An attempt at getting more or different subscribers was attempted in 1837 with advertisements for revised editions of the first four demi-volumes (physical copies of these have not been traced in this study), saying that two volumes (4 Lieferungen) had been printed by November 1837 and deliveries of further ones were to be forthcoming every two months. That attempt must also have failed as no further demi-volumes are known to have been printed after 1837.

The demi-volumes (Lieferungen) were issued initially with two per year; the first parts of all demi-volumes were issued without title pages (no wrappers were found during this study) so no year dates were printed in the announcements of those demi-volumes. Years were printed when the second demi-volume was issued, which completed the volume and contained the title page. Dates of publication of a month or day within a month based on the contemporary literature were found for



368 Ascăris — Aschilag.

ten, welche ſich trennen laſſen, die äußere iſt dünn, glatt und durchſichtig, die innere dick, gerunzelt, verſchieden gefärbt. — Bei den kleinen Arten iſt der Oeſophagus verhältnißmäßig länger und hat eine keulenförmige Geſtalt, nach welcher eine bis zwei kugelige Erweiterungen folgen, welche man den erſten und zweiten Magen genannt hat; der übrige Theil des Inteſtinalcanals iſt enger und hat nur einige leichte Biegungen.

Der Unterſchied der Geſchlechter giebt ſich durch die Größe kund, die Männchen ſind kleiner.

Das männliche Geſchlechsorgan beſteht aus einer doppelten Ruthe, zum Aus- und Einſchieben, das weibliche zeigt eine äußere Oeffnung, von welcher eine Scheide nach dem Uterus führt, der ſehr kurz iſt und in zwei lange Canäle endigt, die aus zwei deutlichen Häuten beſtehen, und mit einer großen Menge Eier gefüllt ſind, die eine ovale Form, eine runzelige Oberfläche und in der Mitte einen dunkeln Punct haben. Eine oder ein Paar Arten ſcheinen indeß lebendige Junge zu gebären.

Die Ascariden ſcheinen ihr Wachsthum in kurzer Zeit zu vollenden, einige ſind kaum eine halbe Linige lang, während andere eine Länge von anderthalb Schuhen erreichen. Dieſe Würmer ſind ſehr gemein, und manche Thiere ernähren mehrere Arten derſelben, von welchen einige in großer Anzahl beiſammen, andere einzeln leben. Die meiſten leben im Inteſtinalcanal, einige unter dem Peritoneum, in den Lungen u. ſ. w.

Die am häufigſten vorkommende Art iſt A. lumbricoides. Der cylindriſche Körper iſt an beiden Enden gleichmäßig verdünnt, der Kopf klein und deutlich, die Höcker rundlich, zuſammengeneigt, die Oberfläche des Körpers mit zahlreichen Cirkelſtrichen umgeben, vom Kopf nach dem Schwanz laufen zwei tiefe Seitenfurchen. Dieſer Wurm wird auf funfzehn Zoll lang, ſeine Farbe iſt ein ſchmutzig oder roſenröthlich weiß. Er bewohnt die dünnen Därme mehrerer Thiere und auch der Menſchen, und verurſacht beſonders bei Kindern häufig die ſogenannte Wurmkrankheit.

Ascia, *Scopoli* (Insect.), ſiehe Papilio.

Ascia, *Mühlfeld*, Schnauzenfliege (Insect.). Dieſe Dipterengattung gehört zur Familie der Syrphen, und hat folgende Kennzeichen: die Antennen vorgeſtreckt, dreigliederig, das dritte Glied länglich zuſammengedrückt, vor der Mitte mit einer nackten Rückenborſte; das Untergeſicht eingedrückt, eben, unten vorſtehend; Hinterleib vorne verengt; Hinterſchenkel verdickt, unten ſtachelig; Flügel parallel aufliegend. Dieſe Inſecten leben den ganzen Sommer hindurch auf Blumen, Sträuchern und Hecken. Typus iſt Syrphus podagricus, *Fabricius* (*Panzer*, Faun. LIX., 16.).

Ascavias-Vake (Ornith.) Unbeſtimmter Vogel in Nigritien.

Aschilag (Aves). Eine Art Seevogel, welcher zu gewiſſen Zeiten die Felſen von St. Kilda bewohnt, aber zu unvollſtändig beſchrieben iſt, als daß man ihn beſtimmen könnte.

Fig. 2. Sample page from Volume 1 of the *Wörterbuch* (1825) showing entries, including the one for the Diptera genus *Ascia*, where *Syrphus podagricus* is designated as the type species, the earliest subsequent designation for that nominal genus.

all demi-volumes issued except Lieferung 17, for which only the year "1833" was found in a listing of it in 1837.

The atlas plates have been consulted but are not detailed in this study as the organisms depicted on the plates are not new and the plates themselves are, for the most part, those taken from previously published plates in Bertuch's *Bilderbuch für Kinder* and consisted of common species of plants and animals. The September 1824 description of the *Wörterbuch* stated that costs for subscribing could be kept low because no new plates had to be prepared since the publisher had 800 plates from which to choose that had already been used in Bertuch's *Bilderbuch für Kinder* (Anonymous 1824). Each volume that was issued along with plates for the atlas contained an explanation of the plants and animals figured on each plate, which was checked for any new scientific names.

Table 1. **Dating of the *Wörterbuch der Naturgeschichte***
(Date in square brackets is interpolated. See below for explanation of dates of publication.)

Vol.	Pt.	Contents	Pages	Plates	Printed Year	Date of Publication
1*	1	Aal–Aphyllanthes	1–288	1–10	—	9 May 1824
1*	2	Aphyllanthes–Birgus	289–560 + [v]	11–20	1825	Jan 1825
2*	1	Birostrites–Caprifolium	1–256	21–30	—	17 May 1825
2*	2	Caprimulgus–Chaixia	257–468	31–40	1825	2 Oct 1825
3	1	Chala–Coenogonium	1–288	41–50	—	15 Apr 1826
3	2	Coenogonium–Crotonopsis	289–560	51–60	1826	19 Sep 1826
4	1	Crotophaga–Diamant	1–288	61–70	—	6 May 1827
4	2	Diamant–Eisenschüssig Kupfergrün	289–580	71–80	1828	13 Dec 1827
5	1	Eisenschwarz–Fallenia	1–288	81–90	—	22 Jul 1828
5	2	Fallopia–Garidella	289–544	—	1829	23 Jun 1829
6	1	Gariofilate–Graphypterus	1–272	—	—	Jul 1829
6	2	Grappe–Herinaceus	273–512	—	1829	16 Mar 1830
7	1	Herion–Hymenaria	1–256	91–100	—	Nov 1830
7	2	Hymenatherum–Justicia	257–512	—	1831	Feb 1831
8	1	Justicia–Kupfercarbonateis	1–256	—	—	2 Oct 1831
8	2	Kupfercarbonateis–Lepuropetalon	257–542	—	1832	3 Apr 1832
9	1	Lepus–Lynchnophora	1–256	—	—	[before 6 Oct] 1833
9	2	Lychnophorites–Mauhlia	257–574	—	1833	6 Oct 1833
10	1	Maulkin–Mollipennes	1–256	—	—	12 Apr 1835
10	2	Mollis–Myzostyle	257–582	—	1836	Jul 1836
11	1	Naatsjoni–Oceanides	1–272	—	—	Nov 1837

* First 4 demi-volumes were advertised as being reprinted in 1837. These were not consulted in this study.

Each Lieferung [= demi-volume] was issued as follows:

[Lieferung 1. **Aal–Aphyllanthes]**. **9 May 1824**.

[Froriep, L.F. von] [1824]. *Wörterbuch der Naturgeschichte, dem gegenwärtigen Stande der Botanik, Mineralogie und Zoologie angemessen.* Landes-Industrie-Comptoir, Weimar. Pp. 1–288.

REMARKS: The first demi-volume of text and the first 10 plates of the atlas were announced in the May issue of the ATGM as having been displayed at the Leipzig Easter Book Fair [which took place on Jubilate Day, three weeks after Easter (18 April 1824)], and started on 9 May 1824) (Laeven 1992).

[Lieferung 2. Aphyllanthes–Birgus]. January 1825.

[Froriep, L.F. von] 1825. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 289–560 + [iv]. [With title page to entire volume 1 labeled as "Erster Band. A – Bir. Hierzu die Lieferungen 1 und 2. (Taf. 1–20) des Atlas. 1825".]

REMARKS: Dated from an advertisement in the January 1825 issue of the *Allgemeine Typographischer Monats-Bericht*. Contents of this Lieferung are from the advertisement in IZEW.

[Lieferung 3. Birostrites–Caprifolium]. 17 May 1825.

[Froriep, L.F. von] [1825]. *Wörterbuch der Naturgeschichte*.... Landes-Industrie-Comptoir, Weimar. Pp. 1–256.

REMARKS: The first three demi-volumes of the Wörterbuch were issued by June 1825 according to Froriep's second volume of the *Notizen,* which announced their publication among other works published by the Landes-Industrie-Comptoir on its back wrapper. However, an earlier date (17 May 1825) for this third demi-volume was obtained from the IZEW. This part was reviewed in the August 1825 issue of *Isis* (Oken).

[Lieferung 4. Caprimulgus–Chaixia]. 2 October 1825.

[Froriep, L.F. von] 1825. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 257–468. [With title page to entire volume 2 labeled as "Zweiter Band. Bir–Chai. Hierzu die Lieferungen 3 und 4. (Taf. 21–40) des Atlas. 1825".]

REMARKS: The fourth demi-volume [= second part of second volume] was announced by the publisher in the ATGM and the *Annalen der Physik* as sold at the Michaelmesse [St. Michael's Day] Book Fair in Leipzig in 1825, which took place on the first Sunday after St. Michael's Day [= 2 October for 1825] (Laeven, 1992).

[Lieferung 5. Chala–Coenogonium]. 15 April 1826

Landes-Industrie-Comptoir [1826]. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 1–288.

REMARKS: This first part of volume three was announced by the publisher in the ATGM as being sold at the Easter Book Fair in Leipzig [= 15 April 1826].

[Lieferung 6. Coenogonium–Crotonopsis]. 19 September 1826.

[Froriep, L.F. von] 1826. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoire, Weimar. Pp. 289–560. [With title page to entire volume 3 labeled as "Dritter Band. Cha–Cro. Hierzu die Lieferungen 5 und 6. (Taf. 41–60) des Atlas. 1826".]

REMARKS: This part was dated from its advertisement in IZEW.

[Lieferung 7. Crotophaga–Diamant]. 6 May 1827.

[Froriep, L.F. von] [1827]. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 1–288.

REMARKS: This first part of volume four was announced by the publisher in the ATGM as being sold at the Easter Book Fair in Leipzig [= 6 May 1827].

[Lieferung 8. Diamant–Eisenschüssig-Kufergrün]. 13 December 1827.

[Froriep, L.F. von] 1827. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 289–580. [With title page to entire volume 4 labeled as "Vierter Band. Cro–Eisen. Hierzu die Lieferungen 7 und 8. (Taf. 61–80) des Atlas. 1828".]

REMARKS: This part was dated from its advertisement in IZEW.

[Lieferung 9. Eisenschwarz–Fallenia]. 22 July 1828.

[Froriep, L.F. von] [1828]. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 1–288.

REMARKS: This part was dated from its advertisement in IZEW.

[Lieferung 10. Fallopia–Garidella]. 23 June 1829.

[Froriep, L.F. von] 1829. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 289–544. [With title page to entire volume 5 labeled as "Fünfter Band. Eisen–Garidella. Hierzu die Lieferungen 9 (Taf. 81–100) des Atlas. 1829".]

REMARKS: This part was dated from its advertisement in IZEW.

[Lieferung 11. Gariofilate–Graphypterus]. July 1829.

[Froriep, L.F. von] [1829]. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 1–272.

REMARKS: This part was dated from its notice in *Isis* (Oken); IZEW advertised it in its 4 August 1829 issue.

[Lieferung 12. Grappe–Herinaceus]. 16 March 1830.

[Froriep, L.F. von] 1830. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 273–512. [With title page to entire volume 6 labeled as "Sechster Band. Gariofilate–Herinaceus. 1830".]

REMARKS: This part was dated from its advertisement in IZEW.

[Lieferung 13. Herion–Hymenaria]. November 1830.

[Froriep, L.F. von] [1830]. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 1–288.

REMARKS: This part was dated from the date of its advertisement in *Isis* (Oken).

[Lieferung 14. Hymenatherum–Justicia]. February 1831.

[Froriep, L.F. von] 1831. *Wörterbuch der Naturgeschichte* .... Landes-Industrie-Comptoir, Weimar. Pp. 289–560. [With title page to entire volume 7 labeled as "Siebenter Band. Herion–Justicia. Hierzu die Lieferungen 10 (Taf. 91–100) des Atlas. 1831".]

REMARKS: This part was dated from the date of its advertisement in *Isis* (Oken); IZEW advertised it is its 7 June 1831 issue.

[Lieferung 15. Justicia–Kupfercarbonateis]. 2 October 1831.

[Froriep, L.F. von] [1831]. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 1–256.

REMARKS: This part was dated from its listing as for sale in the *Buchmesse* of the Leipzig Michaelmesse Fair, which started on this date.

[Lieferung 16. Kupfercarbonateis–Lepuropetalon]. 3 April 1832.

[Froriep, L.F. von] 1832. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 257–542. [With title page to entire volume 8 labeled as "Achter Band. Justicia–Lepuropetalon. 1832".]

REMARKS: This part was dated from its advertisement in IZEW. The full volume 8 was reviewed in the April 1834 issue of *Isis* (Oken).

[Lieferung 17. Lepus–Lynchnophora]. Before 6 October 1833.

[Froriep, L.F. von] [1833]. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 1–256.

REMARKS: There is no date printed on this Lieferung. The only date found for it is the "1833" listed in the *Medicinisch Schriftsteller-Lexicon* in 1837. It is presumed to have been issued prior to Lfg. 19, which came out on 6 October 1833.

[Lieferung 18. Lychnophorites–Mauhlia]. 6 October 1833.

[Froriep, L.F. von] 1833. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 257–574. [With title page to entire volume 9 labeled as "Neunter Band. Lepus–Mauhlia. 1833".]

REMARKS: Advertised as for sale the Michelmesse Book Fair in Leipzig, which started on 6 October 1833.

[Lieferung 19. Maulkin–Mollipennes]. 12 April 1835.

[Froriep, L.F. von] [1835]. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 1–256.

REMARKS: Dated from the *Augsburg Allgemeines Zeitung*.

[Lieferung 20. Mollis–Myzostyle]. July 1836.

[Froriep, L.F. von] 1836. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 257–582. [With title page to entire volume 10 labeled as "Zehnter Band. Maulin–Myzostyle. 1836".]

REMARKS: Dated from its notice in *Isis* (Oken).

[Lieferung 21. Naatsjoni–Oceanides]. November 1837.

[Froriep, L.F. von] [1837]. *Wörterbuch der Naturgeschichte* ..... Landes-Industrie-Comptoir, Weimar. Pp. 1–272.

REMARKS: Dated from the *Blätter für Literarische Unterhaltung*; also noticed in the November 1837 issue of *Isis* (Oken).

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Adrian Pont kindly supplied the English translation of the 1837 quote concerning the publisher's progress report on the speed of delivery of the subscribed parts of the *Wörterbuch*. Miguel Alonso Zarazaga and Adrian Pont reviewed the submitted manuscript and their suggestions and corrections have helped improve the paper.

Dedication

This paper is dedicated to the memory of one of the best friends of my life, Lu Eldredge. His encouragement and feedback on my bibliographic projects including publication dating were the fuel I needed to keep me going, even when it initially seemed I could not find all the resources I needed to complete my research. I learned an incredible amount from him: about books, good food, bibliography, history, good food, marine biology, invasive species, good food, and life's many inherent problems and how to deal with them. Brewing up a fresh pot of coffee was all the invitation he needed to sit down for a chat in my office every morning and begin the workday the best way possible for good colleagues and friends. That chair is now empty. I will sorely miss him.

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The Endemic Hawaiian Mantis Shrimp, *Parvisquilla sinuosa* (Edmondson, 1921) (Crustacea: Stomatopoda: Squillidae)

Shane T. Ahyong
Australian Museum, 6 College St., Sydney, NSW 2010, Australia, and School of Biological,
Earth & Environmental Sciences, University of New South Wales, Kensington, NSW 2052;
email: shane.ahyong@austmus.gov.au

Abstract. The endemic Hawaiian mantis shrimp, *Parvisquilla sinuosa* (Edmondson, 1921), is redescribed based on the holotype and additional specimens. The new material includes the first known male of the species, whose morphology confirms the presence of sexual dimorphism in uropodal protopod length, as observed in other species of *Parvisquilla*. Of the three known species of *Parvisquilla*, *P. sinuosa* is unique in having a dorsally carinate rather than dorsally tuberculate telson characteristic of its congeners, *P. multituberculata* (Borradaile, 1898) and *P. dominguez* Ahyong & Erdmann, 2003.

Introduction

Twenty species of mantis shrimp (Stomatopoda) are currently known from the Hawaiian Islands (Eldredge & Miller 1997, Ahyong 2002), of which one species, *Parvisquilla sinuosa* (Edmondson, 1921), is apparently endemic. *Parvisquilla sinuosa*, however, is poorly documented, having neither been adequately described nor figured. The species is redescribed and figured here based on the holotype and other material. The present study is dedicated to the memory of Lu Eldredge for his major contributions to Hawaiian zoology and for making the holotype of *P. sinuosa* available for study before his unfortunate passing.

Methods

Morphological terminology largely follows Ahyong (2001, 2012a). Measurements are given in millimeters. Total length (TL) is measured from the apex of the rostral plate to the apices of the submedian teeth of the telson. Carapace length (CL) is measured along the dorsal midline and excludes the rostral plate. Corneal Index is given as 100CL divided by the cornea width. Specimens examined are deposited in the Bernice P. Bishop Museum, Honolulu (BPBM); and Zoological Museum, University of Copenhagen (ZMUC).

Systematics

Squillidae Latreille, 1802

Parvisquilla Manning, 1973

Parvisquilla sinuosa (Edmondson, 1921)

Coronida sinuosa Edmondson, 1921: 295–297, fig. 2. — Edmondson, 1946: 243. — Townsley, 1953: 419–421, figs. 16–17. — Hiatt, 1954: 20, pl. 4: fig. 8h. — Manning, 1963: 322. — Eldredge, 1965: 17. —Holthuis, 1967: 8.

Parvisquilla sinuosa. — Manning, 1973: 299. — Manning, 1995: 22. — Ahyong, 2002b: 838. — Ahyong & Erdmann, 2003: 347. — Schram & Müller, 2004: 184.

Paravisquilla [sic] *sinuosa*. — Eldredge & Miller, 1997: 11.

Holotype. BPBM S526, female (TL 17 mm), Waikīkī Reef, Honolulu, Oʻahu, among dead coral, coll. C.H. Edmondson, 1921.

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Other material examined. ZMUC CRU20560, 1 damaged male, 2 females (TL 11–12 mm), Honolulu, 20–80 m, in coral, coll. Th. Mortensen, 5 May 1915.

Diagnosis. Abdominal somite 6 and telson with numerous slender, straight and curved, dorsal carinae, without upright tubercles. Telson median carina single, undivided along midline. Uropodal protopod, exopod and endopod without dorsal spines or tubercles.

Description of holotype. Dorsal integument smooth, polished. Eye elongate, length twice width; cornea broadened, bilobed, not extending beyond antennular peduncle segment 1; corneal index 459–568. Ophthalmic somite anterior margin triangular. Ocular scales broad, truncate, anterior margin oblique to midline. Antennular somite elongate, extending anteriorly well beyond apex of rostral plate. Antennular peduncle as long as CL. Antennular somite dorsal processes low, angular. Antennal protopod unarmed, without spines or papillae. Antennal scale slender, 0.3CL; entire margin setose.

Rostral plate triangular, length about half width; apex rounded; lacking carinae. Carapace strongly narrowed anteriorly; without dorsal carinae; anterolateral angles blunt; gastric grooves distinct; cervical groove indistinct; posterior margin unarmed.

Raptorial claw dactylus with 4 teeth; outer proximal margin with three, triangular lobes, proximal two acute, distal slightly inflated, blunt. Carpus dorsal margin with short distal tooth. Propodus pectinate; occlusal margin fully pectinate, with 3 movable spines proximally. Merus outer inferodistal margin rounded.

Mandibular palp absent. Maxillipeds 2 and 3 with epipod. Maxilliped 5 basal segment unarmed; merus with broad convex flange on inner margin.

Pereopods 1–3 basal segment unarmed; endopod segments fused, slender, setose distally.

Thoracic somites 5–8 lacking dorsal carinae. Thoracic somite 5 lateral process a short lobe produced diagonally; with blunt triangular ventrolateral lobe. Thoracic somites 6–8 lateral processes broadly rounded. Thoracic somite 8 without sternal keel.

Male pleopod 1 endopod distal 'endite' without lateral lobe; hook process elongate, with pointed apex, as long as tube process.

Abdominal somites 1–5 smooth dorsally, without carinae or spines, pleura blunt posterolaterally. Abdominal somite 6 with slender, unarmed dorsal carinae, otherwise smooth; median carina entire or interrupted; submedian carinae irregularly curved; intermediate carinae irregular, oblique to midline, anteriorly curved laterally; oblique carina between intermediate and lateral carinae; lateral carina straight; posterolateral angle blunt, rounded produced posterolaterally; posterior margin unarmed; triangular ventrolateral projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson thick, inflated, almost twice as wide as long; dorsal surface with numerous slender carinae; median carina with proximal dorsal pit and short posterior spine; accessory median carinae converging at base of posterior spine of median carina; dorsolateral surface with numerous curved, occasionally interconnected and recurved carinae; margins of dorsal surface irregularly carinate and lobulate posteriorly, partially overhanging primary marginal teeth; submedian, intermediate and lateral teeth stout, distinct, acute; submedian teeth with movable apices; prelateral lobe absent; denticles spiniform, submedian 5–8, intermediate 4–9, lateral 1. Telson ventral surface with low postanal swelling.

Uropodal protopod anterior margin produced anteriorly, blunt, rounded; posteriorly terminating in distally bifid, flattened spine, extending posteriorly slightly beyond midlength of endopod (female) or almost to distal three-fourths of endopod (male); with blunt angular projection above exopodal articulation and rounded projection above endopod articulation, otherwise without dorsal spines or tubercles; without ventral spine or tubercle anterior to endopod articulation; protopod inner margin smooth, unarmed.

Uropod exopod proximal segment unarmed dorsally; inner margin straight; outer margin with 10 or 11 movable spines, distalmost reaching almost to midlength of distal segment; distal margin unarmed; Endopod unarmed dorsally.

Colour in life. Transparent white with dark corneas (Edmondson 1921, Townsley 1953).

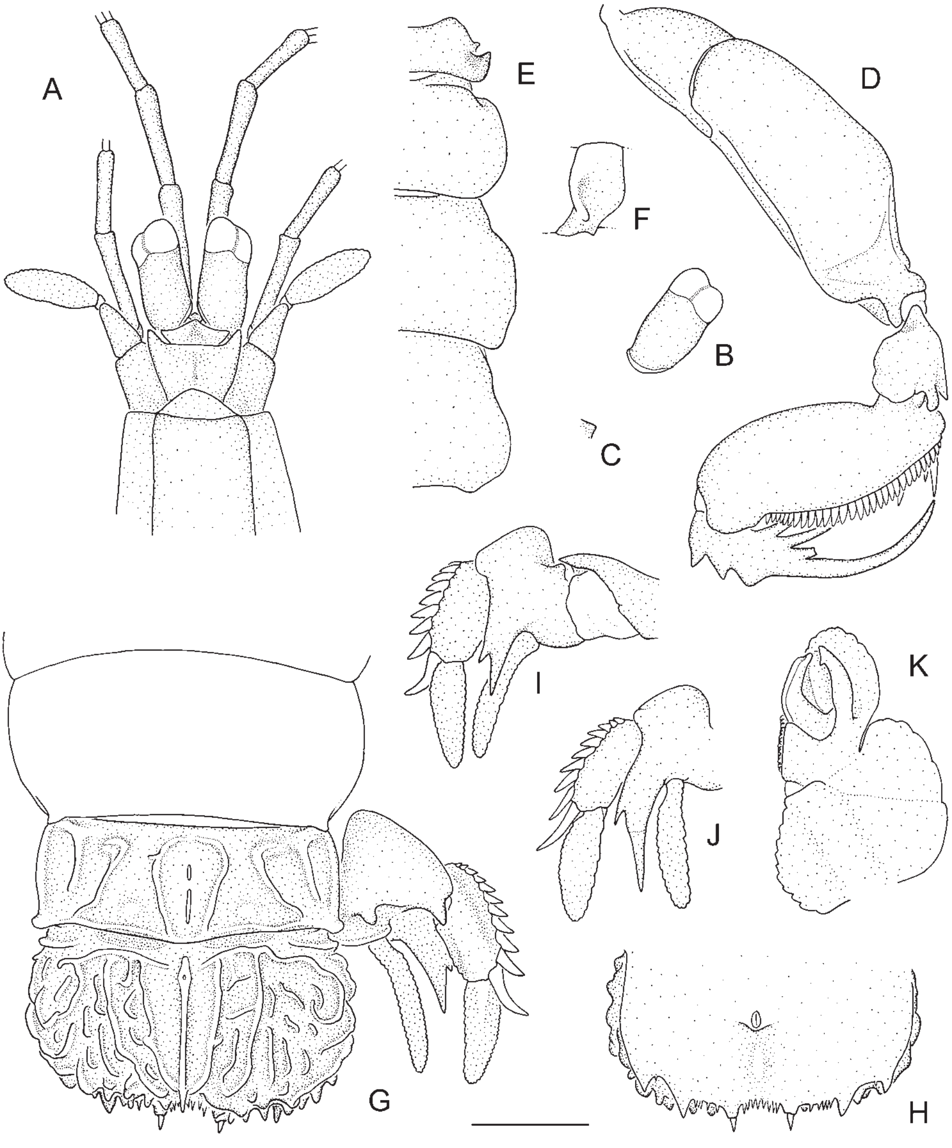

Fig. 1. *Parvisquilla sinuosa* (Edmondson, 1921): **A–I,** holotype female, TL 17 mm (BPBM S526); **J–K**, male (ZMUC CRU20560). **A**, anterior cephalothorax; **B**, right eye; **C**, right dorsal process of antennular somite, lateral view; **D**, right raptorial claw; **E**, thoracic somites 5–8, right dorsal view; **F**, right thoracic somite 5, lateral view; **G**, abdominal somites 5–6, telson and right uropod, dorsal view; H, telson, ventral view; **I–J**, right uropod, ventral view; **K**, right male pleopod 1 endopod, anterior view. Scales: A–J = 1.0 mm, K = 0.5 mm.

Measurements of holotype. TL 17 mm, CL 2.7 mm, antennal scale length 0.8 mm, antennular peduncle length 2.7 mm, cornea width 0.5 mm.

Remarks. *Parvisquilla sinuosa* was originally described in the genus *Coronida* Brooks, 1886, and subsequently transferred to *Parvisquilla* Manning, 1973, alongside *P. multituberculata* (Borradaille, 1898) (type locality: Lifou). A third species, *Parvisquilla dominguez* Ahyong & Erdmann, 2003, was described from Guam. *Parvisquilla* was thought to be a lysiosquilloid (Manning 1978, 1980, 1995), most closely related to the coronidids largely on the basis of the heel on the outer margin of the dactylus of the raptorial claw and elaborate dorsal telson ornamentation. Ahyong (2001) and Ahyong & Erdmann (2003), however, showed that *Parvisquilla* belongs in the Squillidae based on mouthpart, pleopodal and postlarval features.

Variation within the present series is slight. The smallest specimen examined (female, TL 11 mm) may be a juvenile, having less pronounced dorsal telson ornamentation in addition to more numerous and more spiniform submedian and intermediate telson denticles (submedian 7 or 8, intermediate 9 compared to submedian 4–6, intermediate 4 or 5). The present series includes the first known male of the species; it exhibits sexual dimorphism in the more elongate uropodal protopod as reported for the two other species of the genus (Ahyong & Erdmann 2003, Ahyong 2012b).

Parvisquilla sinuosa is unique in the genus for having the dorsal surface of the telson covered with sinuous carinae rather than tubercles as in *P. multituberculata* and *P. dominguez*. *Parvisquilla sinuosa* and *P. dominguez* are presently known only from their respective type localities, whereas *P. multituberculata* ranges widely in the Indo-West Pacific, from the Maldives to the South China Sea, Okinawa, Lifou, Tonga, Samoa, and French Polynesia (Manning 1978, Ďuriš 1987, Ahyong 2002a 2012).

Species of *Parvisquilla* are transparent-white in life, living in crevices and holes in and around the base of corals (Ahyong & Erdmann 2003). All known specimens of *P. sinuosa* were collected from among dead coral heads on Waikīkī Reef, O‘ahu, Hawai‘i (Edmondson 1921, 1946; Townsley 1953).

Distribution. Presently known only from Hawai‘i.

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A Revision of *Danalia* Giard, 1887, *Faba* Nierstrasz & Brender à Brandis, 1930 and *Zeuxokoma* Grygier, 1993 (Crustacea: Isopoda: Epicaridea: Cryptoniscoidea: Cryptoniscidae) with Description of a New Genus and Four New Species

Christopher B. Boyko
Department of Biology, Dowling College, 150 Idle Hour Boulevard, Oakdale, NY 11769, USA
and Division of Invertebrate Zoology, American Museum of Natural History,
Central Park West @79th St., New York, New York 10024, USA, email: cboyko@amnh.org

Abstract. Species belonging to the genera *Danalia* Giard, 1887, *Faba* Nierstrasz & Brender à Brandis, 1930, and *Zeuxokoma* Grygier, 1993 are reviewed. *Danalia* contains species that have mature females that are strongly recurved in shape, cryptoniscus larvae that have reduced and modified pereopods 6 and 7, and that are hyperparasitic on rhizocephalans or directly parasitic on crab hosts. Most species of *Danalia* are in need of recollection and redescription. The generic placement of *Danalia caulleryi* Nierstrasz & Brender à Brandis, 1923 is questioned on the basis of female morphology. *Faba* contains species with females that are linear in shape and are all parasites directly on shrimp hosts. *Faba* is a junior synonym of *Zeuxo* Kossmann, 1880, a preoccupied name previously replaced by *Zeuxokoma*, which is the correct name for the genus. Two new species are described in *Zeuxokoma*, *Z. musaeformis,* **n**. **sp**. and *Z. elongata,* **n**. **sp**., representing the first species described in the genus from both the eastern and western Atlantic, respectively. A new genus, *Avada*, **n**. **gen**., is erected for those species distinguished from *Danalia* by having females with a compact, weakly recurved shape and cryptoniscus larvae with more modified and more reduced pereopods 6 and 7 than those seen in *Danalia* spp. Two new species are described in *Avada*: *A. kedavra,* **n**. **sp**. and *A. eldredgei,* **n**. **sp**. Keys to the genera are provided based on female and cryptoniscus characters.

Introduction

The genus *Danalia* was erected by Giard (1887) for isopod parasites of rhizocephalans that differed from those found on *Peltogaster* (e.g., *Cryptoniscus paguri* Fraisse, 1878) and for two species of *Zeuxo* Kossmann, 1872 that parasitized decapods. Giard (1887) erected *Danalia* because the "appendices terminaux sont de dimension inégales au lieu de former quatre lobes égaux comme chez les types étudiés par Kossmann" [terminal appendages are of unequal size instead of forming four equal lobes as in the types studied by Kossmann]. Although this appears to only differentiate the genus from *Zeuxo*, it also differentiates it from *Cryptoniscus sensu stricto,* as the type species, *C. paguri*, does not have 4 elongate lobes on the attachment structure—it has only 2 rounded ones. Giard's (1887) logic in erecting *Danalia* is hard to follow because he used only the inequality in attachment lobe size as seen in specimens of *Danalia pellucida* Giard, 1887 to distinguish this species from those of *Zeuxo*, but he placed four additional species in *Danalia* without comment as to the shapes of their attachment lobes: *Cryptoniscus larvaeformis* Giard, 1874, *Cryptoniscus curvatus* Fraisse, 1878, *Danalia dohrnii* Giard, 1887, and *Zeuxo longicollis* Kossmann, 1880. Giard (1887) also did not comment on the fact that the shape of the attachment lobes was quite variable, especially during development (see Fraisse 1878a, Caullery 1908).

Currently, there are a dozen species of cryptoniscoids either originally or later placed in *Danalia*, excluding *D. lobiancoi* Giard & Bonnier, 1890, which is a *nomen nudum* (see Grygier 1993, and herein). The species were erected based on the form of the females and, in most cases, the selection of host, with no consideration of the larval characters of the cryptoniscus. Taxonomy based on host identity was in line with the now-discredited concept of Giard & Bonnier (e.g., Giard & Bonnier 1890) that each host bears its own unique parasite fauna and each species of parasite will

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be found on only a single host species. Cryptoniscus larvae and neotenous males, which are very useful as sources for specific and generic characters, are unknown in all species except *D. curvata* (type species), *D. hapalocarcini*, and "*Danalia* 2" of Shiino (1952).

As noted by Grygier (1993), about half of the species of *Danalia* (*caulleryi*, *dohrnii*, *gregaria*, *larvaeformis*, *longicollis*, *pellucida*) are extremely poorly known. Only *D. caulleryi*, a parasite of the decapod *Galathea australiensis* Stimpson, 1858, was illustrated (but may not be a *Danalia* species, see below), and all suffer from very brief, and in some cases nearly non-existent, descriptions. None of the others can be recognized as separate species based on the original descriptions unless they are again collected from the type host (all are from rhizocephalans parasitizing decapods). Grygier (1993) did not include *D. porcellanae* in his list of species, but this was clearly an oversight, as the species was mentioned elsewhere in the paper as previously having been placed in *Danalia* by Altes (1982).

Of the described species in *Danalia*, females of both *Danalia caulleryi* and D. *porcellanae* differ in many respects from the other species. In the case of *D. caulleryi*, its short, thick lobes and development of external segmented plates contrast with the narrow, extending lobes and lack of such plates seen in other species of *Danalia*. This suggests that *D. caulleryi* may belong to another genus. Superficially, it resembles a *Cabirops* (Cryptoniscoidea: Cabiropidae, see Boyko 2013) but appears to have an attachment process that *Cabirops* species lack. Females of several species of *Cabirops* and *Danalia* exhibit an amazing degree of convergence in gross morphology that has led to considerable taxonomic confusion (Boyko 2013, and herein).

The proposal of *Danalia* by Giard (1887) left two species remaining in *Zeuxo*: *Zeuxo porcellanae* Kossmann, 1872 and *Z. alphei* Kossmann, 1872. Giard (1887) wrote: "Je suis bien convaincu qu'une étude plus complete montrera que ce dernier [*Z. alphei*] diffère aussi génériquement du *Zeuxo porcellanae*" [I am convinced that a more complete study will show that the [*Z. alphei*] also differs generically from *Zeuxo porcellanae*]. This has indeed proved to be the case. Currently, *Zeuxo porcellanae* is considered a species of *Danalia* (since its transfer there by Caullery 1908), while *Z. alphei* remains in this monotypic genus, now known as *Zeuxokoma* Grygier, 1993 because *Zeuxo* Kossmann, 1872 is preoccupied (see Grygier 1993, and below). Due to *Zeuxo* being preoccupied, *Faba* Nierstrasz & Brender à Brandis, 1930 would become the next available name for the genus but *Faba* itself is preoccupied by *Faba* Fischer, 1883 (Mollusca), so the correct name for the genus must be *Zeuxokoma* Grygier, 1993.

Danalia and *Zeuxokoma* (= *Zeuxo* Kossmann *non* Templeton) were, before 1930, the only two genera of Cryptoniscidae known where the female isopods possessed 4-lobed attachment structures. In 1930, Nierstrasz & Brender à Brandis erected *Faba*, a third genus of Cryptoniscidae with 4-lobed attachment structures, despite their concern that the similarity of the attachment structures in *Faba* and *Danalia* was convergent and not necessarily indicative of a close relationship. Females of cryptoniscid isopods present few morphological characters useful in elucidating relationships so, in the absence of information about the potentially more informative cryptoniscid stage of any *Faba* species, the presence of the 4-lobed attachment structure does suggest a close relationship between *Faba*, *Danalia,* and *Zeuxokoma*.

Faba is distinct from *Danalia* as females of *Faba* are mature (bearing eggs or embryos) with a linear sac-like morphology without the bilobate U-shape as seen in species of *Danalia*. However, there is no obvious distinction between *Faba* and *Zeuxokoma* and, based on host and insertion method, they appear synonymous. *Zeuxokoma alphei* is poorly known, based only on Kossmann's (1872) brief description regarding its "viel geringere Krümmung, den mehr endständigen Mund, und die weniger massenhaft verzweigten Canäle des Lacunensystems" [much lower curvature, more terminal mouth and less massive branched canal of the lacunae system] and single illustration of the female sac on the alpheid host (type specimens now lost). Although subsequent discovery of parasites on alpheid hosts (see below) indicates that *Faba* is a junior synonym of *Zeuxokoma*, the type species of *Zeuxokoma* is so poorly known that it would be premature to identify any known specimens as *Z. alphei*.

As surmised by Giard (1887), *Zeuxo porcellanae* is not a species of *Danalia* despite its superficial resemblance to species in that genus (see below under *Avada*, n. gen.). This was also suggested when Shiino (1952) described but did not name three species that he ascribed to *Danalia*. Three decapod hosts were reported [*Pachygrapsus crassipes* Randall, 1840, *Pugettia quadridens* (De Haan, 1839), and *Petrolisthes japonicus* (De Haan 1849)], each with a different species of *Danalia*.

The differences in pereopod 6 and 7 morphology of the cryptoniscus larvae (pereopod 6 with only 3 segments and a hyperextended terminal segment; pereopod 7 with bifurcated terminal segment) are sufficient to establish a new genus, *Avada*, for "*Danalia* 2" of Shino (1952) which also must be described as a new species. The morphology of the terminal segment of pereopod 6 in *Avada,* n. gen. is similar to that seen in species of *Danalia* (larvae of *Zeuxokoma* unknown), albeit much longer and much more distally recurved. This structure appears apomorphic and is considered a synapomorphy of *Danalia* and *Avada,* n. gen. The female of "*Danalia* 2" is also quite different from those of typical *Danalia* species in its lack of 2 clear elongate lobes with a spatial separation between them and with irregular dorsal lobes present. Therefore, a new genus for "*Danalia* 2" is erected based on both female and cryptoniscus characters. It would be preferable to have a larger character set as the basis for separation of the genera, but this will have to wait until detailed descriptions and redescriptions of further species can be accomplished.

Avada, n. gen. contains Shiino's "*Danalia* 2" (described herein as *Avada kedavra,* n. sp.), "*Danalia* 1" (not described), and "*Danalia* 3" (not described). *Danalia porcellanae* (Kossmann, 1872) is likewise transferred to this new genus as it has the same basic morphology as Shiino's "*Danalia* 3." In fact, as mentioned by Shiino (1952), "*Danalia* 3" is likely the same species as *Avada porcellanae* and is included in synonymy with it here. "*Danalia* 1" of Shiino (1952), is also likely to be a member of *Avada*, but the original description is so limited that it is not advisable to describe it at this time. A new species from Hawai'i, *A. eldredgei*, is also described. As with *Danalia*, some species of *Avada* parasitize rhizocephalans on decapods (e.g., *Danalia* 1), while some parasitize crab hosts (*A. kedavra,* n. sp., *A. porcellanae*, *A. eldredgei* n. sp.).

The present paper summarizes all species that are or have been placed in *Danalia*, *Zeuxo*, *Zeuxokoma*, or *Faba*, with description of a new genus, *Avada*, to include *Zeuxo porcellanae* and related taxa, and four new species: Two in *Zeuxokoma* and two in *Avada*.

Material and Methods

Specimens were borrowed from or are deposited in the following institutions: Bernice P. Bishop Museum, Honolulu, Hawai'i (BPBM), Florida Museum of Natural History (UF), Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM), Naturalis Biodiversity Center, Leiden (RMNH), National Science Museum of Tokyo (NSMT), University Museum of Bergen Zoological Museum (UBZM), Department of Invertebrate Zoology, Smithsonian National Museum of Natural History (USNM), and Zoological Museum of Amsterdam (ZMA, now in RMNH). Length of the isopods is given as total length (TL), the maximum distance from the attachment end to the opposite end of the specimen (including if U-shaped, as in *Danalia* species), whereas that of the host is given as carapace length (CL, inclusive of rostrum).

Systematics

Cryptoniscidae Kossmann, 1880

Danalia Giard, 1887

Danalia Giard, 1887: 47–50. Type species. *Cryptoniscus curvatus* Fraisse, 1878, by subsequent designation of Grygier (1993).

Other described species. *D. larvaeformis* (Giard, 1874), *D. longicollis* (Kossmann, 1880), *D. dohrnii* Giard, 1887, *D. pellucida* Giard, 1887, *D. ypsilon* Smith, 1906, *D. gregaria* Caullery, 1908, *D. caulleryi* Nierstrasz & Brender à Brandis, 1923, *D. inopinata* Harant, 1925, *D. hapalocarcini* Fize, 1955.

Diagnosis. Mature female: elongate and strongly recurved. Strongly convex dorsal margin with weakly to moderately pronounced lobes (6–10), ventral side strongly concave, with large median gap between lobes. Attachment trunk variable in length with four short to elongate flexible and fragile attachment lobes. Thickened antero-ventral shield area small to moderate in size. Hyperparasitic on sacculinid rhizocephalans or parasitizing crab hosts.

Cryptoniscus (described only for *D. curvata* and *D. hapalocarcini*): Body tear-drop shaped, cuticular surface smooth. Eyes with irregular pigment most prominent around medially directed edge. Antennule of 3 articles, first (basal) article smooth, anterior margin smooth, posterior margin and surface smooth, article 2 triangular, article 3 with 2 flagella and bundle of aesthetascs. Antennae of 9 articles (4 peduncular and 5 flagellar), flagellar articles much narrower than peduncular articles. Pereomeres with entire (not toothed) quadrangular coxal plates 1–7. Pereopods 1 and 2 subequal in size, gnathopodal with dactyli entire (non-bifid). Pereopods 3–5 ambulatory, smooth. Pereopod 6 of 4 segments; basis elongate, broadening distally, ischium quadrangular, approximately 1/3 length of basis, merus about 1/4 size of ischium, fourth segment (fused dactylus and propodus?) long and slender, tapering toward tip, approximately as long as ischium and basis combined. Pereopod 7 of 4 segments, basis similar in shape to that of pereopod 6 but smaller; ischium short, subquadrate; carpus small and cylindrical; terminal segment elongate, undivided, tapering to distal tip, recurved at tip.

Remarks. The species are listed in chronological order of description and the list contains all taxa currently or formerly placed in *Danalia*, with reference to their current status. Females of *Danalia* spp. differ from those of *Zeuxokoma* in being strongly recurved whereas those of *Zeuxokoma* are linear. Females of *Danalia* spp. can be distinguished from those of *Avada* n. gen. in that those of *Danalia* present two elongate lobes with a large gap between them on the ventral side whereas those of *Avada* n. gen. have short irregular lobes with little to no gap between them. Females of *Danalia* have very soft, flexible attachment hooks that are easily broken while those of *Zeuxokoma* and *Avada* n. gen. have strongly sclerotized hooks. The cryptoniscus larvae of *Danalia* spp. have a smooth antennular segment 1, a 4-segmented pereopod 6 with the terminal segment being approximately as long as the basis and ischium combined and pereopod 7 with the terminal segment entire. This contrasts with the cryptoniscus larvae of *Avada* spp. that have a toothed antennular segment 1, a 3-segmented pereopod 6 with the terminal segment being much longer than the basis and ischium combined and pereopod 7 with the terminal segment bifid.

***Danalia porcellanae* (Kossmann, 1872)**

Remarks: See *Avada porcellanae* n. comb., below.

***Danalia larvaeformis* (Giard, 1874)**

Cryptoniscus larvaeformis Giard, 1874: 243; Delage, 1884: 665; Giard, 1887: 48–49; Stebbing, 1893: 403; Grygier, 1993: 187, 190, 192.

Danalia larvaeformis:—Giard, 1887: 50-51; Bonnier, 1900: 197, 384; Richard, 1900: 73; Caullery, 1908: 589; Wimpenny, 1927: 6; Bourdon, 1963: 423; Altes, 1982: 27; Grygier, 1993: 188.

Danalia larvae-formis (sic) Fize, 1956: 27.

Type host and locality:—Unknown number of female and cryptoniscus syntypes from *Sacculina carcini* Thompson, 1836 (Sacculinidae) infesting *Carcinus maenas* (Linnaeus, 1758) (originally as *Cancer maenas*) (Portunidae) from the coast of Bretagne, France (Atlantic).

Other hosts and localities. Same host rhizocephalan and crab from Roscoff, France (Bourdon, 1963; Øksnebjerg, 2000).

Forms known. Female and cryptoniscus.

Material examined. None.

Remarks. The original description leaves much to be desired in terms of characters that would distinguish this species from any other in *Danalia*. Although subsequent collections have been made (Bourdon 1963), no specimen has ever been illustrated or described in detail.

Danalia curvata **(Fraisse, 1878)**

Fig. 1

Cryptoniscus curvatus Fraisse, 1878a: 257–269, 287, 291, pl. 12, figs. 4, 9, pl. 14, pl. 15, figs. 55, 56; Fraisse, 1878b: 434; Giard, 1887: 48–49; Grygier, 1993: 187, 190, 192.

Zeuxo curvata:—Kossmann, 1880: 125.

Danalia curvata:—Giard, 1887: 51; Stebbing, 1893: 403; Bonnier, 1900: 168, 197, 384; Giard, 1900: 73; Smith, 1906: 99-104, pl. 1, fig. 4, pl. 7, figs. 22-30; Caullery, 1908: 583, 589, 591, 596, 597, figs. A1–6, B1–7, C1–4, D1–4, E1–7, pl. 26, figs. 1–20; Lo Biaco, 1909: 593, 609; Wimpenny, 1927: 6; Fize, 1956: 27; Snodgrass, 1956: 50–52, fig. 19; Nielsen & Strömberg, 1965: 54; Altes, 1982: 28–29, fig. 3; Grygier, 1993: 188; Øksnebjerg, 2000: 72, fig. 3A.

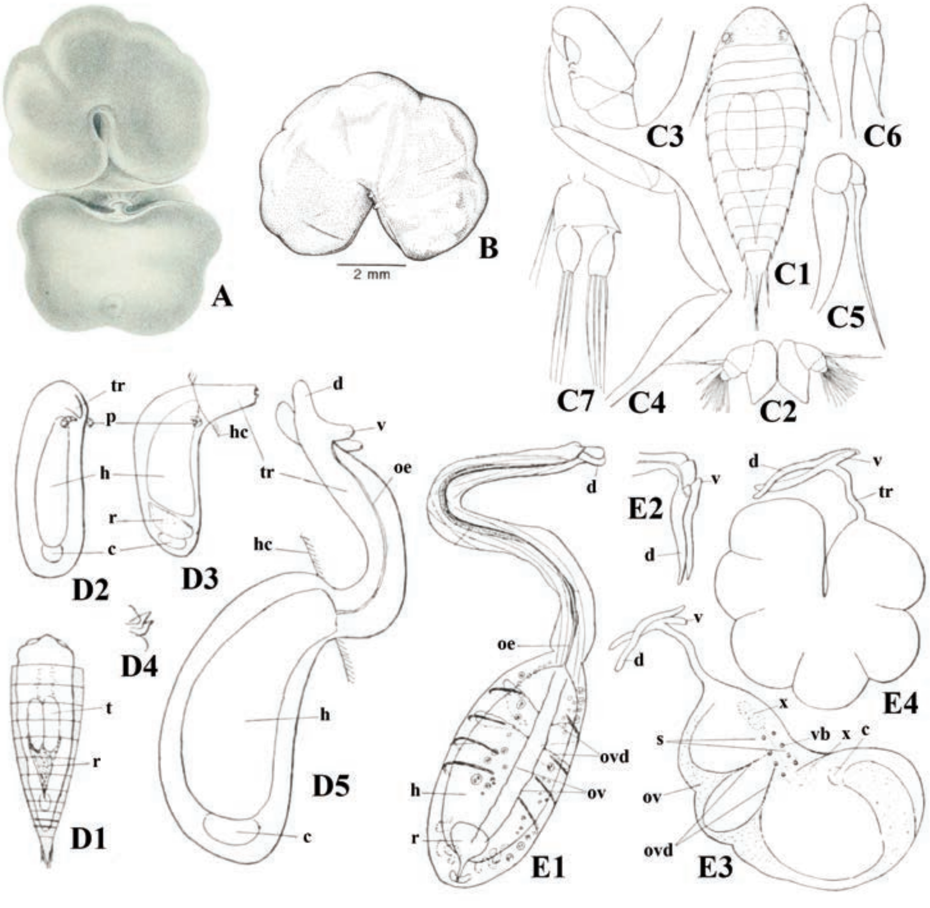


Figure 1. *Danalia curvata* Fraisse, 1878. **A**, female (upper) on host rhizocephalan (lower). **B**, female (hook and trunk lacking). **C**, cryptoniscus larva: C1, dorsal view, C2, antennules, C3, pereopod 2, C4, pereopod 4, C5, pereopod 6, C6, pereopod 7, C7, pleopod 5. **D**, metamorphosis of female from cryptoniscus: D1, molting of cryptoniscus to juvenile female, D2, D3, young females, D4, close up of trunk denticles (precursor to hooks), D5, more advanced female with trunk and hook development. **E**, anatomy of female: E1, dorsal view, E2, end of trunk with hooks, E3, nearly adult female but not yet recurved, E4, adult female in U-shape. c, heart; d, dorsal hooks of proboscis; h, liver; hc, host carapace; oe, esophagus; ov, ovary; ovd, oviducts; p, second pereopod; r, rectal bladder; s, longitudinal grooves of brood cavity; t, testes; tr, trunk; v, ventral hooks of proboscis; vb, ventral buds; x, holes in brood chamber. A from Fraisse, 1878; B from Øksnebjerg, 2000; C–E from Caullery, 1908. Not to scale.

Type host and locality. 20+ female and cryptoniscus syntypes from *Drepanorchis neglecta* (Fraisse, 1878) (originally as *Sacculina neglecta*) (Sacculinidae) infesting *Inachus communissimus* Rizza, 1839 (originally as *Inachus scorpio* Fabricius, 1798) (Inachidae) from Naples, Italy.

Other hosts and localities. Same rhizocephalan and decapod host, Naples and Sicily, Italy (Smith 1906, Caullery 1908, Øksnebjerg 2000).

Forms known. Female and cryptoniscus.

Material examined. 1 mature syntype female, 7.6 mm (RMNH CRUS.I.1389), infesting syntype of *Drepanorchis neglecta* (8.5 mm), Naples, Italy, date unknown, coll. P. Fraisse.

Remarks. *Danalia curvata* is by far the most completely described and illustrated of the species in the genus, primarily from the works of Fraisse (1878a) and Caullery (1908). Fraisse (1878a) was not exact in the number of specimens examined, but there were at least 20 adult females and numerous cryptonisci. Fraisse (1878a: pl. 14, fig. 32) did not illustrate pereopods 6 or 7 of the cryptoniscus larva (only 5 pairs shown), but Caullery (1908: fig. B5, B6, herein, figs. C5, C6) illustrated both. Grygier (1993) dated Fraisse's taxon from 1877, but that work was a dissertation not published in the sense of the ICZN (Fraisse 1877). *Danalia curvata* was made available from Fraisse (1878a), with a good description as well as illustrations.

The material examined here was originally in the collection of Hugo Frederik Nierstrasz (1872–1937) at the University of Utrecht but was transferred to Leiden in 1946 (*fide* L.B. Holthuis correspondence files in RMNH). The original label does not indicate type status but does identify the specimens as being collected by Fraisse, making their type status likely; later RMNH labels give the status as "?type" and "syntype." It is likely that several Mediterranean species of *Danalia* are synonymous with *D. curvata*, but larval and molecular characters are needed to make this determination.

Danalia longicollis (Kossmann, 1880)

Fig. 2A

Zeuxo longicollis Kossmann, 1880: 124–125, pl. 11, figs. 8–9; Giard, 1887: 49.

Danalia longicollis:—Giard, 1887: 51; Bonnier, 1900: 198, 384; Richard, 1900: 73; Caullery, 1908: 589; Wimpenny, 1927: 6; Fize, 1956: 27; Altes, 1982: 28; Grygier, 1993: 187–188, 190, 192.

Type host and locality. 3 female syntypes from *Sacculina* sp. (probably *S. leptodiae* Guérin-Ganivet, 1911) (Sacculinidae) infesting *Leptodius exaratus* (H. Milne Edwards, 1834) (originally as *Chlorodius* (*Leptodius*) *exaratus*) (Xanthidae) from the Red Sea.

Other hosts and localities. None.

Forms known. Female only.

Material examined. None.

Remarks. This species is poorly described and no characters are given that would distinguish it from others in the genus but it is the only *Danalia* known from the Red Sea. Although the host rhizocephalan was not identified to species in Kossmann (1880), it is likely *Sacculina leptodiae* Guérin-Ganivet, 1911, as that is the only rhizocephalan known from *Leptodius exaratus* in the Red Sea (Boschma 1955).

Danalia dohrnii Giard, 1887

Fig. 2B

Cryptoniscus curvatus Fraisse, 1878a: 293, pl. 12, fig. 12 (not *Cryptoniscus curvatus* Fraisse, 1878).
Danalia Dohrnii Giard, 1887: 54; Caullery, 1908: 589, 593.
Danalia dorhni:—Giard & Bonnier, 1890: 391; Stebbing, 1893: 403; Bonnier, 1900: 197, 384; Richard, 1900: 73; Altes, 1982: 27; Øksnebjerg, 2000: 59.
Danalia dohrnii:—Caullery, 1908: 593; Grygier, 1993: 188, 190, 192.
Danalia Dohrni:—Wimpenny, 1927: 6; Fize, 1956: 27.

Type host and locality. 3 female syntypes from *Sacculina benedeni* Kossmann, 1872 (a probable synonym of *S. carcini* Thompson, 1836) (Sacculinidae) infesting *Pachygrapsus marmoratus* (Fabricius, 1787) (originally as *Grapsus varius* Latreille, 1803) (Grapsidae) from Naples, Italy.

Other hosts and localities. None.

Forms known. Female only.

Material examined. None.

Remarks. This species was erected by Giard (1887), who made the name available by indication through reference to the figure of Fraisse (1878a) that illustrated three very immature female specimens on a single host rhizocephalan (Fig. 2B, herein). There was no description provided at that time or subsequently. Presumably, Giard (1887) considered this to be a new species on the basis of the different host choice (both rhizocephalan and crab), and perhaps also on the basis of the parasite occurring as multiples individuals on a single rhizocephalan, although this is also known for *D. curvata* (see Smith 1906: pl. 1, fig. 4). The correct original spelling of the species name is *dohrnii*, as given by Giard (1887; see also ICZN Articles 31.1.1 and 33.4).

Giard & Bonnier (1890) listed "*Danalia Dohrnii*" from "*Grapsisaccus Benedeni* Kossmann" (= *Sacculina benedeni* Kossmann, 1872) from the Gulf of Naples but without mentioning the identity of the associated decapod host. Bonnier (1900) listed the species as "*Danalia Dohrnii* Giard" infesting "*Sacculina Benedeni* Kossmann" from "*Pachygrapsus marmoratus* Fabricius" (= *Pachygrapsus marmoratus* (Fabricius, 1787) (Grapsidae) from Naples. The genus name *Grapsisaccus* must take the authorship of Giard & Bonnier (1890) with the type (and sole) species *Sacculina benedeni* Kossmann, 1872. *Grapsisaccus* is a synonym of *Sacculina* and *S. benedeni* is a synonym of *Sacculina carcini* Thompson, 1836.

Danalia pellucida Giard, 1887

Danalia pellucida Giard, 1887: 51; Bonnier, 1900: 198, 384; Richard, 1900: 73; Caullery, 1908: 589; Wimpenny, 1927: 6; Fize, 1956: 27; Altes, 1982: 27; Grygier, 1993: 188, 190, 192.

Type host and locality. Unspecified number of syntypes from *Sacculina triangularis* Anderson, 1862 (Sacculinidae) from *Cancer pagurus* Linnaeus, 1758 (Cancridae) from Penbrom and Croisic, France (Atlantic).

Other hosts and localities. None.

Forms known. Female only.

Material examined. None.

Remarks. This name was made available from Giard's (1887) meager description "les appendices terminaux sont de dimension inégales au lieu de former quatre lobes égaux comme chez les types étudiés par Kossmann" [= *Zeuxo porcellanae* and *Z. alphei*] [terminal appendages are of unequal

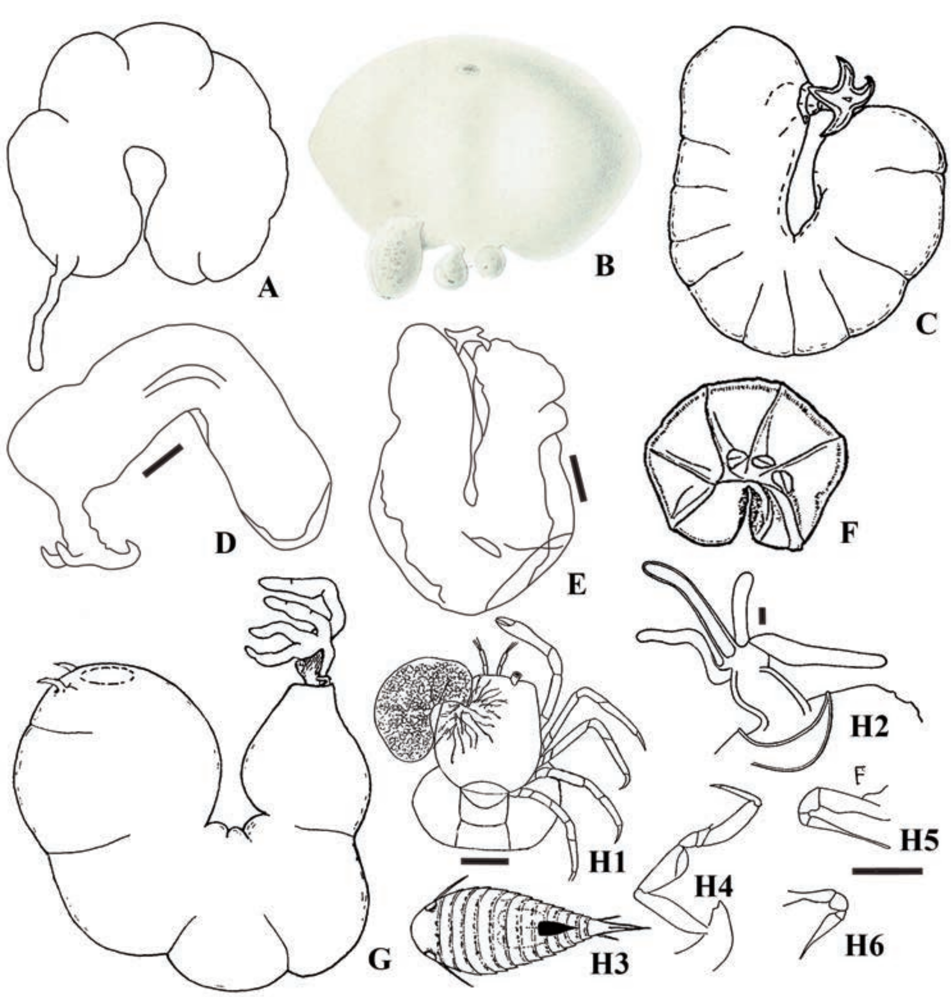


Figure 2. **A**, *Danalia longicollis* (Kossmann, 1872), attachment hook lacking. **B**, *Danalia dohrnii* (Giard, 1887), showing three individuals on a single *Sacculina benedeni* Kossmann, 1872, host. **C–E**, *Danalia ypsilon* Smith, 1906 with attachment hooks. **F**, *Danalia caulleryi* Nierstrasz & Brender à Brandis, 1923, attachment hooks lacking. **G**, *Danalia inopinata* Harant, 1925, with attachement hooks. **H**, *Danalia hapalocarcini* Fize, 1955: H1, adult female on host *Hapalocarcinus marsupialis* Stimpson, 1859; H2, close-up of attachment hooks; H3, cryptoniscus larva; H4–H6, cryptoniscus pereopods 4-6, respectively. A, from Kossmann, 1874; B, from Fraisse, 1878; C, from Altes, 1982; D, E, USNM 1251726; F, from Nierstrasz & Brender à Brandis, 1923; **G**, from Harant, 1925; H, from Fize, 1955. Scale = 0.1 mm (H2, H4–H6), 0.25 mm (D), 0.5 mm (E), 1 mm (H1) (rest not to scale).

size instead of forming four equal lobes as in the types studied by Kossmann]. This is the same character used by Giard (1887) to justify erecting the genus and there was no distinction made between *D. pellucida* and the other four taxa placed by Giard (1887) in *Danalia*; the species was not illustrated. Recollection from the type rhizocephalan host on *C. pagurus* is necessary to determine the status of the species. Although Giard (1887) used the characters of this species as the basis for erecting *Danalia*, Grygier (1993) wisely chose the more completely described *Cryptoniscus curvatus* as the type species, given the near complete lack of information about *D. pellucida*. The number of syntypes is unknown, but as the species was stated to occur at more than one location, there were at least two specimens.

Danalia lobiancoi Giard & Bonnier, 1890 (*nomen nudum*)

Danalia Lo Biancoi Giard & Bonnier, 1890: 391; Bonnier, 1900: 198, 384; Richard, 1900: 73.
Danalia Lobiancoi:—Wimpenny, 1927: 6.
Danalia lobiancoi:—Fize, 1956: 27; Altes, 1982: 27; Grygier, 1993: 189-190.

Remarks. Giard & Bonnier (1890) listed "*Danalia Lo Biancoi*" from "*Portunascus corrugatus* Gd" from the Gulf of Naples but without mentioning the identity of the associated decapod host. Bonnier (1900) listed the species as "*Danalia Lo Biancoi* Giard" infesting "*Sacculina corrugatus* Giard" from "*Portunus corrugatus* Leach" [= *Liocarcinus corrugatus* (Pennant, 1777)] (Polybiidae) from Naples. As there was no description or indication of either the cryptoniscid or the rhizocephalan host at that time (or at any time subsequently), the names of the species *lobiancoi* (emended, see Grygier 1993) and *corrugatus*, as well as the nominal genus *Portunascus* are all *nomina nuda*. Boschma (1937, 1955) suggested that *Portunascus corrugatus* is probably a synonym of *Sacculina carcini* (Sacculinidae). If true, then this parasite is probably identical to either *D. larvaeformis* or *D. dohrnii* (also known from Naples) or perhaps all three are synonymous, but those two species are poorly described. Topotypic collections from type hosts are needed.

Danalia ypsilon Smith, 1906

Figs. 2C–E

"sacculinée" A. Milne Edwards & Bouvier, 1900: 278.
Danalia ypsilon Smith, 1906: 100, pl. 7, fig. 32: Caullery, 1908: 589, 594; Guérin-Ganivet, 1911: 74; Wimpenny, 1927: 1–7, figs. 1–3; Veillet, 1942: 1–4; Veillet, 1945: 194–196, 303, 319–325, 336, figs. 30–31; Fize, 1956: 27; Boschma, 1958: 34; Altes, 1982: 23, 25–26, 28–29; Grygier, 1993: 189–190; Øksnebjerg, 2000: 48.
Danalia gypsilon (sic) Altes, 1982: fig. 4.2.

Type host and locality. Female holotype from *Galathea dispersa* Bate, 1859 (Galatheidae) from unspecified locality [Naples].

Other hosts and localities. Infesting *G. dispersa* from Naples (Smith 1906, Øksnebjerg 2000) and Beaulieu-sur-Mer, France (Mediterranean) (Wimpenny 1927); infesting *Galathea intermedia* Lilljeborg, 1851 from Cape Verde (A. Milne Edwards & Bouvier 1900) and Sète, France (Mediterranean) (Veillet 1942); infesting *Galathea bolivari* Zariquiey Álvarez, 1950; Bay of Cadaqués, Spain (herein).

Forms known. Female (described), cryptoniscus (undescribed, see Veillet 1942).

Material examined. 3 mature females, 3.9-4.0 mm (USNM 1251726), infesting *G. intermedia* (4.6 mm CL), one per host, St. SL8, Cape Verde Islands, 17 June 2011, coll. unknown; 1 mature female (6.7 mm) (RMNH CRUS.I.1737), infesting *G. bolivari* (9.1 mm CL), Bay of Cadaqués, Spain, 3–17 Aug 1950, coll. L.B. Holthuis.

Remarks. Smith (1906) did not provide any description for this species, only an illustration, and the type series only includes the single specimen illustrated. Wimpenny (1927) described the female form from two specimens and provided illustrations. Veillet (1942) discussed the mode of parasitism of this species and an associated rhizocephalan, *Lernaeodiscus galatheae* [now *Triangulus galatheae* (Norman & Scott, 1906); see Boyko & Harvey 2000] on a galatheid host. The new material examined in this study confirms the presence of the species in Cape Verde, as originally reported [erroneously as a "sacculinée" by A. Milne Edwards & Bouvier (1900); see Guérin-Ganivet 1911]. Although the species occurs in both the Lusitania and Tropical East Atlantic (TEA) Provinces (cf. Briggs & Bowen 2012), there are other known instances of crustaceans with a primarily Lusitanian distribution [e.g., *Albunea carabus* (Linnaeus, 1758), *Scyllarus pygmaeus* (Bate, 1888)] that also occur in the TEA.

The specimens from Cape Verde Island were all attached to the thin ventral cuticle of the ventral third pleomere of each host. The Spanish specimen is attached on the ventral surface at the junction of the third and fourth pleomeres. The body of *D. ypsilon* is strongly recurved and with less developed external lobes than seen in most of the species of *Danalia* where this character is known (e.g., *D. curvata*, *D. longicollis*, *D. inopinata*).

***Danalia gregaria* Caullery, 1908**

Danalia gregaria Caullery, 1908: 593, 589, 597; Lo Bianco, 1909: 607; Wimpenny, 1927: 6; Fize, 1956: 27; Nielsen & Strömberg, 1965: 53; Altes, 1982: 27; Grygier, 1993: 189–190, 192; Øksnebjerg, 2000: 65.

Type host and locality. 11 female and 8 male syntypes from *Sacculina goneplaxae* Guérin-Ganivet, 1911 (originally as *Sacculina* sp.) (Sacculinidae) infesting *Goneplax rhomboides* (Linnaeus, 1758) (Goneplacidae) from Naples, Italy.

Other hosts and localities. None.

Forms known. Female and cryptoniscus.

Material examined. None.

Remarks. Caullery (1908) stated that he could not find any differences between the cryptonisci of *D. curvata* and *D. gregaria*, nor were any characters of the females consistently different between the two species. In fact, Caullery (1908) specifically stated he was following "la règle de Giard," that states each host bears a different species of parasite. Given the fact that both *D. curvata* and *D. gregaria* are known from multiple specimens on their rhizocephalan hosts (though they are different host species) from the same locality (Naples) and lacking any morphological grounds for separating them, the two species are likely to be synonyms. However, a more detailed study of topotypic material of *D. gregaria* from the type host is needed before taking such action.

***Danalia caulleryi* Nierstrasz & Brender à Brandis, 1923**

Fig. 2F

Danalia caulleryi Nierstrasz & Brender à Brandis, 1923: 62, pl. 4, fig. 1, pl. 9, figs. 35a–b; Altes, 1982: 28; Grygier, 1993: 189–190.
Danalia Caulleryi:—Wimpenny, 1927: 6.
Danalia caullery (sic) Fize, 1956: 27; Nielsen & Strömberg, 1965: 53.

Type host and locality. Female holotype from *Galathea australiensis* Stimpson, 1858 (Galatheidae) from Banda ("Paternoster-Inseln"), Indonesia.

Other hosts and localities. None.

Forms known. Female only.

Material examined. Holotype female (ZMA CRUS.I.100624), 8.2 mm, ex *Galathea australiensis* (not in jar), Stn. 37, 27 m, dredge, coral and coral sand, close to reef, Sailus Ketjil, Paternoster Islands, Flores Sea, 30–31 March 1899, coll. Siboga Expedition.

Remarks. The female holotype (and only known specimen) of *D. caulleryi* superficially resembles the general morphology of *D. curvata* (e.g., Fraisse 1878a: pl. 14, fig. 39; Øksnebjerg 2000: fig. 3A), but shows external segmentation and plate development similar to that seen in species of *Cabirops* Kossmann, 1884. Nierstrasz & Brender à Brandis (1923) noted that the attachment portion of the holotype could not be found, but direct observation of the holotype shows that some kind of attachment process was present but was broken off (presumably when the specimen was removed from the host), which all *Cabirops* species (brood chamber parasites of isopods) lack. Based on the morphology, this species is not a *Cabirops* but probably not a *Danalia* either. However, because the only known specimen is lacking the attachment process, its proper placement cannot be determined without additional material.

Danalia fraissei **Nierstrasz & Brender à Brandis, 1925 (=** ***Cabirops fraissei*****)**

Danalia fraissei Nierstrasz & Brender à Brandis, 1925: 1–2, 7, pl. 1, figs. 1–6.
Cabirops fraissei — Boyko, 2013: 107 (complete synonymy), 112, fig. 3.

Material examined. Syntype female (RMNH CRUS.I.1390), 1.87 mm, ex "*Ergyne rissoi*" Nierstrasz & Brender à Brandis, 1925 [= *Cancricepon choprae* (Nierstrasz & Brender à Brandis, 1925)] (not in jar) ex *Domecia acanthophora* Desbonne, 1867 (not in jar), Caracas Bay, Curaçao, 7 April 1920, coll. C.J. van der Horst.

Remarks. Now placed in *Cabirops* (Cryptoniscoidea: Cabiropidae) (see Boyko 2013). The syntype female was originally in the collection of Hugo Frederik Nierstrasz (1872–1937) at the University of Utrecht but was transferred to Leiden in 1946 (*fide* L.B. Holthuis correspondence files in RMNH). The original label does not indicate type status but as there was only a single female described by Nierstrasz & Brender à Brandis (1925), this must be the female syntype. Later RMNH labels give the status as "type?" and "syntypes" but the cryptoniscus syntype is lost (the only other isopod in the jar is, inexplicably, a terrestrial isopod). The host brachyuran is given on the label as *Domecia acanthophora* but was cited by Nierstrasz & Brender à Brandis (1925) as *D. hispida* Eydoux & Souleyet, 1842. Guinot (1964) determined that *D. hispida* is a strictly Pacific species.

Danalia inopinata **Harant, 1925**

Fig. 2G

Danalia inopinata Harant, 1925: 1–3, unnumbered figure; Wimpenny, 1927: 6; Harant, 1931: 373; Fize, 1956; 27; Nielsen & Strömberg, 1973: 88; Altes, 1982: 27–28, fig 4.1; Grygier, 1993: 189–190; Øksnebjerg, 2000: 60.

Type host and locality. Female holotype from *Sacculina* sp. (probably *S. gerbei* Guérin-Ganivet, 1911, see Øksnebjerg 2000) (Sacculinidae), infesting *Pilumnus hirtellus* (Linnaeus, 1761) (Pilumnidae), from Sète, France (Mediterranean).

Other hosts and localities. *Sacculina gerbei* infesting *Pilumnus spinifer* H. Milne Edwards, 1834 from Baie de Banyuls, France (Mediterranean), 3 m depth (see below).

Forms known. Female only.

Material examined. None.

Remarks. The name of the host rhizocephalan was given by Harant (1925) only as "*Sacculina* sp."; its identity is inferred from the fact that the only *Sacculina* known from *Pilumnus hirtellus* is *S. gerbei*. However, the authorship of *S. gerbei* is not "Giard, 1887" (per Guérin-Ganivet 1911), "Bonnier, 1887" (per Boschma 1955), nor even "Giard *in* Bonnier, 1887" (per Øksnebjerg 2000). Bonnier (1887) merely listed the name as "*Sacculina Gerbei* Giard" without any description, illustration or indication; the name is therefore not available from Bonnier (1887). The first person to use the name and provide a description and illustration, thereby making the name available, was Guérin-Ganivet (1911). I have seen a good quality photograph of *D. inopinata* on the DORIS website (http://doris.ffessm.fr) showing *D. inopinata* parasitizing the same rhizocephalan (*S. gerbei*) but from a new crab host (*P. spinifer*). It can be distinguished from the other well-described species of *Danalia* by its posterior end being markedly more swollen than the anterior and bearing two hook-like structures.

***Danalia* sp. Utinomi, 1944**

"Parasite" Utinomi, 1944: 696–697, fig. 4.

Host and locality. Three females from *Pseudocryptochirus viridis* Hiro, 1938 (Cryptochiridae) (one host with two parasites) from Japan.

Other hosts and localities. None.

Form known. Female.

Material examined. None.

Remarks. Utinomi (1944) remarked on the similarity of these specimens to the parasitic "copepod" *Faba*, but noted they were "not quite the same." The recurved body and external lobes place these specimens in *Danalia*.

***Danalia hapalocarcini* Fize, 1955**

Fig. 2H

Danalia hapalocarcini Fize, 1955: 2444–2447, figs. 1-4; Fize, 1956: 22–28, figs. 15–18; Altes, 1982: 28–29; Grygier, 1993: 189–190.

Type host and locality. One female and three cryptoniscus syntypes from *Hapalocarcinus marsupialis* Stimpson, 1859 (Cryptochiridae) from Nhatrang, Vietnam.

Other hosts and localities. None.

Forms known. Female and cryptoniscus.

Material examined. None.

Remarks. Despite the unusual insertion of the female parasite into the dorsal carapace of the host crab, this species is clearly a *Danalia*. The female shows the characteristic U-shape and bears a 4-pronged attachment processes (Fig. 2H2); the cryptoniscid has the dactyli of pereopods 6 and 7 (Figs. 2H5, 2H6) elongate and tapering and very similar in shape and proportion to those seen in *D. curvata*.

***Danalia* sp. Øksnebjerg, 2000**

"?*Danalia* sp." Øksnebjerg, 2000: 67.

Host and locality. Four females from one host specimen *Sacculina zariquieyi* Boschma, 1947 (Sacculinidae) infesting *Monodaeus couchii* (Couch, 1851) (Xanthidae) from Turkey (Aegean Sea).

Other hosts and localities. None.

Form known. Female.

Material examined. None.

Remarks. Although these parasitic isopods were only provisionally identified by Øksnebjerg (2000), the host choice strongly suggests they belong to *Danalia*. As there are no other records of *Danalia* from the Aegean Sea, Turkey, or the host rhizocephalan, their identity is unknown.

Zeuxokoma Grygier, 1993

Zeuxo Kossmann, 1872: 332–333 (junior homonym of *Zeuxo* Templeton, 1840: 203 [Crustacea: Tanaidacea]). Type species: *Zeuxo alphei* Kossmann, 1872, by subsequent designation of Grygier (1993).

Zeuxokoma Zimmer, 1927: 763; Neave, 1940: 700 (unavailable).

Faba Nierstrasz & Brender à Brandis, 1930: 1–2 (junior homonym of *Faba* Fischer, 1883: 602 [Mollusca]). Type species: *Faba setosa* Nierstrasz & Brender à Brandis, 1930, by original designation.

Zeuxokoma Grygier, 1993: 190, 193 (new replacement name for *Zeuxo*). Type species: *Zeuxo alphei* Kossmann, 1872, automatic.

Other described species. *Z. setosa* (Nierstrasz & Brender à Brandis, 1930), **n**. **comb**., *Z. glabra* (Nierstrasz & Brender à Brandis, 1930), **n**. **comb**., *Z. luetzeni* (Høeg & Bruce, 1988), **n**. **comb**., *Z. musaeformis,* **n**. **sp**., *Z. elongata,* **n**. **sp**.

Diagnosis. Female: Elongate relatively linear smooth sac with pronounced thickened anteroventral shield; internal subdivisions present in mature females but external lobes lacking; trunk short relative to body with 4 stout strongly sclerotized attachment hooks. Parasitizing shrimp hosts directly. Cryptoniscus unknown.

Remarks. Although Grygier (1993) stated only that he was designating *Zeuxo alphei* as the type species of *Zeuxokoma*, he was also designating it as the type species of *Zeuxo* Kossmann *non* Templeton, which was replaced by *Zeuxokoma*, as per ICZN Article 67.8. Nierstrasz & Brender à Brandis (1930) made the puzzling statement that "the embryos of *F. glabra* certainly are those of copepods; and no doubt *Faba* belongs to the Epicaridea," but the mention of copepods was clearly a lapsus for isopods, possibly caused by a poor translation from the original German to English (this was their only paper published in English). That this was an error is confirmed by SEM study of embryos extracted from a *Z. glabra* female (see below).

Females of *Zeuxokoma* spp. differ from those of *Danalia and Avada,* n. gen. in being mature in a relatively linear sac shape, whereas those of *Danalia* and *Avada,* n. gen. are recurved. The attachment hooks of females of *Zeuxokoma* are strongly scleratized and similar to those of *Avada,* n. gen., but very different from the soft, flexible attachment hooks of *Danalia*.

Zeuxokoma alphei (Kossmann, 1872)

Fig. 3A

Zeuxo alphei Kossmann, 1872: 333, pl. 18, fig. 11; Kossmann, 1874: 134, pl. 7, fig. 11; Bonnier, 1900: 196, 198, 384, fig. 32a; Richard, 1900: 73; Grygier, 1993: 188–190, 192–193.

Danalia (*Zeuxo*) *alphei*:—Wimpenny, 1927: 6; Fize, 1956; 27; Grygier, 1993: 188.

Faba alphaei (sic):—Altes, 1982: 21, 30.

Type host and locality. Holotype female from "*Alpheus*" sp. (Alpheidae), Philippines.

Other hosts and localities. None.

Forms known. Female only.

Material examined. None.

Remarks. Although Kossmann (1872) gave the host as *Alpheus* sp., it is unidentifiable beyond Alpheidae. Attempts to locate the type specimen were unsuccessful and it is probably lost; recollection of topotypic material is needed to settle the specific identity of the species. Based on the shape of the holotype, the host choice, and locality, it is possible that *Z. alphei* is identical with *Z. glabra* and/or *Z. luetzeni*. However, the insertion point (in the region of the mouthparts) is unusual and the shape of the body is very elongate while being more curved than seen in other *Zeuxokoma* specimens.

Despite Grygier's (1993) selection of *Zeuxo alphei* as the type species of *Zeuxokoma* (and, automatically, the type species of *Zeuxo* Kossmann *non* Templeton), the combination *Zeuxokoma alphei* does not appear anywhere in Grygier's work.

***Zeuxokoma* sp. van Kampen & Boschma, 1925**

Thompsonia sp. van Kampen & Boschma, 1925: 58–59, pl. 1, fig. 31, text fig. 44; Høeg & Lützen, 1993: 369.

Host and locality. Female from *Alpheus malleodigitus* (Spence Bate 1888) (Alpheidae), 15 m), Sulu Archipelago, Philippines.

Other hosts and localities. None.

Forms known. Female only.

Material examined. None.

Remarks. Høeg & Lützen (1993) first suggested that this record of a "rhizocephalan" actually belonged to the genus *Faba* (now *Zeuxokoma*). The figures given by van Kampen & Boschma (1925) do not resemble any of the described species of *Zeuxokoma* and it may be an undescribed species, although possibly not belonging to this genus based on the semispherical shape of the body.

***Zeuxokoma setosa* (Nierstrasz & Brender à Brandis, 1930), n. comb.**

Fig. 3B

Faba setosa Nierstrasz & Brender à Brandis, 1930: 2–3, figs. 1–5; Altes, 1982: 30; Grygier, 1993: 190.

Type host and locality.—Holotype female from *Spirontocaris holmesi* Holthuis, 1947 (originally as *S. bispinosa* Holmes, 1900) (Hippolytidae), 167 fathoms (= 305.4 m), off central California, USA.

Other hosts and localities. None.

Forms known. Female only.

Material examined. Holotype female (USNM 62732), 7.3 mm, ex *Spirontocaris holmesi* Holthuis, 1947 (8 mm CL), 167 fms (= 305.4 m), 38°17'N, 123°29'W, Albatross Station 3170, off central California, USA.

Remarks. The female holotype is mature, as evidenced by embryos filling the sac. Very limited segmentation can be observed in this specimen and the anteroventral shield is very small (barely extending beyond the area where the trunk inserts into the body). Nierstrasz & Brender à Brandis (1930) described the species as having a row of six tubercles on the left side of the body and in having the body sparsely set with long setae. However, examination of the "tubercles" (Fig. 3B2) shows them to be nothing more than larger embryos placed close to the inner surface of the transparent cuticle. The "setae" (Fig. 3B5) are not a part of the organism, and are inserted into the cuticle with the tapered end pointing into the body of the specimen. The "setae" are actually foreign matter embedded in the holotype, probably during capture with the host. They appear quite similar to glass sponge (Porifera: Hexactinellida) spicules. Despite this "loss" of characters, this species is still easily distin-

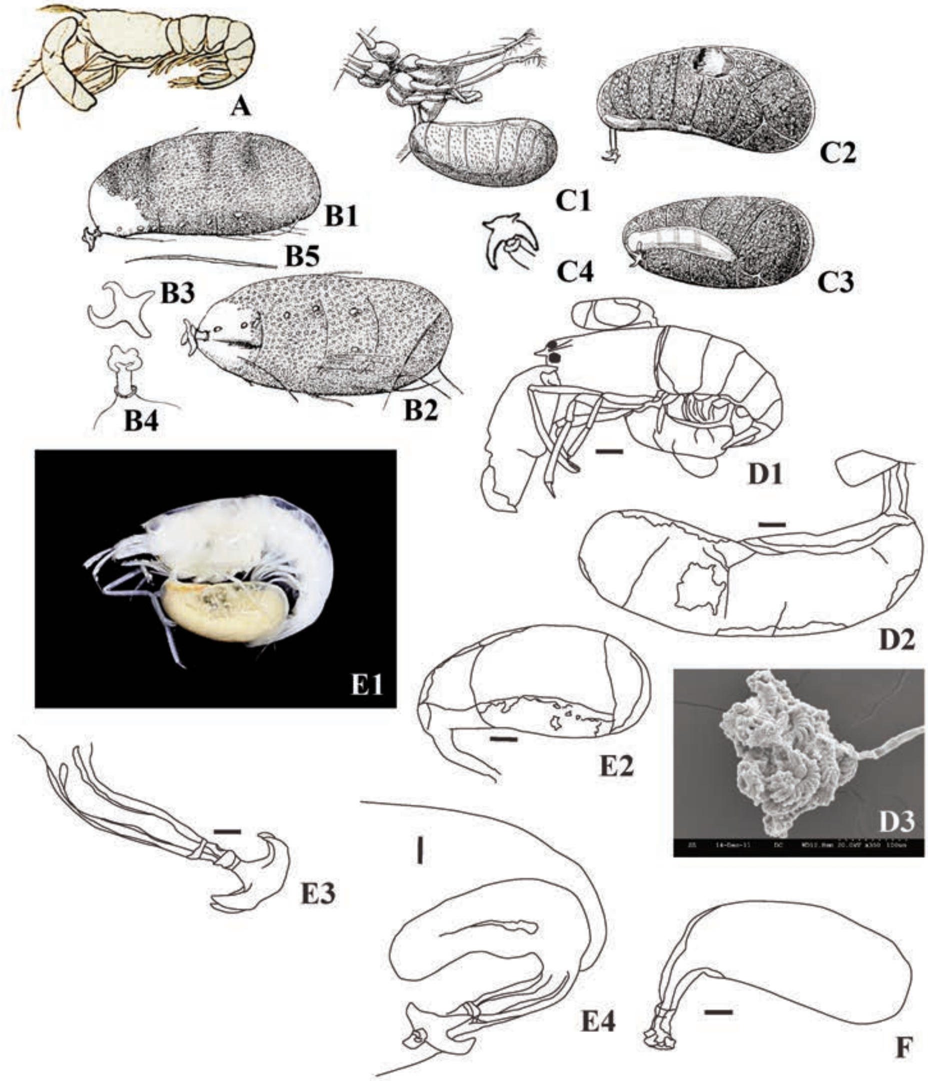


Figure 3. **A**, *Zeuxokoma alphei* (Kossmann, 1872) on alpheid host. **B**, *Zeuxokoma setosa* (Nierstrasz & Brender à Brandis, 1930): B1, adult female holotype, lateral view; B2, same, ventral view; B3, attachment hooks, head-on view; B4, attachment hooks and stalk, lateral view; B5, "seta" (= sponge spicule?). **C–E**, *Zeuxokoma glabra* (Nierstrasz & Brender à Brandis, 1930): C1, adult female holotype showing insertion on ventral abdomen of alpheid host; C2, same, lateral view; C3, same, ventral view; C4, attachment hooks, lateral view; D1, three females attached to one *Alpheus lobidens* De Haan, 1849; D2, adult female, lateral view; D3, embryos from female; E1, adult female and alpheid host; E2, same, lateral view; E3, same, attachment hooks and trunk, lateral view; E4, same, ventral view. **F**, *Zeuxokoma luetzeni* (Høeg & Bruce, 1988), holotype female. A, from Kossmann, 1874; B, from Nierstrasz & Brender à Brandis, 1930; C, from Nierstrasz & Brender à Brandis, 1930; D3, BPBM S15989; E, UF 20176; F, NTM CR 005275. Scale = 0.1 mm (D3), 0.2 mm (E3), 0.25 mm (E4, F), 0.5 mm (D2), 0.625 mm (E2), 1.43 mm (D1) (rest not to scale).

guished from the others in the genus by the small shield located circumanteriorly, the compact, bean-shaped body, and the very short attachment stalk. It is the only *Zeuxokoma* known from a hippolytid host and the only one known from the west coast of North or South America.

***Zeuxokoma glabra* (Nierstrasz & Brender à Brandis, 1930), n. comb.**

Figs. 3C–E

Faba glabra Nierstrasz & Brender à Brandis, 1930: 3–4, figs. 6–11; Altes, 1982: 30; Grygier, 1993: 190.

Holotype host and locality. Holotype female on unidentified alpheid shrimp (originally as *Crangon* sp.), Waikīkī reef, Honolulu, O‘ahu, Hawai‘i, USA.

Other hosts and localities. *Alpheus lobidens* De Haan, 1849, Hawaii Institute of Marine Biology reef flat, Kāne‘ohe Bay, O‘ahu, Hawai‘i, USA; *Alpheus* sp. (Alpheidae), Moorea, Society Islands, French Polynesia.

Forms known. Female only.

Material examined. Female holotype (RMNH CRUS.I.1373) (5.6 mm) from *Alpheus* sp. (4.5 mm CL), Waikīkī reef, Honolulu, O‘ahu, Hawai‘i, USA, coll. C. H. Edmondson; 1 ovigerous female (6.3 mm) plus two other mature females (5.0, 4.3 mm) from *Alpheus lobidens* De Haan, 1849 (6.7 mm CL), Hawaii Institute of Marine Biology reef flat, Kāne‘ohe Bay, O‘ahu, Hawai‘i, USA, 29 March 1979, coll. W.J. Cooke (BPBM S15989);1 mature female (5.8 mm) from *Alpheus* sp. (damaged, sex indeterminate, 4.5 mm CL, UF 20175), Papetoai, Moorea, outer slope in *Pocillopora eydouxi* Milne Edwards & Haim, 1860, rubble, 6 m, Society Islands, French Polynesia, 18 May 2009, coll. M. Leray (UF 20176).

Redescription. Mature female: 4.3–6.3 mm long; elongate, widening distally, slightly recurved; surface smooth, without lobes; internal segmentation visible through cuticle; shield approximately 1/2 length of body, restricted to anteroventral region. Trunk moderately long (approximately 1/2 anteroventral shield length) and inserted into body at ca. 90° angle, 4 recurved attachment lobes. Directly parasitizing alpheid shrimp host.

Remarks. The holotype was long considered lost (L. Eldredge, pers. comm.) and, given the difficulty in identifying species in this family, one of the newly reported specimens of Hawaiian material cited here was going to be designated as a neotype. However, the holotype was located in the RMNH in June 2014. Although the species was stated to have its “type in the Bishop Museum” (Nierstrasz & Brender à Brandis 1930), Nierstrasz never actually sent the specimen to the Bishop Museum and, in 1946, it was transferred along with his other Utrecht collections to the RMNH (*fide* L.B. Holthuis correspondence files in RMNH). This species may be identical with *Z. alphei*, but that species is poorly described and illustrated and the holotype is lost, so this cannot be determined without topotypic material of Z. *alphei*. It may also be identical with *Z. luetzeni* and that also needs recollection. Molecular techniques will probably be necessary to determine if similar species (e.g., *Z. alphei*, *Z. luetzeni*) are synonymous with *Z. glabra*.

The attachment of the holotype to the host was ventrolateral to the left fifth pereopod (Fig. 3C1), whereas the French Polynesian specimen (Fig. 3E1) was attached at the base of the second pereopod on the right side of the host. The host of the newly reported Hawaiian material (Fig. 3D1) bears three mature female *Zeuxokoma* specimens: the largest was attached medioventrally between the pleopods on the fourth pleomere, the next largest was attached on the ventral surface of the pleuron of the first pleomere on the right side, and the smallest was attached high on the pleuron of the second pleomere on the right side. Although this host was infested by three female parasites, it still carried eggs; suggesting that the energy drain of infestation by cryptoniscoids did not result in parasitic castration.

Embryos (Fig. 3D3) from a 5.0 mm Hawaiian specimen possess characters typical of isopod embryos (cf. Boyko & Wolff 2014) and not characters of copepods, as per Nierstrasz & Brender à Brandis's (1930) erroneous statement.

Zeuxokoma luetzeni **(Høeg & Bruce, 1988), n. comb.**

Fig. 3F

Thompsonia luetzeni Høeg & Bruce, 1988: 246–249, figs. 1–3; Høeg & Lützen, 1993: 369.
"Thompsonia luetzeni… a parasitic isopod related to the genus *Faba*" Høeg & Rybakov, 1992: 606.
"Thompsonia luetzeni… an isopod related to *Faba*" Grygier, 1993: 191.
"*Thompsonia*" *luetzeni* Grygier, 1993: 193.

Type host and locality. Holotype female (NTM Cr005275) and paratype female from *Alpheus parvirostris* Dana, 1852 (Alpheidae), from colonies of *Galaxea fasicularis* (Linnaeus, 1767), 26°26'N, 127°43'E, Zanpa-Misaki, Okinawa, Ryukyu Islands, Japan.

Other hosts and localities. None.

Forms known. Female only.

Material examined. Holotype mature female, 2.4 mm, type locality and host (2.8 mm CL), 24 Oct 1984, coll. H. Yamashiro.

Remarks. The holotype is mature (contains embryos) and was found inserted ventrally in the sternite of the first pleomere of the host. Two parasitized hosts are known (each bearing one parasite, the holotype and paratype). Originally described as a rhizocephalan, this species has been recognized as a cryptoniscid isopod since it was mentioned as such by Høeg & Rybakov (1992), and was thought to be a *Faba* (now *Zeuxokoma*), as indicated by Grygier (1993). The present paper marks the formal transfer of the species into this isopod genus. Because the original description considered the parasite as a rhizocephalan, there were no comparisons to any species of cryptoniscoid isopods. Examination of the holotype shows no characters that could be used to differentiate it from *Z. glabra* but given the substantial geographic distance between type localities (Japan and Hawaii), it would be premature to synonymize the two taxa in the absence of cryptoniscus larval and/or molecular data.

***Zeuxokoma musaeformis*, n. sp.**

Fig. 4A

Danalia sp. Brinkmann, 1984: 211–213, figs. 4–8; Støve, 1985: 83, 85–87.
Danalia musaeformis (Brinkmann MS name) Støve, 1985: 85 (unpublished dissertation, unavailable name).

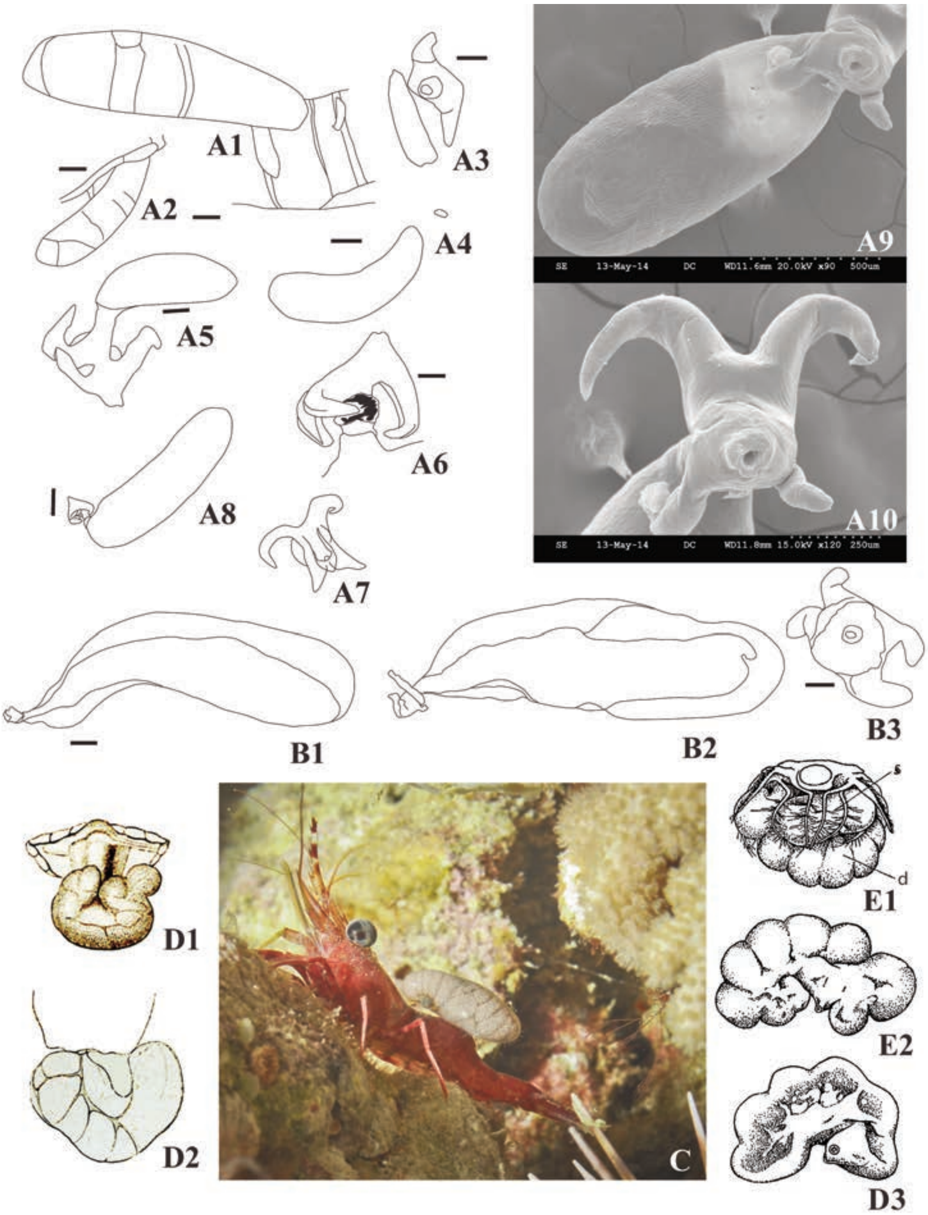
Type host and locality. *Pandalina profunda* Holthuis, 1946 (Pandalidae) from Herdlaosen, Herdla, Norway.

Other hosts and localities. None.

Forms known. Female only.

Etymology. From the Latin *musa* + *formis*, referring to the banana shape of the parasite. This is the name used by Brinkmann Sr. in his unpublished manuscript as cited by Støve (1985).

Material examined. Holotype mature female, 6.0 mm, infesting female *P. profunda* (7.0. mm CL), Herlaosen, Herdla, Norway, coll. A. Brinkmann, 28 Oct 1939 (UBZM 98208); 7 paratype immature and mature females, 3.6–9.0 mm (UBZM 63862) mm, infesting 3 female *P. profunda* (6.5–12.6 mm CL, one female with three parasites, one with two, one with one), same data as holotype; 5 paratype juvenile females, 0.6–2.6 mm (UBZM 98209), infesting *P. profunda* (no host in vial), Herdlaosen, Herdla, Norway, coll. A. Brinkmann, 25 July 1939; 1 female paratype, 5.4 mm (UBZM 98210), infesting *P. profunda* (no host in vial), Herdlaosen, Herdla, Norway, 14 July 1939, coll. A. Brinkmann; 1 female paratype, 1.6 mm (UBZM 64096), infesting *P. profunda* (no host in vial), Herdlaosen, Herdla, Norway, 10 Aug 1938, coll. A. Brinkmann; 2 mature females, 3.1–3.6 mm (UBZM 63857), infesting female *P. profunda* (carapace damaged), Herdlaosen, Herdla, Norway, 25 July 1939, coll. A. Brinkmann; 2 mature females, 3.9–8.3 mm (USNM 1251727), infesting two female *P. profunda* (one 8.7 mm CL, one posterior ½ of specimen only, Hardangerfjord, Norway, 12 Aug 2011, coll. C. Noever.



Description. Female: 0.6–9.0 mm long; mature females elongate, slightly widening distally, slightly recurved; surface smooth, without lobes, internal segmentation visible (Fig. 4A1); anteroventral shield small, confined to region around trunk (Fig. 4A9); 2 small ovate perforations in cuticle on either side of midline ventrally in shield region (Fig. 4A9). Trunk moderately extended, inserted into body at ca. 90° angle, with 4 recurved attachment lobes (Fig 4A10); mouth ovate with large anterior semicircular lip and small posterior subquadrate lip (Fig. 4A10). Found parasitic on pandalid shrimp.

Remarks. Brinkmann Jr. (1984) and Støve (1985) repeated the assertion of August Brinkmann Sr. (unpubl.) that this species of *Danalia* parasitizes *Sylon hippolytes* M. Sars, 1870, at its attachment point with the pandalid hosts and (presumably) then can be found on the pandalid host when the rhizocephalan dies. Examination of the present material does not support this hypothesis. No specimens of *Danalia musaeformis* n. sp. have been collected in conjunction with *Sylon* on pandalid hosts, and there is no evidence of prior *Sylon* parasitism on any of these *Danalia*-infested hosts. This species most closely resembles *Z. glabra* but does not have a well-developed anteroventral shield. Because Brinkmann, Sr. considered this species to belong to *Danalia* (in Brinkmann Jr. 1984), he only compared it to *D. curvata*; according to Brinkmann, Sr. (in Brinkmann Jr. 1984), mature females are ivory in color in life.

The small ovate perforations in the shield region (Fig. 4A9) are of unknown function and were not observed on specimens of other species in the genus. They may be oviductal pores (sensu Shiino 1952) but, if so, they are less numerous and concentrated in the shield region in *Zeuxokoma* compared to those seen in *Danalia* (compare Fig. 4A9 with Fig. 1E3). The shape of the shield region is similar to that seen in *Z. setosa*, being found surrounding the anterior region and not extended ventrally as seen in *Z. glabra*.

Three cryptoniscid larvae (ex UBZM 64096) were found among the material of *Z. musaeformis* from UBZM and it was hoped that these would allow the first description of larvae from this genus. Unfortunately, they all were cryptoniscid larvae of a bopyroid species (4 antennal flagellae, pereopods 6 and 7 not different from 5) not a cryptoniscoid (5 antennal flagellae, pereopods 6 and 7 different than 5). The antennules of the cryptoniscid larvae are identical to those illustrated and described by Hansen (1916: 203–205, pl. 15, figs. 11a–d) for *Bopyroides hippolytes* (Krøyer, 1838) and differ from those of *B. cluthae* (Scott, 1902) as described and figured by Bourdon (1968). This appears to the first record of *B. hippolytes* on *Pandalina profunda*, while *B. cluthae* (Scott, 1902) is known from *P. brevirostris*.

Figure 4. **A**, *Zeuxokoma musaeformis* n. sp.: A1, adult female showing attachment to *Pandalina profunda* Holthuis, 1949; A2, another adult female and host pleopod; A3, immature female partially developed attachment hooks (body, left, detached from head, right); A4, adult female (left) and very immature female (right, as small dot), showing size variation during development; A5, immature female showing large attachment hooks relative to small body; A6, close up of attachment hooks, lateral view; A7, close up of attachment hooks, anterior view; A8, adult female, lateral view. A9, immature female, arrow indicating ovate perforations in shield region. A10, same, close up of head region. **B**, *Zeuxokoma elongata* n. sp.: B1, adult female paratype. Lateral view; B2, adult female holotype, lateral view; B3, close up of attachment hooks, head-on view. **C**, *Zeuxokoma* sp. on *Cinetorhynchus hendersoni* (Kemp, 1925). **D**, *Avada porcellanae* (Kossmann, 1872): D1, adult female with porcelain crab abdomen, external lateral view; D2, another adult female and porcelain crab abdomen, external lateral view. D3, adult female from Japan, internal lateral view. E, *Avada* sp. (Shiino, 1952): E1, adult female (d), external lateral view, showing attachment to *Sacculina imberbis* Shiino, 1943 (s) host on *Pachygrapsus crassipes* Randall, 1840 abdomen; E2, adult female, external lateral view, removed from sacculinid host. A1–A4, A6–A8, UBZM 63862; A5, UBZM 98209; A9–A10, UBZM 64096. B, USNM 103736; C, courtesy of Shawn Miller; D1, D2, from Kossmann, 1874; D3 from Shiino, 1952; E1 from Shiino, 1952. Scale = 0.16 mm (A5, A6, A7), 0.2 mm (A3), 0.25 mm (A 10, B3), 0.5 mm (A1, A9), 0.625 (A8), 1 mm (A2, B1, B2), 1.43 mm (A4) (rest not to scale).

***Zeuxokoma elongata* n. sp.**

Fig. 4B

Type host and locality. *Nematocarcinus cursor* A. Milne Edwards, 1881 (Nematocarcinidae), off Mississippi Delta, Gulf of Mexico, 600 fms (= 1097 m).

Other hosts and localities. None.

Forms known. Female only.

Etymology. From the Latin *elongatum*, referring to the very elongate shape of the parasites.

Type host and locality. Holotype female, 14.3 mm (USNM 1251741), 4 paratype females, 10.4–16.4 mm (USNM 103736) infesting two female *N. cursor*, 31.3–31.4 mm CL (only one parasite still attached to host), Sta. 1426, 29°07'N, 87°54'W, off Mississippi Delta, 600 fms (= 1097 m), 24 Sept 1955, coll. R/V *Oregon*.

Description. Mature female: 10.0–16.4 mm long; elongate, widening distally, not recurved; surface smooth, without lobes; anteroventral shield small. Trunk short with 4 recurved attachment lobes. Found parasitizing nematocarcinid shrimp hosts.

Remarks. The only specimen still attached to a host is located ventrally between the second and third pleomeres. This species can be distinguished from all others in the genus by its large size (smallest mature specimen larger than largest mature specimen of any other species; largest specimen nearly 50% larger than largest specimen of any other species) and elongate body with very short trunk and small anteroventral shield region (although the poor preservation makes identification of the size of the shield region difficult). The only other species in the genus with a comparably short trunk is *Z. setosa*, but in that species the body is bean-shaped and not elongated.

Zeuxokoma sp.

Fig. 4C

Host and locality. *Cinetorhynchus hendersoni* (Kemp, 1925) (Rhynchocinetidae), 1881, small cave, 25 ft (= 7.6 m), reef pocket, Kadena steps, Okinawa, Japan, photographed 8 April 2012 on night dive (approximately 7:45 pm) by Shawn Miller.

Other hosts and localities. None.

Forms known. Female only.

Material examined. None (specimen photographed alive, not collected).

Remarks. Based on the appearance of the female and given the locality where the specimen was observed, the most likely identification for this parasite is *Z. luetzeni* (possibly identical with *Z. alphei*) that was also collected in Japan. However, all specimens of *Z. luetzeni* and *Z. alphei* were found on alpheid hosts, and those parasites are not known to insert on the dorsal surface of the host's abdomen. The only other host species belonging to Nematocarcinoidea (*Z. elongata* n. sp.) is found in the Gulf of Mexico and is morphologically different in female parasite shape (short trunk not arising from the parasite at ca. 90° angle, parasite proportionally much thinner compared to length). The combination of host choice, infestation position, and body shape all suggest that this specimen is not identical to *Z. luetzeni*, Z. *alphei*, or *Z. elongata,* n. sp. Collection of specimens is needed to determine the identity of the *Cinetorhynchus*-infesting *Zeuxokoma*.

Avada, n. gen.

Danalia:—Shiino, 1952: 329–335 (not *Danalia* Giard, 1887).

Type species. *Avada kedavra*, n. sp.

Other species. *Avada porcellanae* (Kossmann, 1872), **n. comb.**, A. sp. *sensu* Shiino, 1952, *A. eldredgei,* **n. sp**.

Etymology. The genus is named after the killing curse uttered by Lord Voldemort in J.K. Rowling's *Harry Potter* series. For a host to be parasitized by a species of *Avada* is to suffer probable reproductive death by sterilization.

Diagnosis. Female: Strongly convex dorsal margin smooth (Fig. 5B1) or divided into 7–9 lobes (Fig. 5A1), ventral side shorter, shallow medial indentation. Attachment trunk short with four short strongly sclerotized attachment lobes (Figs. 5B2, 5B5). Parasitizing sacculinid rhizocephalans or crab hosts.

Cryptoniscus (only known for *A. kedavra,* n. sp.): Head anterior margin with triangular median region reflexed posteroventrally (visible in ventral view) (Fig. 5A3). Antennule of 3 articles (Fig. 5A3), first (basal) article smooth, anterior margin with 2 spines, covered by reflexed median of anterior head margin, article 2 triangular with one transverse ridge medially, article 3 with 2 flagella (inner with 3 long setae, outer with 2 shorter setae) and bundle of aesthetascs. Pereopods 1 and 2 (Fig. 5A5) subequal in size, ischium with elongate lateral spine. Pereopods 3–5 (Fig. 5A6, 5A7) ambulatory. Pereopod 6 (Fig. 5A8) of 3 segments; basis elongate, hourglass shape, ischium approximately 2/3 length of basis, third segment extremely long and slender, tapering toward recurved tip, more than 2x as long as ischium and basis combined. Pereopod 7 (Fig. 5A9) of 4 segments, basis similar in shape to that of pereopod 6 but smaller; ischium short, subquadrate; carpus small and cylindrical; terminal segment long, slender, subdivided by median slit into ventral and dorsal portions, dorsal portion 2x length of ventral, recurved at tip.

Remarks. Although only a single species is known with cryptoniscus larvae, possible morphological synapomorphies for the larvae in this genus are the presence of two teeth on the anterior margin of the first segment of the antennule (see below, also see Nielsen & Strömberg, 1965) and the terminal segments of pereopods 6 and 7 which are different in shape and proportions from those of larvae in other genera (where known). Differences between the new genus and *Danalia* and *Zeuxokoma* are given in the Remarks for those two genera.

Avada porcellanae (Kossmann, 1872), n. comb.

Fig. 4D

Zeuxo porcellanae Kossmann, 1872: 333, pl. 18, figs. 9–10, 12; Kossmann, 1874: 134, pl. 7, figs. 9–10, 12; Kossmann, 1880: 124; Kossmann, 1884: 459; Giard, 1887: 48–50; Bonnier, 1900: 196, 198, 384, fig. 32b; Richard, 1900: 73; Altes, 1982: 21; Grygier, 1993: 187, 189, 192.
Cryptoniscus porcellanae Fraisse, 1878b: 421.
Danalia porcellanae Caullery, 1908: 589, 630; Grygier, 1993: 189.
Danalia (*Zeuxo*) *porcellanae* Wimpenny, 1927: 6; Altes, 1982: 28; Grygier, 1993: 188.
Danalia (*Zeuxo*) *porcellana* (sic) Fize, 1956: 27.
"Danalia du Japon sur… *Petrolisthes*" Fize, 1956: 27.
Danalia 3 Shiino, 1952: 334–335, figs. 1A, E.

Type host and locality. 2 female syntypes from unidentified porcelain crabs, Philippines.

Other hosts and localities. *Petrolisthes japonicus* (De Haan, 1849) (Porcellanidae) from Seto, Japan.

Forms known. Female only.

Material examined. Female (ZMA CRUS.I.261172), 6.8 mm, ex *Porcellana streptochira* Miers, 1884 [= *Lissoporcellana quadrilobata* (Miers, 1884)] (not in jar), Stn. 50, Bay of Badjo, west coast of Flores, Indonesia, 16–18 April 1899, coll. Siboga Expedition.

Remarks. This parasite is very irregular in shape with 8 or 9 variably-shaped lobes dorsally. Kossmann (1872) illustrated the hook-like attachment lobes that are similar to those seen in *A. eldredgei,* n. sp., also from a porcelain crab host but differing from this species by its smooth dorsal surface that lacks lobes. Nierstrasz & Brender à Brandis (1923) reported on another specimen from Indonesia but did not illustrate it. Examination of that specimen shows that it is nearly identical both in general morphology and the shape of the attachment hook to the specimen illustrated by Kossmann (1872; fig. 4D1 herein). Shiino (1952) suggested that his *Danalia* 3 might be identical with Kossmann's *porcellanae*. Although Kossmann's (1872) description is meager and his illustration is not detailed, both sets of specimens appear to belong to the same species. The mature parasite is orange-red in color (*fide* Shiino, 1952).

Avada sp.

Fig. 4E

Danalia 1 Shiino, 1952: 330–331, figs. 1c, d.
"Danalia du Japon sur… *Sacculina"* Fize, 1956: 27.
D[*analia*] sp. Altes, 1982: 28.

Host and locality. 1 female specimen from *Sacculina imberbis* Shiino, 1943 (Sacculinidae), infesting *Pachygrapsus crassipes* Randall, 1840 (Grapsidae), from Seto, Japan.

Other hosts and localities. None.

Forms known. Female only.

Material examined. None.

Description. Female (modified from Shiino, 1952): 11.4 mm long, yellowish in color, irregular in shape. Strongly convex dorsal margin divided into 9 lobes, ventral side shorter, medially indented. Trunk short, bifurcated into two branches which each bifurcate again. Parasitizing sacculinid rhizocephalan on grapsid crab host.

Remarks. The female morphology is very much like that of other *Avada* species, but the original description, lacking the cryptoniscus and any illustrations of the attachment process, is not sufficient to warrant description of the species at this time. Based on the description of the attachment process as having four lobes, but one pair borne on each half of a subdivided trunk, this taxon appears distinct from *A. porcellanae* and *A. eldredgei,* n. sp., which each have four short attachment lobes borne on a single undivided stalk.

***Avada kedavra*, n. sp.**

Fig. 5A

Danalia 2 Shiino, 1952: 331–334, figs. 1B, 2; Nielsen & Strömberg, 1965: 53.
"*Danalia* du Japon sur… *Pugettia*" Fize, 1956: 27.

Type host and locality. 1 female (holotype) and 3 cryptoniscus larvae (paratypes) infesting *Pugettia quadridens* (De Haan, 1839) (Epialtidae) from Seto, Japan.

Other hosts and localities. None.

Forms known. Female and cryptoniscus.

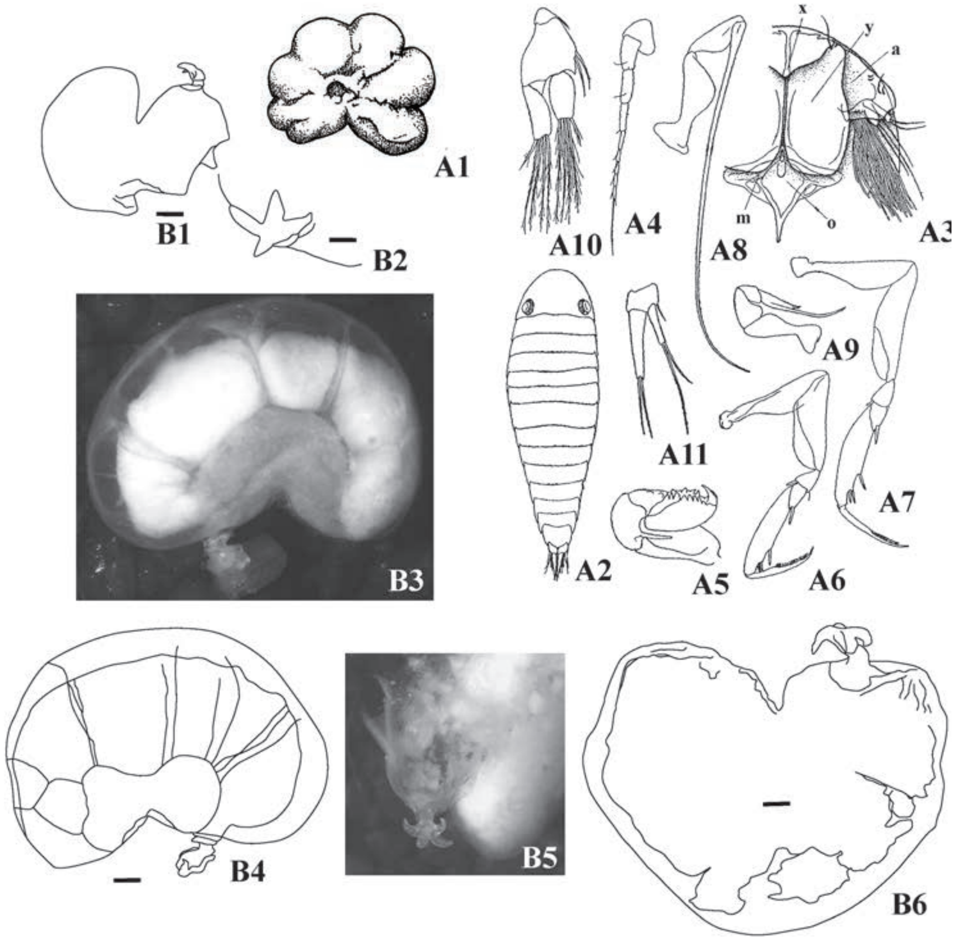


Figure 5. **A**, *Avada kedavra* n. sp.: A1, adult female, lateral view; A2-A11, cryptoniscus larvae: A2, dorsal view; A3, ventral view of head and antennule; A4, antenna; A5, pereopod 2; A6, pereopod 4; A7, pereopod 5; A8, pereopod 6; A9, pereopod 7; A10; pleopod 1; A11, uropod. **B**, *Avada eldredgei* n. sp.: B1, adult female, lateral view; B2, same, close up of attachment hooks; B3, adult female, lateral view; B4, same, opposite side, lateral view; B5, adult female, close up of attachment hooks; B6, same, lateral view. A, from Shiino, 1952; B1, B2, BPBM S16162; B3, B4, BPBM S16160 (holotype); B5, B6, BPBM S16161. a, antennule, m, mandible, o, oral cone, x, frontal lobe of head, y, basal segment of antennule. Scale = 0.25 mm (C2), 0.32 (C4, C6), 0.625 (C1) (rest not to scale).

Etymology. The species name in conjunction with the genus name completes the killing curse uttered by Lord Voldemort in J. K. Rowling's *Harry Potter* series.

Material examined. None. The holotype is the specimen figured by Shiino (1952: figs. 1B, 2) deposited in NSMT. It may be one of the specimens currently catalogued as NSMT-Cr 14504 but attempts to confirm its current status and condition though contact with the relevant curator were unsuccessful.

Description. Female (modified from Shiino 1952): 4.5 mm long, yellowish in color; semi-circular in shape. Strongly convex dorsal margin divided into 7 lobes, ventral side shorter, medially indented. Attachment hook shape and trunk length unknown. Directly parasitizing epialtid crab host.

Cryptoniscus (modified from Shiino 1952): Body tear-drop shaped, 0.96 mm length, strongly convex dorsally (Fig. 5A2). Cuticular surface smooth. Head anterior margin ovate in dorsal view but with triangular median region reflexed posteroventrally (visible in ventral view (Fig. 5A3x), posterior margin straight, widest at posterolateral junction with pereomere 1 (Fig. 5A2). Diffuse, moderately large eyes located proximolaterally, eyes with irregular pigment most prominent around medially directed edge (Fig. 5A2). Antennule of 3 articles (Fig. 5A3), first (basal) article smooth, approximately 2 times longer than broad, anterior margin with 2 spines, covered by reflexed median of anterior head margin, posterior margin and surface smooth (Fig. 5A3y), article 2 triangular with one transverse ridge medially (Fig. 5A3a), overhanging terminal article, article 3 with 2 flagella (inner with 3 long setae, outer with 2 shorter setae) and bundle of aesthetascs (Fig. 5A3). Antennae of 9 articles (4 peduncular and 5 flagellar) (Fig. 5A4), flagellar articles much narrower than peduncular articles, peduncular articles each with 1 subterminal setae, flagellar articles each with 1 terminal seta, proximal flagellar article longest, flagellar articles 2–5 of approximately equal length, terminal article with 1 long seta. Oral cone anteriorly directed (Fig. 5A3o).

Pereomere 5 broadest, tapering anteriorly and posteriorly. Body pigmentation lacking. Pereomeres with entire (not toothed) quadrangular coxal plates 1–7. Pereopods 1 and 2 subequal in size, short and stout, gnathopodal with dactyli entire (non-bifid) (Fig. 2A5), ischium with elongate lateral spine, merus with 2 low small lobes on inner margin, propodus and carpus nearly fused, carpus with acute denticles in 2 rows along inner border, dactylus with 2 or 3 acute spines on outer margin. Pereopods 3–5 (Figs. 5A6, 5A7) ambulatory, smooth; dactyli long, straight, slender, smooth margins, with ventral setal comb, tip hooked via ventral indentation of margin; propodi straight, medially inflated (progressively more inflated from pereopod 3 to 5), 1 stout ventral seta at 1/3 from distal margin and 2 smaller setae near junction with dactylus; carpi of pereopods 3–5 with one stout terminal ventral seta; meri with one thin terminal dorsal seta; ischium proportionally longer from pereopod 3 to 5. Pereopod 6 (Fig. 5A8) of 3 segments; basis elongate, hourglass shaped, being constricted 1/3 from proximal margin with ventral triangular expansion in distal ½; ischium approximately 2/3 length of basis, narrow proximally and moderately expanded distoventrally; third segment (homology uncertain) extremely long and slender, tapering toward recurved tip, more than 2x as long as ischium and basis combined and nearly 1/3 of total body length. Pereopod 7 (Fig. 5A9) of 4 segments, basis similar in shape to that of pereopod 6 but smaller; ischium short, subquadrate; carpus small and cylindrical; terminal segment (homology uncertain) long, slender, subdivided by median slit into ventral and dorsal portions, dorsal portion 2x length of ventral, recurved at tip, ventral portion with 2 distal spinules.

Pleon with 5 pleopods composed of basis (sympod), exopod, and endopod (Fig. 5A10). Sympod 2-jointed: small proximal portion triangular with short setae at inner angle, larger distal portion similar in shape, with 2 medially directed setae, endopod with 4 long plumose setae and 1 short plumose seta on outer margin, exopod with 4 plumose setae and 1 short plumose setae on inner margin. Pleotelson quadrangular, uropodal endopods approximately twice as long as exopods, basis with 1 distolateral seta, endopods and exopods with 2 long simple terminal setae (Fig. 5A11).

Remarks. The presence of dorsal lobes on the female distinguishes this species from *A. eldredgei* n. sp. The highly symmetrical shape of the body contrasts with the asymmetrical shape seen in *A. porcellanae*. This is the only species in the genus with a well described cryptoniscus larva that provides additional characters distinguishing the genus from the *Danalia*. The homology of the terminal segments of pereopods 6 and 7 are not clear; they could be fused dactyli and propodi (and in the case of pereopod 6, also meri) or one or more of the other segments could be lacking with the terminal segment being a hyperextended dactylus.

Despite attempts to ascertain if the material studied by Shiino (1952) still exists in NSMT, I was not able to locate it. It is definitely not in the collections of either the Seto Marine Lab or the Mie University, institutions where Shiino worked.

***Avada eldredgei*, n. sp.**

Fig. 5B

"*Sacculina*-like form" Edmondson, 1946: 226.
Lernaeodiscus sp. Boschma, 1953: 190-191.
"close to… *Danalia porcellanae*" Boyko & Harvey, 2000: 673.

Type host and locality. 3 females, each infesting a single *Pachycheles pisoides* (Heller, 1965) (Porcellanidae) from Hawai‘i.

Other hosts and localities. None.

Forms known. Female only.

Etymology. The species is named after Lu Eldredge (1938–2013) whose knowledge of the Hawaiian fauna, especially the marine invertebrates was exceptional. His generous nature will be sorely missed. His assistance in planning The Crustacean Society meeting in Honolulu in 2011 was invaluable, and his welcoming of his colleagues into his home is fondly remembered.

Material examined. 1 mature female holotype, 3.5 mm (BPBM S16160, Fig. 5B3, 5B4), infesting female *P. pisoides* (3.5 mm CL) (ex BPBM 3427), Kahala, O‘ahu, Hawai‘i, April 1931, coll. C.H. Edmondson; 1 mature female paratype, 4.0 mm (BPBM S16161, Fig. 5B5, 5B6), infesting male *P. pisoides* (4.0 mm CL) (ex BPBM 4314), Kawela, O‘ahu, Hawai‘i, 10 July 1937, coll. unknown; 1 mature female paratype, 4.3 mm (damaged) (BPBM S16162, Fig. 5B1, 5B2), infesting female *P. pisoides* (4.3 mm CL) (ex BPBM 5902), Mā‘ili Point, O‘ahu, Hawai‘i, 10 July 1953, coll. C.H. Edmondson.

Description. Female, length 3.5–4.3 mm. Body of female sac-like, composed of two stout lobes weakly recurved with small indentation on ventral surface medially. Outline of body smooth, without lobes. Body with developing ovarian tissue showing internal segmentation (Fig. 5B3, 5B4). Attachment hooks of four short, stout, lobes born on short trunk slightly longer than width of hooks (Fig. 5B5). Directly parasitizing porcelain crab host.

Remarks. Boyko & Harvey (2000) first correctly identified this species as an isopod and not a rhizocephalan. This species can be distinguished from the others in the genus by its smooth outline, lacking in externally differentiated lobes as seen in *A. porcellanae* and A. *kedavra,* n. sp.

Keys to Genera Based on Females and Cryptoniscus Larvae

Females

1a. Female body shape linear, not recurved .... *Zeuxokoma* Grygier, 1993
1b. Female body shape recurved 2
2a. Female body shape strongly recurved, body as two large lobes with large space medially, attachment hooks flexible, not sclerotized .... *Danalia* Giard, 1887
2b. Female body shape weakly recurved, little to no space between right and left sides of body, attachment hooks rigid, sclerotized .... *Avada,* n. gen.

Cryptoniscus larvae (larvae not known for *Zeuxokoma*)

1a. Antennule segment 2 with spines, pereopod 6 with 3 segments, terminal segment longer than basis and ischium combined, pereopod 7 terminal segment bifid .... *Avada,* n. gen.
1b. Antennule segment 2 unarmed, pereopod 6 with 4 segments, terminal segment approximately as long as basis and ischium combined, pereopod 7 terminal segment entire .... *Danalia* Giard, 1887

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Box Jellyfish (Cubozoa: Carybdeida) in Hawaiian Waters, and the First Record of *Tripedalia cystophora* in Hawai‘i

Gerald L. Crow
Waikīkī *Aquarium, University of Hawai'i at Manoa, 2777 Kalakaua Ave., Honolulu,
Hawai'i 96815, USA; email: gcrow@hawaii.edu*

Luciano M. Chiaverano
*Kewalo Marine Laboratory, Pacific Biosciences Research Center, University of
Hawai'i at Manoa, Honolulu, Hawai'i 96813, USA*

Jennifer Crites
Paradise Pen and Photo, Honolulu, Hawai'i 96822, USA

Marat A. Khramov & Brenden S. Holland
*Center for Conservation Research and Training, Pacific Biosciences Research Center,
University of Hawai'i at Manoa, Honolulu, Hawai'i 96822, USA*

Abstract. Box jellyfish represent an ecologically important component of tropical marine planktonic communities, and certain species are notorious for their potent sting. We describe and review the occurrence of three box jellyfish species previously recorded from the Hawaiian Islands, *Carybdea arborifera* (Maas, 1897), *Alatina moseri* (Mayer, 1906), and *Copula sivickisi* (Stiasny, 1926), and newly report a fourth species, *Tripedalia cystophora* Conant, 1897. The latter two species are likely to have been introduced by shipping to Hawai‘i. Although previously reported in Hawai‘i, *Carybdea rastonii* was not confirmed from Hawaiian waters in this study and we suggest it may have been misidentified. Instead, DNA sequence fragments from specimens tentatively identified via morphological characters as *C. rastonii* matched the congener *C. arborifera*. Continued surveillance of box jellyfish is warranted, as the Hawaiian Islands have a well-developed ocean associated tourism, introduction of dangerous stinging jellyfish such as those that cause severe “irukandji” syndrome is of primary concern.

Introduction

In the last three decades jellyfish (cnidarian classes Cubozoa, Scyphozoa, and Hydrozoa) have received increased scientific attention due to their fluctuations in abundance that frequently result in population explosions (i.e., blooms) in marine ecosystems worldwide (see Pitt & Lucas 2014). Jellyfish blooms negatively affect fisheries by clogging nets (Nagata *et al.* 2009, Dong *et al.* 2010), pen aquaculture by causing fish death (Doyle *et al.* 2008, Delannoy *et al.* 2011), power generation and desalination by clogging intake screens (Daryanabard & Dawson 2008), and tourism by stinging swimmers (Fenner & Williamson 1996, Fenner *et al.* 2010).

Box jellyfish, or cubomedusae (Cubozoa), represent the smallest cnidarian class with approximately 50 species (Bentlage *et al.* 2010). However, the basic biology, population dynamics and species identity are poorly understood (Kingsford & Mooney 2014). Box jellyfish have complex eyes with sophisticated visual acuity (Martin 2004, Nilsson *et al.* 2005, Kozmik *et al.* 2008) enabling active predation (Hamner *et al.* 1995, Buskey 2003), obstacle avoidance (Garm *et al.* 2007), and even navigation using terrestrial landmarks (Garm *et al.* 2011). Cubomedusae exhibit complex phototactic, courtship and mating behaviors (Lewis & Long 2005), unique to this group. Perhaps their most notorious feature is their extremely dangerous venom (Tibballs *et al.* 2012). Most species within this class can cause medically significant stings (Gershwin *et al.* 2010), and while toxicity varies

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from species to species, the class includes the world's most venomous marine creature, *Chironex fleckeri* (Fenner & Williamson, 1996), which can kill an adult human within minutes. Most box jellyfish prefer calm tropical and subtropical near-shore marine habitats, areas that are frequently shared with tourists, fishermen, surfers and divers. This overlap of recreation with box jellyfish often results in dangerous encounters (Fenner & Williamson 1996, Fenner & Hadok 2002, Huynh *et al.* 2003).

Box jellyfish have been documented in the Hawaiian Islands since 1877 when Theodore Ballieu, a French commissioner to Hawai'i, collected a specimen in Honolulu reported as *Charybdea alata* (Reynaud, 1830) (Ranson 1945, Kay 1972) and placed it in the Muséum National d'Histoire Naturelle in Paris. In 1891, *Carybdea arborifera* (as *Charybdea arborifera* Maas, 1897) was collected in Honolulu surface waters (Maas 1897). In 1902 a five-month survey of the entire Hawaiian Island chain by the Steamer *Albatross* collected 41 *C. arborifera* (as *Charybdea rastonii* Haacke, 1887) off O'ahu, Maui and Kaua'i from 0 to 42 m (Mayer 1906). Twenty-three specimens of a new species, *Alatina moseri* (as *Charybdea moseri* Mayer, 1906) were collected in the same survey from the Northwestern Hawaiian Islands (NWHI) Maro Reef to south of the Island of Hawai'i at the surface to 46 m (Mayer 1906). Galtsoff (1933) reported *A. moseri* (as *Charybdea alata*) during a 1.5 month survey of Pearl and Hermes, NWHI as a one day occurrence on 18 Aug 1930 "appeared in great numbers near southeast island and caused considerable discomfort (from stings) to our divers".

Night surveys in 1996 and 1998 discovered *Copula sivickisi* (as *Carybdea sivickisi* Stiasny, 1926) on the south shore of O'ahu in Mamala Bay (Waikīkī Beach area) and on the west coast of O'ahu in Yokohama Bay (Matsumoto *et al.* 2002), respectively, as well as from Ma'alaea Harbor on Maui in 2005 (Crow *et al.* 2006). An additional survey in Ma'alaea Harbor on Maui in 2004 collected *C. arborifera* (as *C. rastoni*) (Crow *et al.* 2006).

Considering the fact that box jellyfish were recorded as far ago as the 19th century in Hawai'i, surprisingly little information exists regarding their biology and ecology. We summarize here our knowledge of Hawaiian cubomedusae and report the first record of *Tripedalia cystophora* Conant, 1897 in Hawaiian waters.

Methods

We studied the collections of the Bernice P. Bishop Museum (BPBM), Honolulu, the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., and the Muséum National d'Histoire Naturelle, Paris (MNHN). Additional specimens from the National Marine Fisheries Service (NMFS), the University of Hawai'i, Department of Oceanography and those of the first author were also added to the BPBM collection. In addition, we reviewed Hawaiian Ocean Safety and Lifeguard Services (OSLS) records, currently available at the OSLS Leahi St. office. Reports were also taken from newspaper accounts and accessed via the printed index to the Honolulu Advertiser and Honolulu Star-Bulletin 1926–1994 based on key word search (jellyfish, box jellyfish, stings). Printed microfilm accounts are available from the first author. In addition, a search was conducted on the Chronicling America, Library of Congress website: http://chroniclingamerica.loc.gov covering Hawai'i newspapers from 1836–1922 with no reports of box jellyfish in newspaper articles. The website was last accessed on 23 Feb 2014. Newspaper reports were accepted when verification of species identification was possible.

Measurements were made with an analog micrometer (± 0.1 mm) as follows: 1) bell-height (BH): the distance from the upper tip of the bell to velarial turnover, and 2) bell-height to rhopalial opening (BHR): the distance from the upper tip of the bell to the rhopalial niche opening.

We performed preliminary molecular evaluation of each taxon by sequencing one or more DNA markers and conducting BLAST (Basic Local Alignment Search Tool) searches to determine highest probability matches in GenBank.

Table 1. **Records of the box jellyfish *Alatina moseri* on Waikīkī Beach, O‘ahu, and significant records from two other Hawaiian Islands**.

Date(s)	Comments	Source
5 Mar 1948	First time reported in Waikīkī	BPBM D285 records
30 Jun 1951	Swarms on beach;painful stings	Edmondson 1952; BPBM D315
28 May 1962	Queen's surf to Natatorium	Hono. Star Bull. 51:148.
30–31 Dec 1980	First two day episode	BPBM D533
23 Sep 1981	Aggregation over a 4–5 km area	BPBM D555, OSLS
5 Dec 1982	Ala Moana, after Hurricane Iwa	Star Adver. I 13
5 Mar 1988	Mass near Hilton Hawaiian Village	Hono. Advertiser A1/ A3
22 Mar 1990	Hanauma Bay closure	Hono. Advertiser A3
28 Feb 1992	Invasion, Hanauma Bay to Sandy Beach	Hono. Advertiser A1
14 Jun 1993	Invasion, Nanakuli to Makua	Hono. Advertiser A4
15 Jul 1993	3 people stung near Molokini Crater	Hono. Advertiser C6
1998 to 2011	Waikīkī monthly beach counts	Chiaverano *et al.* 2013
3 Dec 2007	Poi‘pu Beach, Kaua‘i	Hono. Advertiser A1

BPBM = Bernice P. Bishop Museum records; Hono. Star Bull. = Honolulu Star Bulletin; Hono. Advertiser = Honolulu Advertiser; OSLS = Ocean Safety and Lifeguard Services records.

Class CUBOZOA Werner, 1972
Order CARYBDEIDA Gegenbaur, 1857

Family ALATINIDAE Gershwin, 2005

Genus *Alatina* Gershwin, 2005

Family and species diagnosis: T-shaped rhopaliar niche ostia with a single upper and two lower covering scales (Gershwin 2005, Bentlage & Lewis 2012, Kayal *et al.* 2012, Smith *et al.* 2012, Lewis *et al.* 2013).

Alatina moseri (Mayer, 1906)

Fig. 1

Synonyms used in Hawaiian literature: *Carybdea moseri* (Mayer, 1906), *Charybdea moseri* Mayer, 1906; *Carybdea alata* Reynaud, 1830, and *Charybdea alata* (Reynaud, 1830).

ECOLOGICAL AND MORPHOLOGICAL INFORMATION: Mayer (1906) captured large specimens about 80 mm high and 47 mm wide (mature at about 67 mm bell height) throughout Hawaiian offshore waters as far as 520 km from the nearest island. Ranson's (1945) report of *C. alata* (a name used by subsequent Hawaiian authors to refer to what is now known as *A. moseri*) is a misidentification of (at the time) an undescribed specimen of *C. arborifera*, as discussed below. Edmondson (1946) specimens have a bell about 2 in wide and nearly twice that height occasionally observed it on the reefs of O‘ahu, this species is typically a pelagic species. The first specimens were reported in Waikīkī on 5 March 1948 with "very powerful stinging cells" (*fide* BPBM Accession Record). Edmondson (1952) reported that "swarms suddenly appeared" at Waikīkī Beach on 30 June 1951 (*fide* BPBM Accession Record). Chu & Cuttress (1954) noted that this species was occasionally encountered on the reefs and unprotected coastline of Hawai‘i. Anonymous (1962) reported a "heavy distribution" from Queen's Surf to the Natatorium in Waikīkī on 28 May 1962. This species has appeared in Waikīkī Beach surveys every month since August 1994 (OSLS records). Thomas *et al.* (2001a) discussed an 8–12 day influx cycle, Chiaverano *et al.* (2013) discussed climatic and oceanographic influences on its abundance on Waikīkī Beach, and Carrette *et al.* (2014) reported on its early life history in laboratory cultures. *A. moseri* specimens examined in Hawaii had simple, bi-fork and tri-fork distal ends of the velarial canals (first author data).

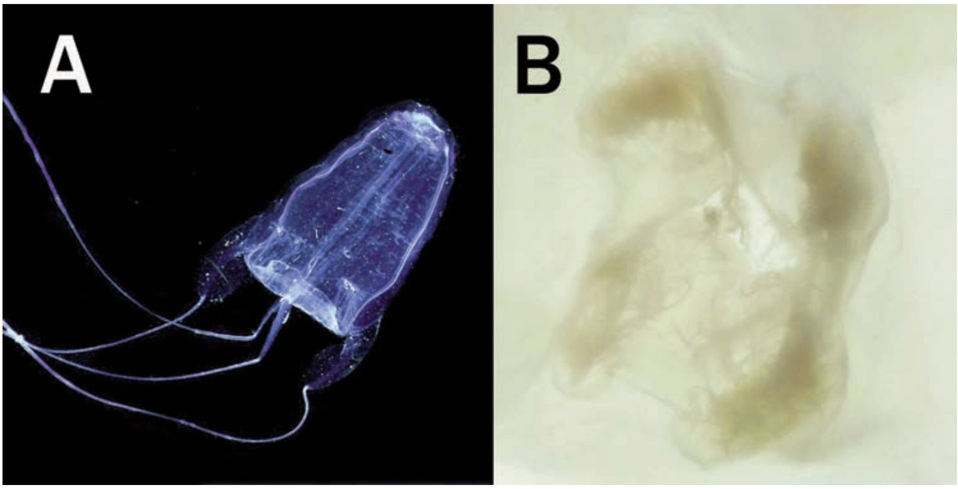

Figure 1. (**A**) Photograph of living *Alatina moseri* collected at Waikīkī Beach, in a kreisel tank, (**B**) Close up of crescentric gastric phacellae.

STINGS AND TOXICOLOGY: References: Tamanaha & Izumi (1996) sting reaction; Thomas & Scott (1997) sting records and first aid; Nagai *et al.* (2000) unique protein sting toxin; Chung *et al.* (2001) venom; Thomas *et al.* (2001a) treatment; Thomas *et al.* (2001b) sting treatment trial; Nomura *et al.* (2002) sting treatment; Yanagihara *et al.* (2002) ultrastructure of nematocyst; Yoshimoto & Yanagihara (2002) heat sting treatment; Ping & Onizuka (2011) sting treatment review 2000 to 2008, and Yanagihara & Shohet (2012) venom cardiovascular effects.

HAWAIIAN SPECIMENS EXAMINED: BPBM D285 Waikīkī Beach 5 Mar 1948; BPBM D315 Waikīkī Beach 30 Jun 1951 (four specimens); USNM 51962 Ala Wai Boat Harbor 1955; BPBM D533 Kūhiō Beach, Waikīkī 31 Dec 1980; BPBM D555 Waikīkī Beach 23 Sep 1981; R V *Oscar Elton Sette* (OES) NOAA/ Pacific Island Fisheries Research Center and UH Manoa, Oceanography night Cobb trawls in the top 200 m of water around Cross Seamount Summit (for trawl details see Drazen *et al.* 2011); BPBM D2302 (BHR 30 mm) < 14 km off Cross Seamount 24 Apr 2008, BPBM D2303 (BHR 23.4 mm) off southwest flank Cross Seamount 30 Apr 2008; BPBM D2304 in cyclonic mid ocean eddy between Cross Seamount and Oʻahu 18°N and 158°W 7 May 2008); BPBM D2271 Magic Island, Ala Moana Beach Park 19 May 2009; BPBM D2269 Cobb Trawl southwest of Keāhole Point, Island of Hawaiʻi SE 12-06 station 30, 21 Aug 2012; BPBM D2270 Waikīkī Beach 24 Feb 2014.

HAWAII DISTRIBUTION: NWHI, Midway Atoll (washed ashore) to Island of Hawaiʻi (Kona side) and south of Hawaiian Islands over Cross Seamount.

RANGE: Widespread throughout Hawaiian Islands and Osprey Reef on Great Barrier Reef, Australia (Bentlage *et al.* 2010). Considered by Bentlage & Lewis (2012) to be an oceanic species in tropical and temperate waters.

REMARKS: This is a widespread, oceanic species recorded since 1902 throughout the entire Hawaiian Archipelago, as well as on the Great Barrier Reef (Mayer 1906, Bentlage *et al.* 2010). As discussed below, *A. moseri* appears to have increased in frequency on Oʻahu since the late 1940s (Table 1). Box jellyfish collections of GLC in 1998 and 2000 along the leeward coastline of Oʻahu ranged from 54.6 to 93.3 mm BH and 22.0 to 66.5 g wet weight.

Chiaverano *et al.* (2013) reported records over a 14-yr period (1998 to 2011) for *A. moseri* that had no seasonality at Waikīkī Beach. Rather, box jellyfish abundance at Waikīkī Beach fluctuated monthly and annually, and correlated with the changes in the North Pacific Subtropical Gyre (NPGO) index. This index displayed a strong positive correlation with primary production and >2 mm zooplankton biomass that potentially translated to increased food availability for *Alatina moseri* medusae. There was no abundance link to the Pacific Decadal Oscillation or to the Multivariate El Nino-Southern Oscillation Index (Chiaverano *et al.* 2013). This species now appears off Waikīkī Beach every month of the year eight to 12 days after the full moon (Thomas *et al.* 2001a; Chiaverano *et al.* 2013) close to the late night or early morning high tide. To date, the polyps for this species in Hawai‘i have not been found in the wild. Starting in 31 March 1989, this species began to show up at Hanauma Bay (east shore), appearing on 18 May 1990 on the west shore (several areas) and on 28 August 1997 at Waimea Bay north shore of O‘ahu (OSLS records).

On Waikīkī Beach during 21 and 22 October 2000, adult *A. moseri* were observed in spawning condition from the hours of 2300 to 0400 (Carrette *et al.* 2014). During spawning events witnessed in buckets at Bonaire, Dutch West Indies, male *A. alata* gonads became cloudy and ruptured in several spots along the distal axis releasing spermatozoa into the gastro-vascular cavity that were then shed through the manubrium into the water. Females took up the spermatozoa into the gastro-vascular cavity, their gonads became opaque and also ruptured in several spots while eggs were concurrently ovulated into gastric sacs for fertilization (Lewis *et al.* 2013). Within several hours embryos were seen circulating through the entire gastro-vascular system, the fertilized eggs were released and the planulae settled out after several days to start development as polyps (Lewis *et al.* 2013). The polyps of *A. moseri* (reported as *A.* near *mordens*) survived in the laboratory at temperatures of 18 to 31 °C and salinities of 22 to 40 ppt (Courtney & Seymour 2013), well within the range of Hawaiian waters. In the laboratory, polyps began to start metamorphosis 31 days post fertilization (Carrette *et al.* 2014). Polyp cysts of *A. moseri* were highly resistant to high salinities (39.3 ppt) and starvation for more than 12 months could still regenerate when conditions stabilize (Courtney & Seymour 2013, Carrette *et al.* 2014).

The sting of this species produces a mixture of toxic and allergic reactions and in acute cases results in local painful, pruritic erythematous dermatitis that may persist for seven months (Tamanaha & Izumi 1996). Heat treatment, particularly hot showers at 44 °C, helped reduce pain from stings (Yoshimoto & Yanagihara 2002).

Family CARYBDEIDAE Gegenbaur, 1856

Genus CARYBDEA Peron & Lesueur, 1810

This family has heart-shaped rhopaliar niche ostia (Gershwin & Gibbons 2009; Bentlage & Lewis 2012).

Carybdea arborifera (Maas, 1897)

Fig. 2

Synonyms used in Hawaiian literature: *Charybdea arborifera* Maas, 1897, (non *Carybdea rastonii* Haacke, 1886, *Carybdea rastoni* Haacke, 1887, *Charybdea rastoni* Haacke, 1887), *Procharybdis cuboides* Haeckel, 1880.

> Original description (Maas 1897): *"Schirm glockenformig bis prismatisch (bei kleineren Exemplaren mehr das erstere), oben flach gewolbt. Gallerte sehr diinn und schlaff. Exumbrella structurlos. Schirmhohe 15, durchmesser 10 mm. Magenrohr etwa 5 (!) mm. lang mit kurzen Mundlappen. Phacellen ein Baumchen in jedem Interradius bildend. Velarium breit, in jedem Quadranten von 4 symmetrisch liegenden und symmetrisch verastelten Canalen durchzogen. Pedalien kaum hervortretend. Tentakel vielmals langer wie die Schirmhohe.*" [Bell is bell-shaped to prismatic (in smaller specimens more the former), top of dome flat. Jelly is very thin and limp. Exumbrella structureless. Bell height 15, diameter 10 mm. Stomach tube about 5 mm long with short oral lobes. Phacellae dendritic in each interradius. Velarium wide, in each quadrant traversed with four symmetrically placed and symmetrically branching canals. Pedalia barely protruding. Tentacles many times longer than the height of the bell.]

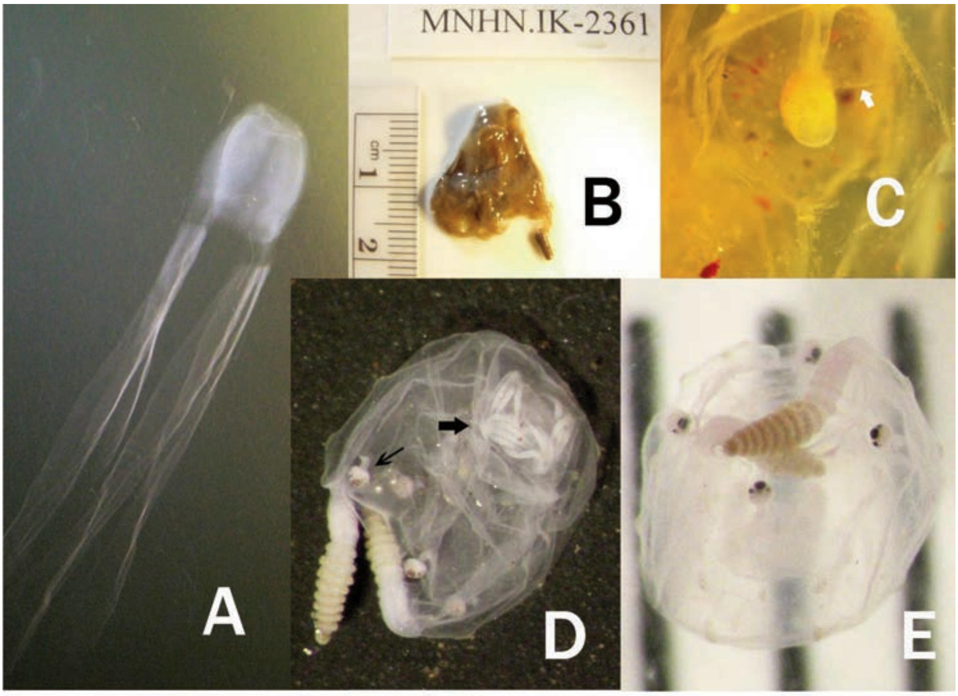

Figure 2. (**A**) Photograph of in situ *Carybdea arborifera* at Kewalo Basin, Oʻahu; (**B**) The 1877 Hawaiian specimen of *Carybdea arborifera* in MNHN; (**C**) Close up of the adult heart-shaped rhopaliar niche ostium of the 1877 *Carybdea arborifera* specimen; (**D**) Juvenile specimen of *Carybdea* from Kāneʻohe Bay, Oʻahu. Note the four gastral filaments in each interradius of juvenile specimen; (**E**) Ventral view of juvenile showing open rhopaliar niche ostium.

Bentlage *et al.* (2010) concluded that *C. arborifera* is a distinct species. Molecular studies (Bentlage *et al.* 2010; this study) have not confirmed the presence of *C. rastonii* in Hawaiʻi. A number of specimens that have been morphologically identified as *C. rastonii* from three Oʻahu localities and were sequenced for this study at two mtDNA loci, 16S and COI (Table 2). However, our 16S gene fragments matched *C. arborifera* in GenBank with a minimum of 99% sequence identity for all specimens, whereas, the match to *C. rastonii* exhibited only 84% sequence identity at maximal query sequence cover (96%) (CQ849116, XQ849117), confirming the identity of the Hawaiʻi specimens as *C. arborifera*. Prior to this investigation, there were no *C. arborifera* COI sequences in GenBank. The top taxonomic match for COI gene fragment was at 81% sequence identity (non-species level match) to the carybdid *Tamoya ohboya* Collins *et al.* (2011), the Bonaire banded box jellyfish.

ECOLOGICAL AND MORPHOLOGICAL INFORMATION: Mayer (1906) reported specimens ranging in size from 11 mm to 35 mm bell height (beginning to mature at about 11 mm bell height) in Hawaiʻi from the 1902 *Albatross* research cruise from Maui, Oʻahu, and Kauaʻi. Crow *et al.* (2006) found *C. arborifera* in Maʻalaea Boat Harbor, Maui by night lighting at the surface.

HAWAII SPECIMENS EXAMINED: MNHN.IK-2361 Iles Sandwich (Hawaiian Islands), 1877, bell height 16.7 mm, labeled as *Carybdea alata*; USNM 52341 (1 specimen) Oʻahu, 3 Jul 1954; USNM 54397 Kāneʻohe Bay, Oʻahu 5 Jul 1972 (5 specimens); BPBM D2272 Kewalo Basin boat harbor, Honolulu, Oʻahu 22 Apr 2004; BPBM D2274 Snug Harbor, Sand Island, Honolulu, Oʻahu 26 May 2004; BPBM D1119 (3 specimens) Maʻalaea Boat Harbor, Maui, 9 Feb 2006; BPBM D1120 (1 specimen) Maʻalaea Boat Harbor, Maui, 7 Feb 2006; BPBM D2273 Lilipuna Pier, Kaneohe Bay, Oʻahu 03 Jul 2013; BPBM D2305 (8 specimens) Kewalo Basin boat harbor, Honolulu, Oʻahu 05 Jul 2006.

HAWAII DISTRIBUTION: Known only from the Hawaiian Islands. Captured at Puniawa Point, Maui in 33 to 77 m, and at Hanalei Bay, Kaua‘i and by surface night lighting in Honolulu Harbor (Mayer, 1906), Kāne‘ohe Bay, Kewalo Basin, Snug Harbor, O‘ahu and Ma‘alaea Harbor, Maui where it was observed feeding on fish on O‘ahu (USNM, and GLC personal observations).

This species appears to have a similar ecological niche as *Carybdea rastonii* in Australia. Matsumoto (1995) reported that adults of *C. rastonii* in Australia have four rhopalia each with six eyes; in the laboratory medusae moved away from dark objects and toward light (white) objects. Medusae were observed near the bottom over sand during daylight and moved to the surface at night or under turbid water conditions (Matsumoto 1995). Stomach contents in Australia consisted of copepods, isopods, amphipods and fishes (Matsumoto 1995).

REMARKS: As noted above, the first specimen of this species from Honolulu (probably Honolulu Harbor) was collected by Ballieu in 1877 and sent to MNHN. The specimen was misidentified as *Carybdea alata*. It is still in the collection (MNHN.IK-2361) and we present photographs of it here (Figs. 2B, C). The species was again captured from Honolulu surface waters in 1891 and described by Maas (1897) as a new species that differs from *rastonii* based on the smooth structure of the bell and the form of gastric phacellae. Mayer (1906) reports *rastonii* from Hawaiian waters (including Honolulu Harbor) but does not discuss *arborifera*. Bigelow (1909) compared specimens from Australia, Tuamotu Archipelago and Hawai‘i and stated that the smooth bell was an artifact of preservation, the gastric phacellae shape represent ontogenetic changes and the similar location data of Honolulu Harbor make it unlikely two species would occur there, therefore, *arborifera* is a probable synonym of *rastonii*. Mayer (1910) stated that *arborifera* was clearly young specimen of *rastonii*. This remained in place until Bentlage *et al.* (2010) showed genetic differences between *arborifera* and *rastonii*.

Family TRIPEDALIIDAE Bentlage, Yanagihara, Lewis, Richards, & Collins, 2010

sensu TRIPEDALIDAE of Conant 1897

Family diagnosis: Sexual dimorphism of the gonads, produces spermatophores and the males have sub-gastric sacs/seminal vesicles (Bentlage & Lewis 2012).

Genus COPULA Bentlage, Yanagihara, Lewis, Richards & Collins, 2010

Copula sivickisi (Stiasny, 1926)

Synonyms used in Hawaiian literature: *Carybdea sivickisi* Stiasny, 1926.

General Description: Key-hole shaped rhopaliar niche ostia (Gershwin, 2005).

ECOLOGICAL AND MORPHOLOGICAL INFORMATION: Matsumoto *et al.* **(**2002) found this species by night lighting at the surface on the south shore of O‘ahu at the Natatorium (a War Memorial fronting Mamala Bay, Waikīkī) on 8 July 1996, and from the west coast of O‘ahu, Yokohama Bay, on 20 March 1998 at the surface during night collecting and fishing operations 1.3 km offshore over 180 to 550 m of water. Crow *et al.* (2006) reported it from night lighting surveys at the water’s surface in Ma‘alaea Harbor, Maui.

HAWAIIAN SPECIMENS EXAMINED: BPBM D1068 (five specimens) Waikīkī Natatorium, 3 Dec 2001; BPBM D1069 (1 specimen) offshore Yokohoma Bay, O‘ahu, 20 Mar 1998; BPBM D1117 (1 specimen) Ma‘alaea Boat Harbor, Maui, 7 Feb 2006; BPBM D1118 (5 specimens) Ma‘alaea Boat Harbor, Maui, 9 Feb 2006.

HAWAII DISTRIBUTION: O‘ahu and Maui, probably established throughout the main Hawaiian Islands.

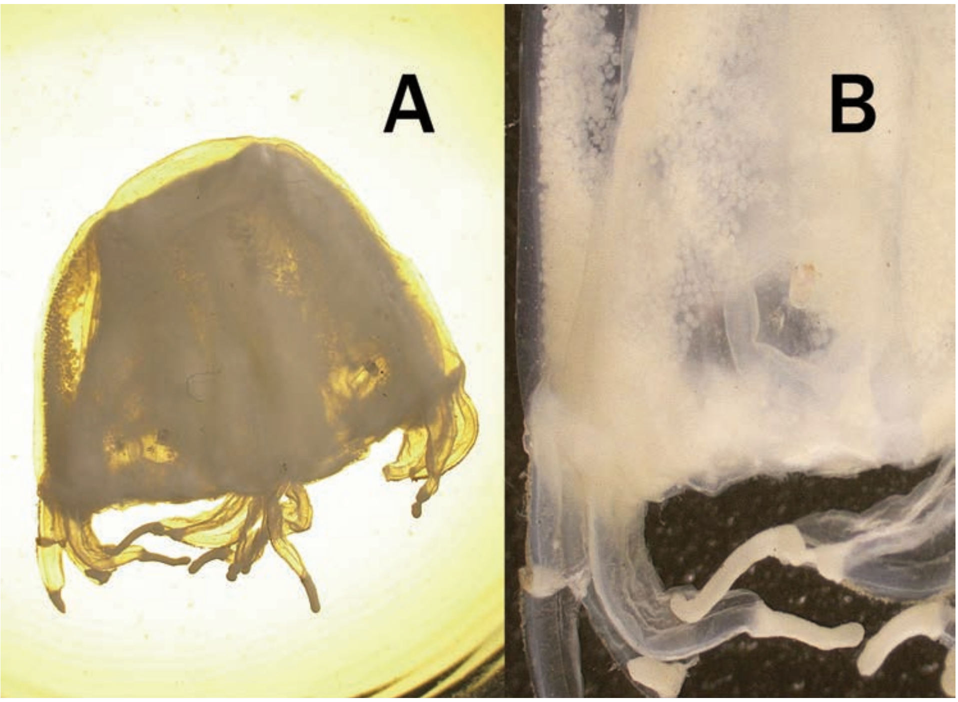

Figure 3. (**A**) Adult female *Tripedalia cystophora* from Enchanted lakes, O‘ahu; (**B**) Close up of eggs in gonadal lamellae of the Hawai‘i specimen.

RANGE: Widespread throughout the Pacific (Philippines, Japan, Hawai‘i, Guam, Vietnam, Thailand, Australia, New Zealand) and Indian Oceans (western Sumatra) (Lewis *et al.* 2008).

REMARKS: *Copula sivickisi* is a small sexually dimorphic cubomedusa ≤14 mm bell diameter with four distinctive adhesive pads that allow attachment to algae, rocks or coral during the day (Hartwick 1991, Long & Lewis 2005). Females with bell diameters larger than 2.5 mm have velar spots and gonads and mature at about 4.5 mm (Lewis *et al.* 2008). During courtship males attach a tentacle to the female and the female is brought in contact with the oral opening of the bell; the male then passes a spermatophore to the female that the female inserts into her manubrium (Lewis & Long 2005, Lewis *et al.* 2008). The female releases an embryo strand to complete reproduction (Lewis & Long 2005). In laboratory culture at 28 °C fertilization to budding was completed in 95 days (Toshino *et al.* 2014). This species is seasonal from May to August in Shirahama, Japan and then presumably dies after reproduction (Lewis & Long 2005). In Hawai‘i, this species was captured in February March, July, and December and probably occurs year round based on capture dates in Matsumoto *et al.* (2002) and Crow *et al.* (2006).

Genus TRIPEDALIA Conant, 1897

Tripedalia cystophora Conant, 1897

Fig. 3

General Description: Medusa with 12 tentacles in four interradial groups with each group having three tentacles. Velarium suspended by four perradial frenula with canals present. Stomach with relatively well developed suspensoria and four horizontal brush-shaped groups of gastric filaments (Conant 1897). Frown-shaped rhopaliar niche ostia (Gershwin 2005).

HAWAIIAN SPECIMENS EXAMINED: BPBM D2256 (9.7 mm BH; 8.3 mm BHR).

HAWAII DISTRIBUTION: A single mature female with eggs was collected 7 August 2011 by Keagan Young at a boat dock near mangroves in the Ka‘elepulu Canal, Enchanted Lakes, O ‘ahu (21°23'25"N, 157°43'45"W). The specimen has been deposited in the Bishop Museum (above).

RANGE: Widespread along tropical and subtropical mangrove habitats: Atlantic (Jamaica, Puerto Rico, Florida, Brazil; Orellana & Collins, 2010), Pacific (Costa Rica; Rodriquez-Saenz & Segura-Puertas 2009), Hawai‘i (herein), Indonesia (Derawan Island, GenBank EU272637, GQ849065) and Indian Oceans (Seychelles, Aldabra Atoll USNM 1078120, USNM 1102214).

REMARKS: Conant (1897) reported this species from the mangrove habitat of Port Henderson and Kingston Harbor, Jamaica. In Puerto Rico, *T. cystophora* feeds on copepods in shafts of daylight within the mangrove prop root forest (Buskey 2003). The visual system is made up of upper and lower lenses, pit and slit eyes (Garm *et al.* 2008). The upper eye lens and pit eye are oriented upward when swimming to help orient to the water surface and terrestrial objects (Garm *et al.* 2008). This allows navigation within the mangrove prop roots and positioning within the canopy (Garm *et al.* 2011). The lower eye lens and slit eye are oriented obliquely downward (Garm *et al.* 2007) presumably for feeding and obstacle avoidance.

Only one specimen of *T. cystophora* is known to date from the Hawaiian Islands. While the single recovered individual was a mature ovigerous female, we do not know if this species is established in Hawai‘i. Since 2011, we have searched for this species in Ka‘elepulu Canal, and nearby regions, both to obtain material for genetic analysis and to determine its status, on 19 August 2011, but without success.

Discussion

Four species of box jellyfish are reported from the Hawaiian Islands: *Alatina moseri*, *Carybdea arborifera*, *Copula sivickisi*, and *Tripedalia cystophora*. *Tripedalia cystophora* actively feeds during the day in the mangroves (Garm *et al.* 2012) while the other three species are nocturnal. *Alatina moseri* is the only species that appears monthly along O‘ahu shorelines and regularly impacts marine recreation, even closing Hanauma Bay on large influx days. Native Hawaiians relied heavily on coastal marine resources and were therefore intimately familiar with nearshore marine flora and fauna of the islands. Using native linguistics as a metric for the presence and importance of various taxa can be instructive, although not definitive, relative to what species were present pre-western contact in 1778. The Hawaiian language includes two names for the Indo-Pacific blue bottle *Physalia utriculus*, *pa‘i malau* and *po‘i malau*, and a generic jellyfish named *pololia*. However, no name was given to the box jellyfish *Alatina moseri* (Pukui & Elbert 1986). It is not clear whether *Alatina moseri* was transported to Hawai‘i with early ship traffic from the western Pacific or it was already wide spread throughout the Pacific basin prior to human mediated transport. Considering the painful nature of the *A. moseri* sting (Tamanaha & Izumi 1996, Yoshimoto & Yanagihara, 2002) it is unlikely that the people of pre-contact Hawai‘i would not have named this animal if it was commonly present in coastal waters.

Alatina moseri is an oceanic species that is present throughout the Hawaiian archipelago and its abundance appears to have increased in the coastal waters of O‘ahu from early 1900s to the late 1980s, including a dramatic increase in abundance since 1948 (Table 1). Beach counts in the 1990s have fluctuated in an oscillating pattern such that its abundance is difficult to predict (Chiaverano *et al.* 2013). Whether coastal alterations on O‘ahu have resulted in increased polyp survival or changing climatic conditions over the 20th century have favored recent proliferation is not clear. Currently, the other populated islands of Maui, Moloka‘i, Kaua‘i, Lāna‘i and Hawai‘i do not experience regular influxes of box jellyfish, although *A. moseri* has been documented offshore throughout the entire archipelago.

Based on genetic data published by Bentlage *et al.* (2010) and this paper, with limited Pacific Ocean sampling *Carybdea arborifera* is currently confirmed only from the Hawaiian Islands.

Table 2. **Hawaii molecular systematic data used as a way to confirm the taxonomic identity of box jellyfish in Hawai‘i**.

All matches to GenBank database had associated expectations values of 0.0 with the exception of COI for *Carybdea arborifera*, which matched *Tamoya ohboya* with an expectation value of 1e-138.

Taxon	**Gene Fragment**	**Locality and date *n* = number of individuals**	**GenBank accession number; fragment length (base pairs)**	**Top taxonomic match and percent sequence identity**
Alatina moseri	COI	Waikīkī Beach, O‘ahu 24 Feb 2014 *n* = 5 50 naut. mi off Kona, Big Island , 21 Aug 2012 *n* = 1	KM200330 (637)	*Alatina moseri* 98% identity JN642336
	18S	Waikīkī Beach, O‘ahu 10 Aug 2004 *n* = 4 Magic Island, O‘ahu 19 May 2009 *n* = 2 50 naut. mi off Kona, Big Island , 21 Aug 2012 *n* = 1 Waikīkī Beach, O‘ahu 24 Feb 2014 *n* = 16	KM200329 (538)	*Alatina mordens*[a] 100% identity GQ849082
Carybdea arborifera	COI	Kewalo Basin, O‘ahu 22 Apr 2004 *n* = 8 Kāne‘ohe Bay, O‘ahu 3 Jul 2013 *n* = 3	KM200333 (656)	*Tamoya ohboya*[b] 81% identity HQ824532
	16S	Snug Harbor, O‘ahu 26 May 2004 *n* = 1 Kewalo Basin, O‘ahu 22 Apr 2004 *n* = 7 Kāne‘ohe Bay, O‘ahu 3 Jul 2013 *n* = 2	KM200331 (585)	*Carybdea arborifera* 99% identity GQ849096
	18S	Snug Harbor, O‘ahu 26 May 2004 *n* = 1 Kewalo Basin. O‘ahu 22 Apr 2004 *n* = 7 Kāne‘ohe Bay, O‘ahu 03 Jul 2013 *n* = 3	KM200332 (528)	*Carybdea arborifera*, *C. mora*, *C branchii*, *C.* cf *rastonii* 100% identity GQ849091 GQ849094 GQ849093 GQ849089

Although the genes coding for 18S ribosomal RNA (18S rDNA) are widely used in phylogenetic reconstruction, this locus tends to have a relatively slow substitution rate, and therefore is most useful in recovering clades representing class and family relationships. Generally this locus cannot resolve congeneric nodes, therefore it is unable to provide the resolution required for species level recognition, such as within the genus *Carybdea*. In addition, there is increasing support, morphological (Bentlage & Lewis 2012; (capture localities, Mayer 1906, 1910) as well as molecular [data presented here and Bentlage *et al.* (2010)], that *Alatina moseri* is synonymous with *A. mordens* and a widespread lineage in the Pacific Ocean, including Hawaii and Australia.

The Hawaiian Islands are clearly vulnerable to marine introductions via ship traffic (ballast water and hull-fouling) and other sources (Carlton 1987, Apte *et al.* 2001). Eldredge & Carlton (2002) estimated 87% of the introduced marine invertebrates were transported to the Hawaiian Islands via hull-fouling, solid ballast and ballast water. Six primary incoming routes of transoceanic vessel-mediated introductions were detected for Hawai‘i, four from the western Pacific and one each from the eastern Pacific coast of North America and French Polynesia (Carlton, 1987). There is evidence that biogeographically isolated, relatively depauperate marine communities such as those of the Hawaiian Islands are highly susceptible to marine invasions (Hutchings *et al.* 2002). Introduced jellyfish *Cassiopea* spp. from two different ocean basins (Holland *et al.* 2004), *Phyllorhiza* sp. and *Aurelia* sp. from the western Pacific Ocean (Dawson *et al.* 2005; Carlton & Eldredge 2009) and *Mastigias* sp. (GLC pers. observ.) have become established in Hawai‘i. At least two of the box jellyfish in Hawai‘i, *Copula sivickisi* and *Tripedalia cystophora* appear to be introduced. Clearly, Hawai‘i is vulnerable to introduction of jellyfish and constant surveillance is necessary to keep additional species, especially the more dangerous “irukandji” taxa, from becoming established.

Worldwide jellyfish populations received relatively little attention until after the 1950s (Purcell, 2012). Natural jellyfish population fluctuations (including 10 yr and 20 yr cycles) in conjunction with solar and climatic cycles and anthropogenic changes to the environment including climate, eutrophication, overfishing, coastal construction, aquaculture and transport of nonindigenous species may have resulted in jellyfish proliferations (Purcell, 2012; Condon *et al.* 2013; Duarte *et al.* 2013). Detailed oceanographic, climatic, systematic and ecological studies are needed to better understand and predict changes in the distributions and the long-term impacts of cubomedusae on coastal ecology and recreation in the Hawaiian Islands. Such data will provide predictive value in our understanding of range expansion and management of established box jellyfish, as well as potential invasion by additional harmful box jellyfish species.

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Key to Table 2: CO1= mitochondrial cytochrome *c* oxidase subunit I; 16S= mitochrondrial rRNA small ribosomal subunit; 18S= nuclear small subunit (SSU) rRNA ribosomal gene

a. Match used to compare GenBank sample JN642336.1 (Smith *et al.* 2012) to this study sample KM200330.

b. There are no entries for 18S gene fragment from *Alatina moseri* in GenBank; however, 100% match from *A. moseri* from Waikīkī this study GenBank KM200329 to *A. mordens* from Australia GenBank GQ849082.1 supports the conclusion that *A. mordens* and *A. moseri* from Hawai‘i could be the same species as was detailed by Bentlage *et al.* (2010).

c. There are no COI sequences for *Carybdea arborifera* in GenBank; closet match is the sequence for *Tomoya ohboya* with an 81% match.

Francois Renoult for providing access to the 1877 specimen from Hawai‘i at the Muséum national d’histoire naturelle, and the Waikīkī Aquarium for providing partial travel fund support to GLC to examine the Paris specimen. We thank Landy Blair, Ralph Goto and James Howe for access to Ocean Safety and Lifeguard Services records, Cheryl Lewis for providing information on USNM specimens, Keagan Young for collecting the *Tripedalia* specimen, and Mark Heckman for several other box jellyfish specimens.

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Porcellanopagurus eldredgei, a New Species of Bivalve-carrying Hermit Crab from Guam (Crustacea: Decapoda: Anomura: Paguridae)

Roy K. Kropp
Pacific Northwest National Laboratory, Marine Sciences Laboratory, 1529 W. Sequim Bay Rd., Sequim, Washington 98382, USA; email: Roy.Kropp@pnnl.gov

Abstract. A new species of bivalve-carrying hermit crab, *Porcellanopagurus eldredgei*, **n.sp.**, from Guam is described and illustrated, based on collections made from a deep-water shrimp trapping program. The new species is recognized primarily by having a straight, rather than curved, supraoribital border.

Introduction

The hermit crab genus *Porcellanopagurus* Filhol, 1885 includes 13 species (McLaughlin *et al*. 2010). Four species (*P. edwardsi* Filhol, 1885; *P. tridentatus* Whitelegge 1900; *P. platei* Lenz, 1902, and *P. japonicus* Balss, 1913) were described between 1885 and 1913, but the fifth species (*P. truncatifrons* Takeda, 1981) was not described until 1981. From 1985 to 2000, an additional eight species were described (*P. nihonkaiensis* Takeda, 1985; *P. belauensis* Suzuki & Takeda, 1987; *P. foresti* Zarenkov 1990; *P. jacquesi* McLaughlin, 1997; *P. adelocercus* McLaughlin & Hogarth, 1998; *P. chiltoni* de Saint Laurent & McLaughlin, 2000; *P. filholi* de Saint Laurent & McLaughlin, 2000; and *P. haptodactylus* McLaughlin, 2000). Komai & Takeda (2006) provided revised descriptions of two species from Japan, *P. japonicus* and *P*. *nihonkaiensis*. Of known species of *Porcellanopagurus*, two were found relatively near the Mariana Islands, *P. truncatifrons* from the Ogasawara Islands and *P. belauensis* from Palau. During a trapping program conducted in the late 1970s to collect deep-water shrimp (*Heterocarpus* spp.) from the sea surrounding Guam (Wilder, 1979), two specimens of *Porcellanopagurus* were collected that were not referable to any known species.

Material and Methods

The description of the morphology of the new species, except for the telson, is based on the holotype. Because of damage to the telson of the holotype, the telson of the paratype is described. Where the state of a particular character found on the paratype differs from that found on the holotype, the state found on the paratype is enclosed by brackets. Abbreviations used are: cl, carapace length; cw, carapace width; ft, feet; m, meters; mm, millimeters; BPBM, Bernice P. Bishop Museum, Honolulu, Hawai‘i.

Family Paguridae

Genus *Porcellanopagurus* Filhol, 1885

Porcellanopagurus eldredgei, new species

Figs. 1–4

Type material. *Holotype*: male, cl. 15.1 mm, cw. 21.7 mm; GUAM, Double Reef, Sta. 96, 1200 ft (354 m); 30 Dec 1976; BPBM S16174. *Paratype*: male, cl. 10.5 mm, cw. 16.1 mm; same collection data, BPBM S16175. Each holding a valve of an undescribed species of *Plicasesta* Vokes, 1963 (Mollusca, Bivalvia, Limidae).

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Fig. 1. *Porcellanopagurus eldredgei* new species, holotype male (BPBM S16174), Guam. Dorsal view.

Description. Shield about 1.4 times broader than long, widening posteriorly, flattened in lateral view; surface roughened by short scalloped ridges bearing simple setae anteriorly, with furrows approximately defining regions of shield; gastric region slightly swollen, anterior portion partly divided by median furrow; posterior part marked by well-defined furrow; lateral borders with numerous simple setae (Figs. 1, 2). First lateral lobe with 3 teeth; anterior tooth rounded, without spine; middle tooth subacute; posterior tooth poorly developed, rounded. Second lateral lobe produced anteriorly, triangular, narrowly rounded at tip. Third lateral tooth (“posterior carapace lateral lobe” of McLaughlin 2000) subtriangular, transverse, not produced anteriorly and broadly rounded at tip. Cardiac region not inflated, faintly defined. Rostrum narrowly triangular, lateral margins straight in dorsal view, very slightly inflated above base of eyestalks, tip rounded. Supraorbital border straight, transverse; external orbital tooth slightly produced anteriorly, rounded, lateral border oblique to median line.

Eyestalk stout, about 2 times longer than rostrum, markedly constricted at middle portion, with scattered simple setae.

Basal article of antenna with serrated spine forming lateral distal angle; mesial angle short, broad, setose. Third segment 1.4 times longer than antennal acicle. Antennal acicle elongate, narrow, longer than second segment.

Distal 5 segments of third maxilliped subequal in length; mesial surface of ischium with longitudinal row of conical teeth (crista dentata) on mesial edge, 1 spine distally near lateral margin; merus slightly longer than ischium, with distal spine on lateral margin; propodus with simple, serrate setae distally on mesial margin; dactylus with numerous serrate setae mesially.

Chelipeds unequal in mass; right cheliped massive (Figs. 3A, B). Merus with dense patch of setae mesially, spines on dorsal and ventral margins. Carpus with oblique rugae, rugae with simple setae on anterior edges; outer surface concave on upper half, convex on lower half. Palm swollen;

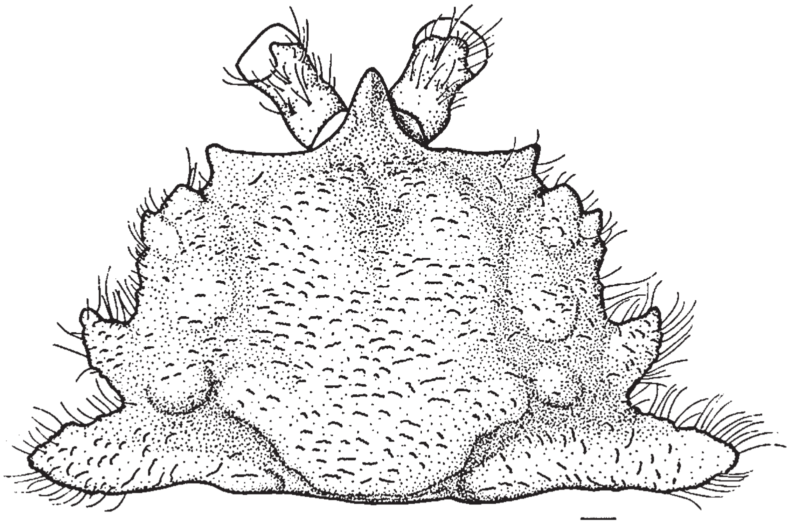

Fig. 2. *Porcellanopagurus eldredgei* new species, holotype male (BPBM S16174), Guam. Dorsal view of anterior part of carapace. Scale = 1.0 mm.

upper margin with low, broad tubercles forming ridge, lower margin with longitudinal rugae becoming flattened circular tubercles forming slight ridge on upper margin, inner surface finely granular. Fixed finger with 6 teeth; dactylus with 7 teeth.

Left cheliped slender (Fig. 3C). Ischium irregularly tuberculate, with elongate simple setae. Merus compressed proximally, lower border tuberculate, dorsal surface ridged, with setae. Carpus slightly greater than merus; outer surface flattened, with regular shallow depression; inner surface inflated; surfaces with scattered rugae, each with setae on distal margin. Palm slightly compressed, with scattered setose rugae. Fingers shorter than carpus, about 2 times length of manus, curved mesially; cutting edges denticulate.

Pereopods 2 and 3 similar in size and shape, (Figs. 4A, B); right pereopod 2 reaching base of fingers of right cheliped; pereopod 3 slightly longer than pereopod 2. Merus bicarinate, irregularly tuberculate on ventral surface; dorsal margin with setae-bearing transverse ridges, surface with scalloped rugae having setae extending from distal margin, without spines. Carpus with longitudinal ridge comprised of scalloped setae-bearing rugaedorsal to midline of lateral surface; dorsal margin similar to that of merus. Propodus with longitudinal depression near lower margin; upper margin similar to that of merus; ventral margin with 8 [6] single or paired movable spines; ventrodistal angle with 3 [2] spines; dorsodistal angle with 2 [1 or 2] smaller spines. Dactylus compressed, with slight longitudinal depression along midline; lateral surface with some setae-bearing rugae; ventral margin with 13 [11 or 12] (pereopod 2) and 14 [14 or 15] (pereopod 3), flattened movable spines increasing in size distally.

Pereopod 4 very setose. Carpus expanded distally on dorsal surface, with scattered setae-bearing rugae. Propodus compressed, dorsal margin scalloped, ventral margin extending beyond joint with dactylus, not pointed terminally, lateral surface slightly concave. Dactylus strongly curved, with terminal spine; ventral surface with conical spines on distal 2/3, increasing in size distally.

Pereopod 5 smaller than pereopod 4, chelate. Propodus moderately setose, with patch of scales distally on dorsal surface; ventral margin densely setose, distal border expanded transversely, spoon-tipped, lined with conical spines. Dactylus broadly flattened; dorsal surface setose, with scales distally; ventral surface concave, distal margin lined with conical spines.

Endopod of uropod elliptical, with 6 [5] rows of scales; exopod of uropod oval, with 11 [9] rows of scales.

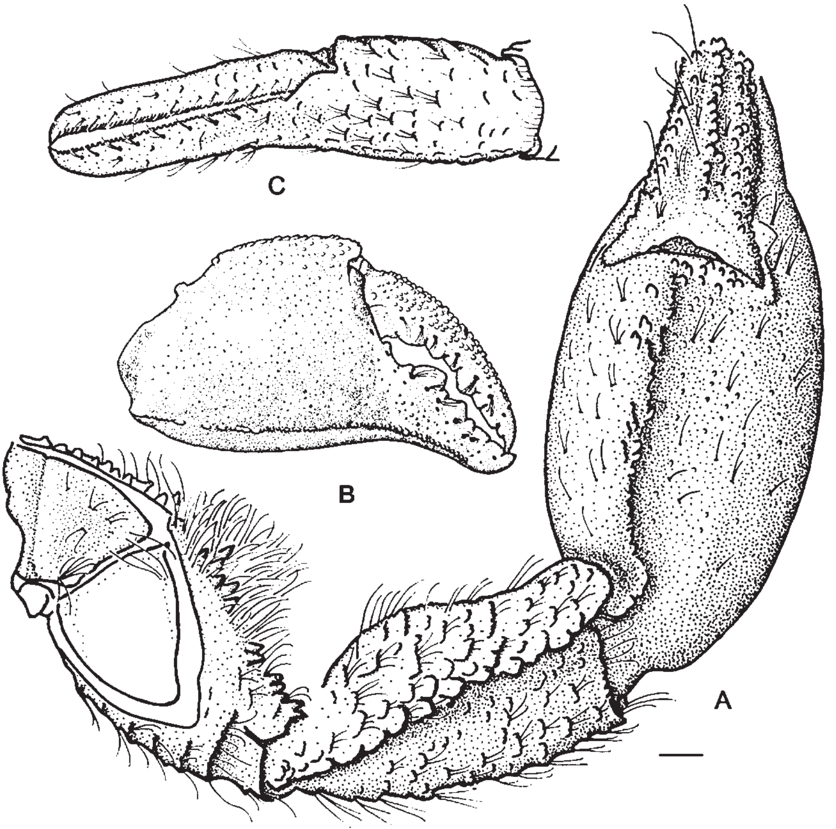

Fig. 3. *Porcellanopagurus eldredgei* new species, holotype male (BPBM S16174), Guam. **A**, mesial view of right cheliped (tip of dactyl not visible). **B**, dorsal view of right cheliped manus. **C**, dorsal view of left cheliped manus. Scales: A, C = 1.5 mm, B = 0.75 mm.

Telson (paratype) wider than long, with median longitudinal depression, with median transverse ridge interrupted mesially by longitudinal depression.

Etymology. The new species is dedicated to, and named for, the late Lucius G. Eldredge who directed the trapping program on which the crabs were collected. Lu was my professor, mentor, and most of all my friend. He and his family made me and many other graduate students feel as though we were part of theirs.

Remarks. The new species is the 14th species of *Porcellanopagurus* to be described. Eleven *Porcellanopagurus* species, including *P. eldredgei*, new species, have a triangular or subtriangular rostrum (McLaughlin 2000). The remaining three species have a truncate rostrum. The species that have a triangular or subtriangular rostrum can be separated into two groups by the form of the second lateral lobe of the shield (posterolateral projection of the carapace), which is bluntly rounded in *P. belauensis*, *P. chiltoni*, *P. edwardsi*, and *P. nihonkaiensis*. The posterolateral projection is acute or subacute in *P. eldredgei*, *P. filholi*, *P. foresti*, *P. jacquesi*, *P. japonicus*, *P. platei*, and *P. tridentatus*. Among these species, the lateral margins of the rostrum are straight in *P. eldredgei*, *P. filholi*, *P. foresti*, and *P. platei* but slightly sinuous in the other three species.

Porcellanapogurus eldredgei can be distinguished from *P. filholi* and *P. foresti* by the transverse orbit, which is moderately to strongly concave in the other species. Additionally, the rostrum is rel-

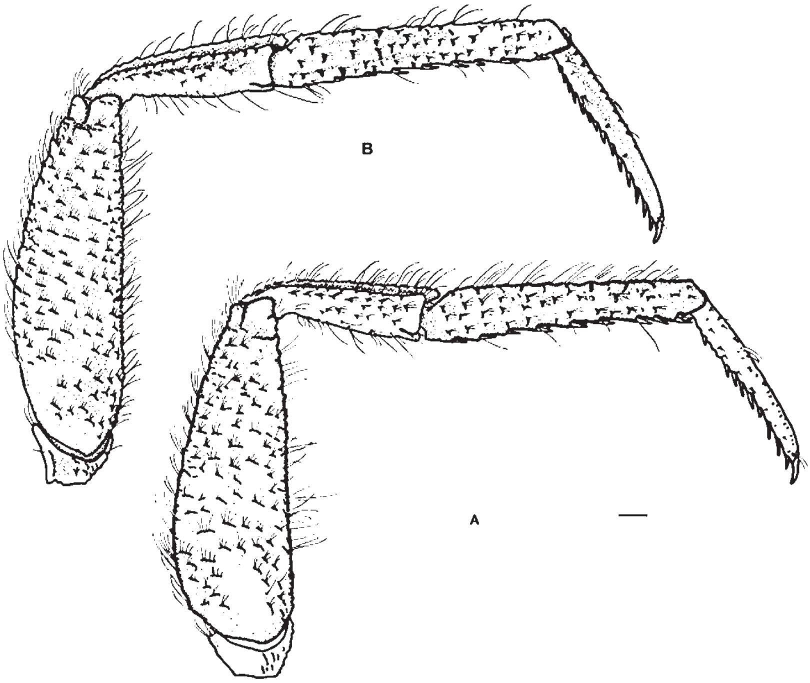

Fig. 4. *Porcellanopagurus eldredgei* new species, holotype male (BPBM S16174), Guam. **A**, lateral view of right pereopod 2; **B**, lateral view of right pereopod 3. Scale: = 1.5 mm.

atively short (extends about half length of the eyestalk, not reaching the base of the cornea) and slightly rounded in *P. eldredgei,* but it is relatively long (overreaches half the length of the eyestalk, reaching or almost reaching the base of cornea) and somewhat to sharply acute in the other two species. The anterolateral angles of the carapace are rounded and weakly directed anteriorly in *P. eldredgei,* but they are rather acute and sharply directed anteriorly in *P. filholi* and *P. foresti*.

Porcellanopagurus eldredgei occurs relatively near the type localities of two other species, *P. truncatifrons* (Ogasawara Islands) and *P. belauensis* (Palau), but it is easily distinguished from them by the combinations of characters discussed above.

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A New Deep-water Species of *Forestiana* (Crustacea: Decapoda: Brachyura: Xanthidae) from Taiwan, with a Clarification of the Name *F. depressa* (White, 1848)

Peter K. L. Ng
*Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore,
Kent Ridge, Singapore 119260, Republic of Singapore; email: dbsngkl@nus.edu.sg*

Abstract. A new species of deep-water xanthid crab, *Forestiana lucius*, is described from Taiwan. The species can easily be distinguished from congeners by its well-developed anterolateral teeth, pigmentation on the chela and form of the male first gonopod. This is the fifth species of *Forestiana* described and the only one known from deep water. *Pilumnus granulatus* Krauss, 1843, is the senior subjective synonym of *Xantho depressus* White, 1848, the type of *Forestiana* Guinot & Low, 2010, and the species should now be known as *Forestiana granulata* (Krauss, 1843).

Introduction

Guinot (1976: 260), in her reappraisal of the Actaeinae Alcock, 1898, redefined several genera using diagnostic characters based on the male thoracic sternum. This included *Forestia* Guinot, 1976, which was defined mainly on its elongated male anterior thoracic sternum (sternites 1–4), the male sternoabdominal cavity reaching to only about a third the length of thoracic sternite 4, and the presence of a longitudinal groove on male thoracic sternite 4 anterior of the sternoabdominal cavity. Guinot & Low (2010) later noted that the name *Forestia* Guinot, 1976, was preoccupied by *Forestia* Trinchese, 1881 (Mollusca) and proposed *Forestiana* as a replacement name. Four species of *Forestiana* are now known: *F. abrolhensis* (Montgomery, 1931), *F. depressa* (White, 1848) (type species by designation), *F. pascua* (Garth, 1985) and *F. scabra* (Odhner, 1925), all from the Indo-Pacific. Recently, a specimen of a new *Forestiana* collected from off deep-water port was obtained in northeastern Taiwan. The description of the new species and comparisons with congeners form the basis of the present paper.

Methods

The terminology used follows that used in Serène (1984). The abbreviations G1 and G2 are used for the male first and second gonopods, respectively. Measurements provided, in millimetres, are of the carapace width and length, respectively. The type specimen is deposited in the National Taiwan Ocean University (NTOU), Keelung, Taiwan.

Taxonomy

Forestiana Guinot & Low, 2010

Forestia Guinot, 1976 (type species *Xantho depressus* White, 1848, by original designation; name preoccupied by *Forestia* Trinchese, 1881 [Mollusca]; gender feminine)
Forestiana Guinot & Low, 2010 (replacement name for *Forestia* Guinot, 1976; gender feminine)

Remarks. The name of the type species, *Xantho depressus* White, 1848b (type locality Philippines), needs to be clarified. This taxon has two synonyms: *Pilumnus granulatus* Krauss, 1843 (type locality South Africa), and *Pilumnus planus* Edmondson, 1931 (type locality Hawai‘i) (cf. Odhner 1925,

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Takeda 1980). While *Pilumnus granulatus* Krauss, 1843, predates *Xantho depressus* White, 1848, as was highlighted by Odhner (1825), the former name has never been used. Odhner (1925: 38) commented that "KRAUSS hat indessen wirklich ein kleines Exemplar der betreffenden Form unter einem anderen Namen beschrieben, nämlich als *Pilumnus granulatus* (Stg. M.), welcher Artname jedoch in Verbindung mit *Actaea* nicht verwendet werden kann". This was probably because the type species of *Actaea* De Haan, 1833, was *Actaea granulata* (Audouin, 1826). However, because this species was originally described in *Cancer*, i.e. as *Cancer granulatus* Audouin, 1826, this name is a junior primary homonym of *Cancer granulatus* Linnaeus, 1758 (which is today a species of *Calappa*, Calappidae) (see discussion in Guinot & Cleva 2011: 112–115). As such, the name *Cancer savignii* H. Milne Edwards, 1834, a junior synonym *Cancer granulatus* Audouin, 1826, has to be used instead, and the species is now known as *Actaea savignyi* (H. Milne Edwards, 1834) (see Ng *et al.* 2008: 194). In any case, *Pilumnus granulatus* Krauss, 1843, is no longer regarded as a member of *Actaea*, as it was during Krauss' (1843) time. Under the terms of Articles 59.2 and 60.2.1 of the Code (ICZN, 1999), *Pilumnus granulatus* Krauss, 1843, is now an available name as it is currently classified in *Forestiana* Guinot & Low, 2010. There is thus no reason to continue using *Xantho depressus* White, 1848, over *Pilumnus granulatus* Krauss, 1843 (cf. Guinot 1976, Ng *et al.* 2008); and the species should now be known as *Forestiana granulata* (Krauss, 1843). The type species for *Forestiana* Guinot & Low, 2010, however, remains as *Xantho depressus* White, 1848, a junior subjective synonym of *Pilumnus granulatus* Krauss, 1843.

***Forestiana lucius*, sp. nov.**

Figs. 1–4

Material examined. Male holotype (12.7 × 9.3 mm) (NTOU), Tashi deep-water port, from deep water greater than 200 m, Ilan Province, northeastern Taiwan, via trawlers, coll. T.-Y. Chan, 19 September 2011.

Diagnosis. Carapace 3M separated by submedian longitudinal groove, frontal margin distinctly bilobate (Figs. 1, 2A, B); external orbital tooth low, forming broad tuberculate lobe with low first anterolateral tooth; rest of margin with 3 well-developed sharp, triangular teeth, third tooth smallest (Figs. 1, 2A); third maxilliped with quadrate merus, anteroexternal angle acute (Fig. 3D); pigmentation on pollex extends to more than half length of palm, forming transverse band across inner surface (Fig. 3F–I); merus, carpus and propodus of ambulatory legs covered with granules and long, short stiff setae which do not obscure surface (Figs. 1, 3E); male abdomen transversely narrow, somite 6 rectangular, lateral margins sinuous, longer than telson (Figs. 3A, 4A); G1 gently sinuous, distal part distinctly hooked with sharply tapering tip, subdistal surfaces with long simple setae and spinules (Fig. 4B–D).

Description. Carapace wider than long; dorsal surface of carapace evenly convex longitudinally and transversely; regions clearly demarcated, separated by distinct grooves, regions covered with numerous granules of varying sizes, those on posterior areas relatively smaller; 3M separated by submedian longitudinal groove (Figs. 1, 2A). Frontal margin distinctly bilobate, lobes separated by deep U-shaped cleft; margins lined by small granules; lateral lobe acutely triangular, clearly separated from frontal margin by low cleft; supraorbital margin granulated; orbit ovate; eye completely filling orbit; peduncle elongated, cornea relatively large, completely pigmented (Figs. 1, 2A, B). External orbital tooth low, tuberculate; not clearly demarcated from first anterolateral tooth, together forming broad tuberculate lobe (Figs. 1, 2A). Anterolateral margin arcuate, with 3 distinct, well-developed sharp, triangular teeth, third tooth smallest; lateral margins and dorsal surfaces covered with small granules; clearly demarcated from gently concave posterolateral margins (Figs. 1, 2A). Posterior carapace margin gently sinuous, granulated; with submarginal row of small granules anterior to it (Figs. 2A, 3C). Suborbital margin distinctly granulated, inner tooth low, broad; pterygostomian, subhepatic and suborbital regions granulated (Figs. 2B). Antennules folding almost laterally; antenna with basal article quadrate, covered with 1 large and 1 small sharp granule, mobile; flagellum short, at

Fig. 1. *Forestiana lucius* sp. nov., male holotype 12.7 × 9.3 mm (NTOU), Taiwan. Color in life (photograph courtesy of T.-Y. Chan).

base of orbital hiatus (Fig. 2B). Epistome transversely rectangular; posterior margin sinuous with with broad median triangle separated by deep median fissure, lateral margins concave; endostome smooth, without ridge (Fig. 2B).

Third maxilliped relatively short; ischium subrectangular, with shallow submedian sulcus, inner margin dentate, margins and adjacent areas granulated; merus quadrate, margins and adjacent areas granulated, median art with several rounded granules, anteroexternal angle acute; exopod stout, distal end reaching to just before distal margin of merus, inner margin with subdistal tooth, flagellum elongate, as wide as merus (Fig. 3D).

Only one cheliped present; outer surfaces with numerous tubercles and granules, with numerous interspersed long and short stiff setae which do not obscure margins or surfaces; inner surfaces relatively smooth (Fig. 3F–I). Basis-ischium lined with small granules; merus short, rounded; carpus ovate, inner angle with numerous rounded granules (Figs. 1, 3F–I). Chelae short, stout, fingers shorter than palm, pigmented black; pigmentation on pollex extending into outer and inner surfaces of palm, outer part forming large triangular patch on distal half of chela, inner part reaching to 2/3 of palm and extending dorsally to margin to form band-like pattern (Figs. 1, 3F–I). Pollex with 3 longitudinal grooves; cutting edge with 5 teeth; tip sharp; dactylus with 2 longitudinal ridges, proximal half of upper margin distinctly granulated, cutting edge with 4–6 teeth of various sizes, tip sharp (Figs. 3F–I).

Ambulatory legs relatively short, stout; second pair longest; fourth pair shortest; surfaces covered with long and short stiff setae which do not obscure surface (Figs. 1, 3E). Basis-ischium surface with small granules. Outer surfaces of merus, carpus and propodus covered with small tubercles or granules (Figs. 1, 3E). Merus dorsal margin armed with numerous sharp sharp granules; ventral margin with smaller sharp granules (Figs. 1, 3E). Dorsal margin of carpus granulated, ventral margin smooth (Fig. 3E). Dorsal margin of propodus tuberculated, ventral margin of carpus with sharp tubercles (Figs. 1, 3E). Dactylus gently curved to almost straight, surface covered with setae; no dactylo-propodal lock discernible (Figs. 1, 3E).

Anterior thoracic sternum elongated, surface distinctly pitted, granulated; sternites 1 and 2 completely fused, triangular, with gently concave lateral margins; separated from sternite 3 by deep

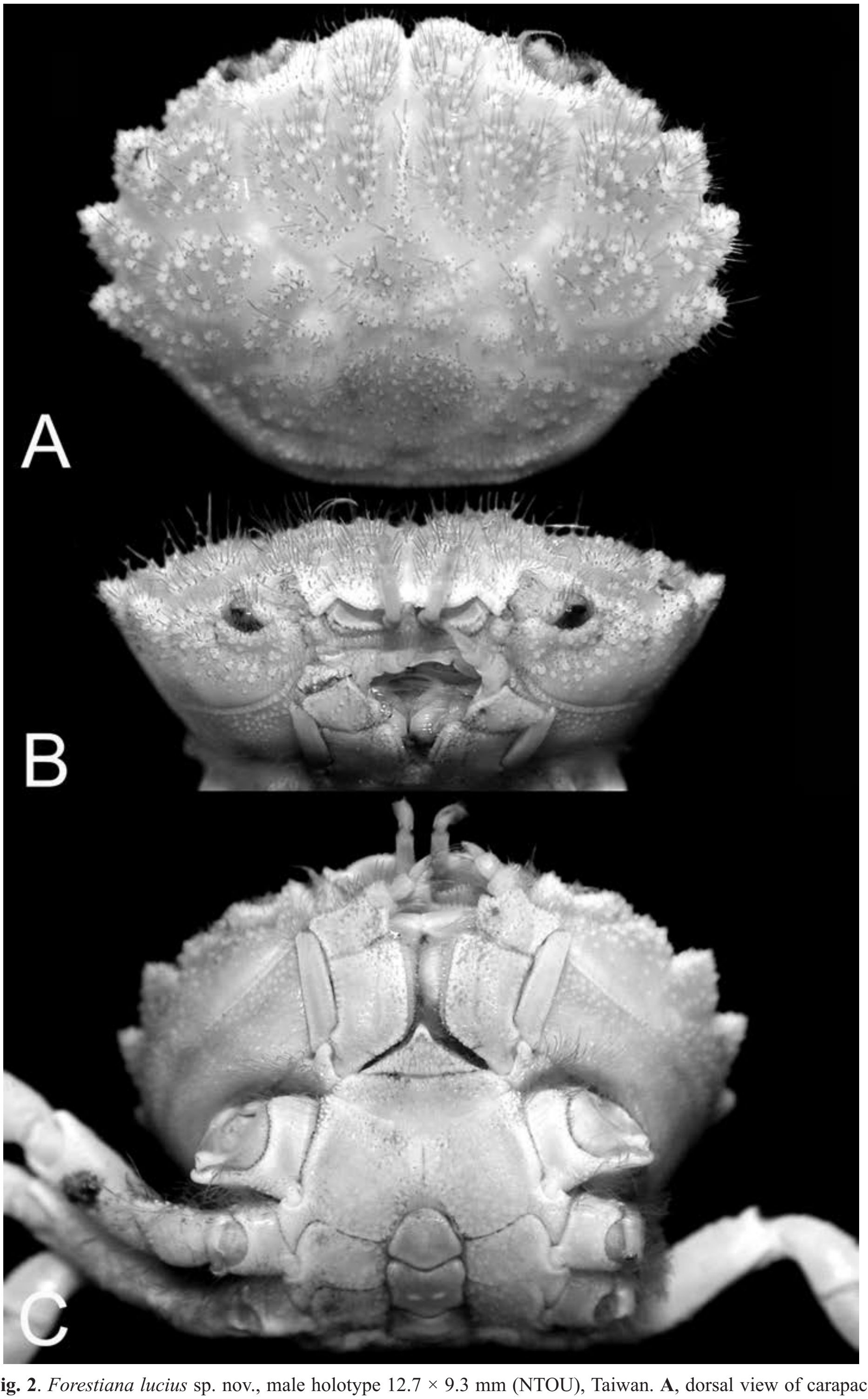

Fig. 2. *Forestiana lucius* sp. nov., male holotype 12.7 × 9.3 mm (NTOU), Taiwan. **A**, dorsal view of carapace; **B**, frontal view of carapace; **C**, ventral view showing anterior thoracic sternum and abdomen.

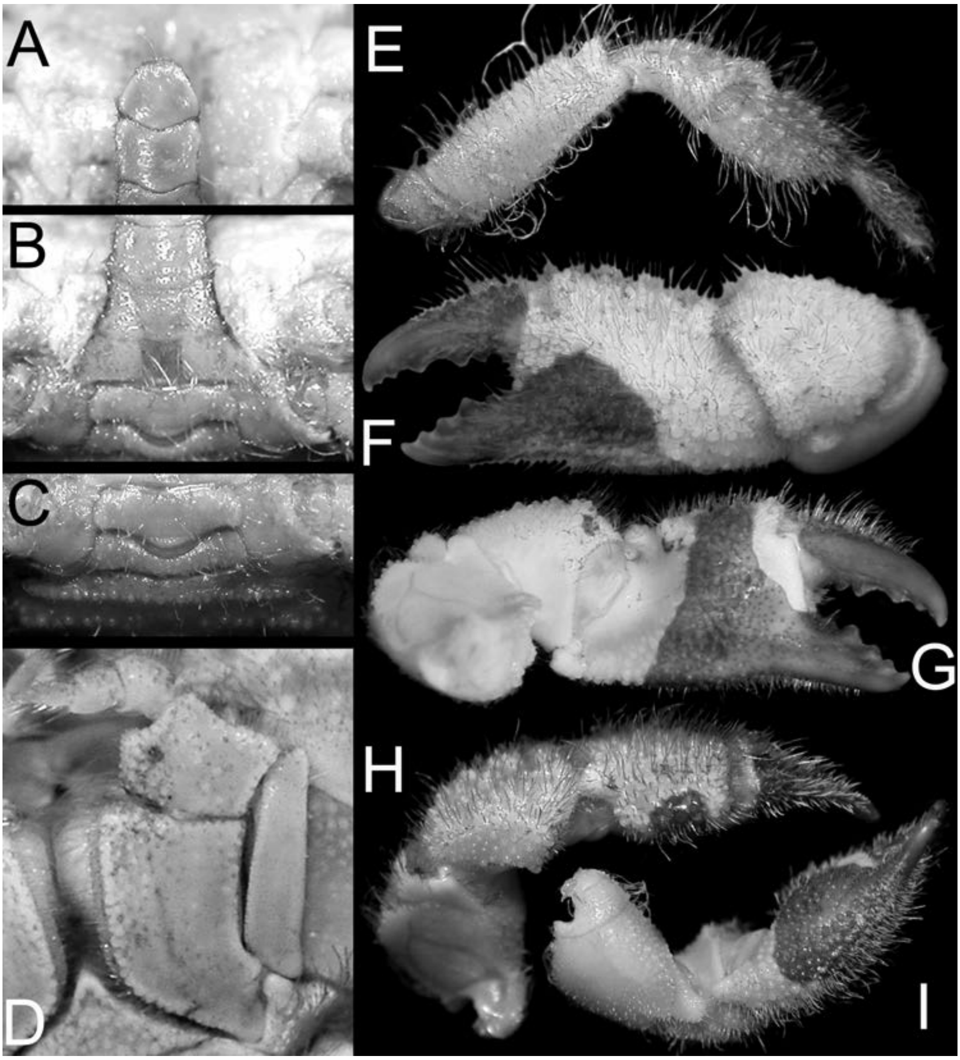

Fig. 3. *Forestiana lucius* sp. nov., male holotype 12.7 × 9.3 mm (NTOU), Taiwan. **A**, male abdominal somite 6 and telson; **B**, male abdominal somites 2–5; **C**, male thoracic somites 1 and 2, and posterior margin of carapace; **D**, left third maxilliped; **E**, right fourth ambulatory leg; **F**, outer view of left chela; **G**, inner view of left chela; **H**, dorsal marginal view of left chela; **I**, ventral marginal view of left chela.

suture; sternites 3 and 4 fused but lateral sutures between them just visible, with shallow submedian grooves discernible; sternite 4 with distinct long, deep longitudinal groove (median line) anterior of sternoabdominal cavity, lateral surfaces granulated; sutures between sternites 4–6 medially interrupted; sutures between sternites 6–8 complete; longitudinal groove (median line) present between sternites 6–8; median part of sternite 6 constricted, very narrow compared to wider median parts of sternites 7 and 8 (cf. pattern 3 of Guinot *et al.* 2013: 263); sternoabdominal cavity reaching to ca. 1/3 length of fused sternites 3 and 4; surfaces near sutures and cavity distinctly granulated, other surfaces pitted to smooth (Fig. 2C). Male abdominal locking mechanism is short peg-like process on anterior third of sternite 5.

Male abdomen transversely narrow; surfaces of somites 1–5 pitted with lateral margins granulated (Figs. 3B, C, 4A). Somites 1 and 2 longitudinally narrow, completely covering surfaces of tho-

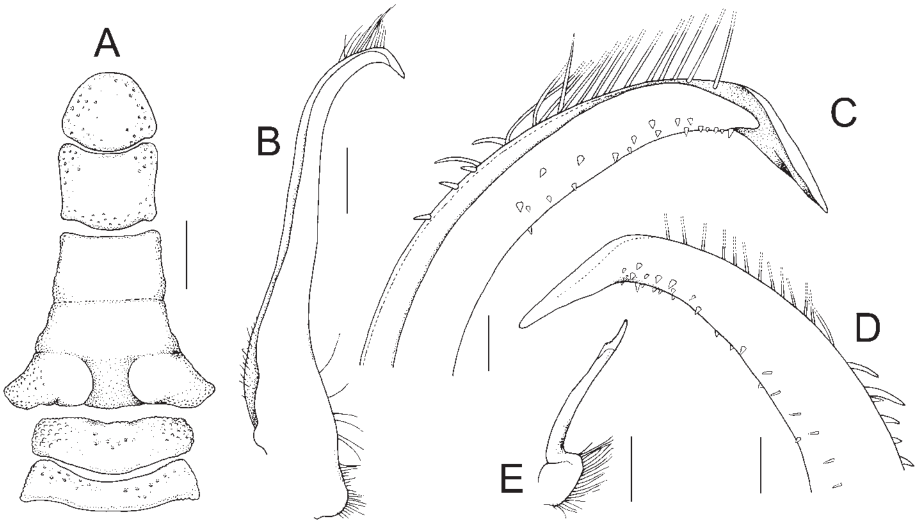

Fig. 4. *Forestiana lucius* sp. nov., male holotype 12.7 × 9.3 mm (NTOU), Taiwan. **A**, male abdomen; **B**, ventral view of left G1; **C**, ventral view of distal part of left G1; **D**, dorsal view of distal part of left G1; **E**, left G2. Scales: A = 1.0 mm; B, E = 0.5 mm; C, D = 0.1 mm.

racic sternum between coxae of last pair of ambulatory legs, sternite 8 completely covered; somites 3–5 completely fused, median sutures barely visible; lateral margins concave; somite 6 rectangular, lateral margins sinuous; slightly longer than telson; telson triangular, lateral margins gently convex, tip rounded (Figs. 3A–C, 4A).

G1 elongate, gently sinuous, distal part distinctly hooked, tip sharply tapering, subdistal surfaces with long simple setae and spinules (Figs. 4B–D). G2 short, ca. a third length of G1; proximal part sinuous, distal part spatuliform (Fig. 4E).

Color. In life (Fig. 1), the carapace, outer surfaces of the cheliped and parts of the ambulatory legs are bright orange. The posterior part of the carapace and ventral surfaces are white. The dark brown pigmentation on the fingers extends substantially into the palm.

Etymology. *Lucius*: named in honor and the memory of Lucius Gilbert Eldredge — an old friend, esteemed colleague and fellow carcinologist, whose many contributions in marine biology as well as his stewardship of the Pacific Science Association have left an indelible mark on Pacific science. Lu’s extensive explorations of the Pacific included Taiwan, and it is therefore appropriate that this new species is named after him. His first name is here used as a noun in apposition.

Remarks. Serène (1984: 103) established *Meractaea* Serène, 1984, a genus which has a male thoracic sternum similar to that of *Forestiana* but the carapace is proportionately broader, the regions have strong rounded tubercles without setae, the ambulatory legs are proportionately longer and the median part of the merus of the third maxilliped has a prominent median tubercle or swelling (cf. Serène 1984; Davie 1993, 1997). The present new species is referred to *Forestiana* because the dorsal surfaces of the carapace are covered with small granules and scattered setae (Figs. 1, 2A, B), the ambulatory meri are relatively short (Figs. 1, 3E) and merus of the third maxilliped has no median swelling or tubercle (Fig. 3D).

All known *Forestiana* species are relatively shallow water species and have been collected in waters less than a hundred metres. *Forestiana granulata* has been reported from South Africa to Philippines, Japan, and Hawai‘i; *F. scabra* is known from Malaysia, Sunda Islands, Vietnam and Australia; while *F. abrolhensis* has been found in Australia and Zanzibar (see Guinot, 1976; Serène, 1984). *Forestiana lucius* sp. nov. is unusual because it was trawled from waters below 200 m. In this respect, *F. lucius* has similar habits to species of *Meractaea* which are found are depths 100 m and deeper (see Serène 1984; Davie 1993, 1997; Komatsu & Takeda 2011).

Forestiana lucius can be distinguished from *F. abrolhensis*, *F. granulata* and *F. scabra* by its prominently developed anterolateral teeth that are large and dentiform (Figs. 1, 2A) (vs. low and rounded in the above three species, see Guinot 1976: pl. 18 figs. 1–3). In its well-developed anterolateral teeth, *F. lucius* resembles *F. pascua* (from Easter Island), which is known only from a female specimen. However, *F. lucius* can be separated from *P. pascua* in having the dorsal surface of the carapace (especially the posterior part) more prominently granulated (Figs.1, 2A) (granules more sparse with the posterior part almost smooth in *F. pascua*, see Garth 1985: fig. 1); the anteroexternal angle of the merus of the third maxilliped more acute (Fig. 3D) (vs. more rounded in *F. pascua*, see Garth 1985: fig. 4); and the fingers of the chela are pigmented black with the pigmentation extending into a large part of the palm (Figs. 1, 3F–I) (vs. fingers brown with the pigmentation not extending to the palm in *F. pascua*, see Garth 1985: figs. 2, 3). The pigmentation pattern on the chela in *F. lucius* is the most extensive in any of the known *Forestiana* species. *Forestiana granulata* and *F. abrolhensis* have the pigmentation on the pollex extending partially onto the lower part of the palm (see Guinot 1976: pl. 18, fig. 1; Serène 1984: pl. 15, fig. D) while in *F. scabra*, it is restricted to the fingers (see Guinot 1976: pl. 18, fig. 2; Serène 1984: pl. 15, fig. E).

The G1 of *F. granulata* and *F. scabra* are quite different, with the distal part gently curved upwards (Guinot 1976: figs. 45a–c) while in *F. lucius*, it is distinctly hooked (Figs. 4B–D). *Forestiana abrolhensis* and *F. pascua* are only known from females.

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The identity of *Leptomithrax sinensis* Rathbun, 1916, and the description of *L. eldredgei,* sp. nov. from Hong Kong (Crustacea: Decapoda: Brachyura: Majidae)

Bertrand Richer de Forges
5, rue Félix Franchette, 98800 Nouméa, New Caledonia
E-mail: b.richerdeforges@gmail.com

Peter K.L. Ng
Lee Kong Chian Natural Museum, Faculty of Science,
National University of Singapore, Kent Ridge,
Singapore 119260, Republic of Singapore
Email: dbsngkl@nus.edu.sg

Abstract. A new species of majid crab, *Leptomithrax eldredgei*, **sp. nov**. is described from Hong Kong. The species is most similar to the poorly known *L. sinensis* Rathbun, 1916, described from Hong Kong only on the basis of a carapace. *Leptomithrax sinensis* is figured for the first time, and differs from *L. eldredgei* in the structure and armature of the carapace.

Introduction

Members of the majid genus *Leptomithrax* Miers, 1876, are separated from species of the closely related genus *Maja* Lamarck, 1801, primarily by having the antennal flagellum distinctly excluded from the orbit (see Sakai 1976, Griffin & Tranter 1986). Fourteen species are recognized at present, all from temperate and cold waters in northwestern Asia and Australasia (Griffin & Tranter 1986, Ng *et al.* 2008). Four species are known from northwestern Asia: *L. edwardsii* (De Haan, 1835), *L. bifidus* (Ortmann, 1893), *L. sinensis* Rathbun, 1916, and *L. kiiensis* Sakai, 1969 (Griffin 1976, Sakai 1976, Griffin & Tranter 1986). In a recent revision of *Maja*, Ng & Richer de Forges (in press) reappraised the taxonomy of *L. kiiensis* and reassigned it to a new genus. *Leptomithrax sinensis* is poorly known species known only from a carapace from East Asia (Rathbun 1916), and has never been figured.

We here diagnose a new species of *Leptomithrax* collected from off Hong Kong. It is compared with its closest congener, *L. sinensis*, and the type carapace of the latter species is figured for the first time.

Methods

Specimens examined are deposited in the Kanagawa Prefectural Museum of Natural History (KPM), Iriuda, Japan; Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (ex Raffles Museum of Biodiversity Research), National University of Singapore; The Natural History Museum (NHM), London, UK; and United States National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., USA. Measurements provided, in millimeters, are of the post-pseudorostral carapace length (base of spines to posterior carapace margin) and the maximum carapace width (across base of spines), respectively. The abbreviation G1 is used for the male first gonopod. We have provided a detailed diagnosis of the new species rather than a full description as it is sufficient at the moment to differentiate it from the similar *L. sinensis* which is known only from a carapace. A full description will be provided later as part of an ongoing revision of *Leptomithrax*.

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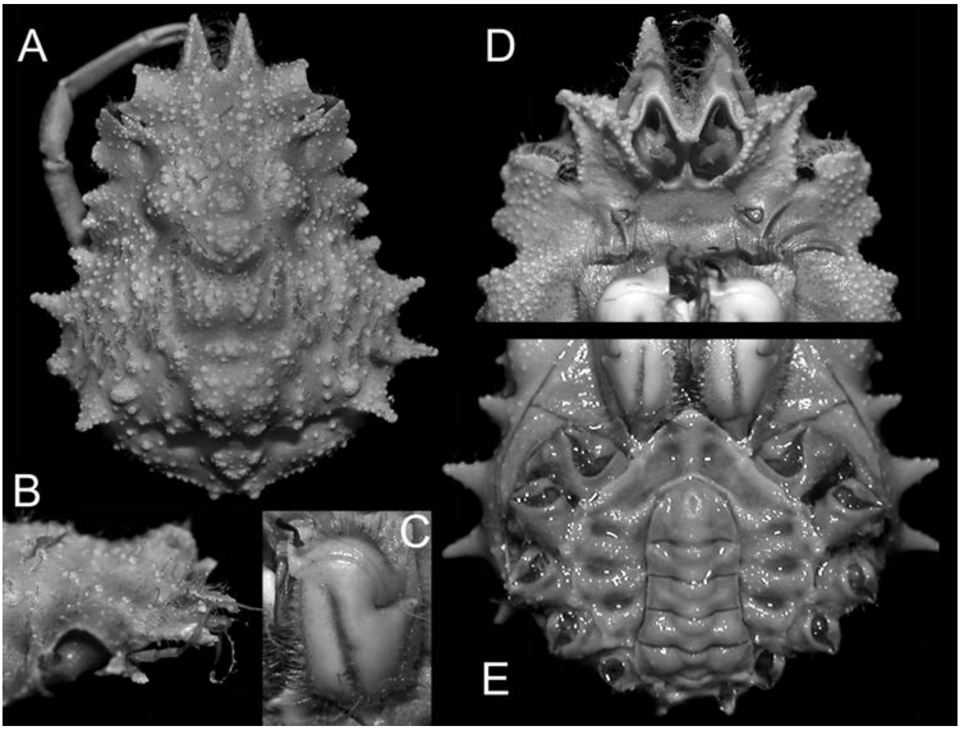

Fig. 1. *Leptomithrax eldredgei,* sp. nov. **A, C, D**, paratype female (21.1 × 17.4 mm) (ZRC 1970.2.17.2), off Hong Kong; **B, E**, holotype male (13.3 × 10.1 mm) (ZRC 1970.2.17.1), off Hong Kong. **A**, overall dorsal view of carapace; **B**, fronto-lateral view of orbits and front showing position of antenna; **C**, left third maxilliped; **D**, ventral view of carapace showing antennae, antennules and epistome; **E**, ventral view showing thoracic sternum and abdomen.

Taxonomy

Leptomithrax eldredgei, **sp**. **nov**.

Figs. 1, 2

Maja sp. – Yang, 1979: 9.

Material examined. Holotype: male (13.3 × 10.1 mm) (ZRC 1970.2.17.1), Cr 2/63, station 24, T./10, Hong Kong, coll. & don. Fisheries Research Station of Hong Kong, 1967. Paratypes: 2 ovigerous females (21.1 × 17.4 mm, 1 broken laterally), 1 female (14.9 × 11.3 mm), 1 crushed specimen (ZRC 1970.2.17.2–5), same data as holotype.

Comparative material examined. *Leptomithrax edwardsii* (De Haan, 1835): 1 female (55.9 × 49.7 mm) (ZRC 2013.1186), Amakusa, Shikizuki, Kyushu, Japan, from fishermen, coll. J. Lai, September 2002. — 8 males (largest 69.8 × 62.8 mm), 7 females (ZRC 2013.1401), Amakusa, Tomioka Port, Kyushu, Japan, coll. J. Lai & S. Arakaki, 7–9 September 2002. — 1 male (75.8 × 69.4 mm) (ZRC 2001.56), Tashi, Taiwan. *Leptomithrax sinensis* Rathbun, 1916: holotype carapace (dried) (32.0 × 25.3 mm) (including spines, 38.3 × 28.8 mm) (USNM 48219), station 5311, South China Sea, near southern Luzon, 21°33'N 116°15'E, 88 fathoms, Philippines, coll. RV *Albatross*, 4 November 1908. *Leptomithrax bifidus* (Ortmann, 1893): 1 dried male (36.5 × 29.4 mm) (KPM NH4024), Kii-Nagashima, Japan, T. Sakai Collection, coll. March 1969. — 2 males (32.5 × 27.5 mm, 27.5 × 20.6 mm) (NHM 1961.11.13.28–29), Seto, Shirahama, Japan, coll. gill nets, I. Gordon & Harada, 1950s.

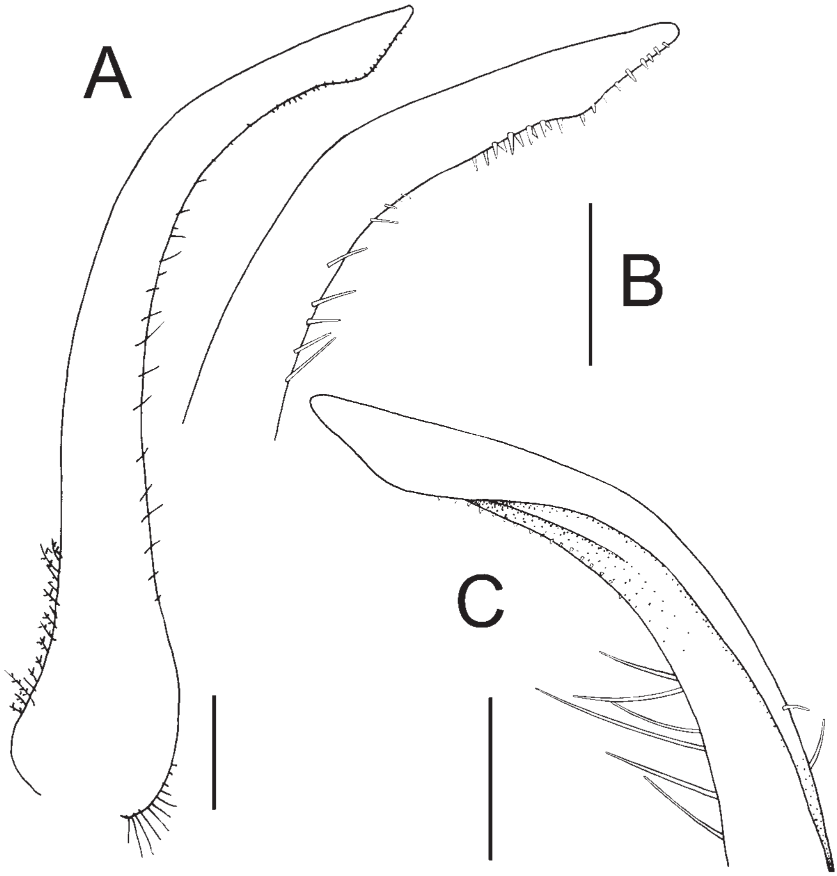

Fig. 2. *Leptomithrax eldredgei,* sp. nov., holotype male (13.3 × 10.1 mm) (ZRC 1970.2.17.1), off Hong Kong. Left G1. A, E = 5.0 mm; B-G = 1.0 mm; F, G, H-J = 0.5 mm. **A**, ventral view; **B**, ventral view of distal part; **C**, dorsal view of distal part.

Diagnosis. Carapace pyriform; dorsal surface with regions distinct, covered with numerous tubercles, granules and clusters of granules (Fig. 1A). Pseudorostral spines short, dorsoventrally flattened, gently diverging, appearing almost subparallel (Figs. 1A, B). Supraocular eave wide, forming sharp posterior angle corresponding to antorbital spine; anterior edge gently expanded; intercalated spine stout, dorso-ventrally flattened, with tip distinctly bifurcated, margins touching antorbital and overlapping postorbital spine; postorbital spine very broad, foliate, outer margin prominently clefted to form 2 distinct lobes; hepatic region with 2 short, blunt, dorsoventrally flattened spines (Figs. 1A, B). Median row of carapace raised, covered with granulated tubercles, no spines; posterior carapace margin with 2 low spines; regions between cardiac and intestinal regions transversely depressed (Fig. 1A). Basal antennal article as wide as long, completely fused with carapace, margins distinctly granulated, internal distal margin forming low tooth, external distal corner with elongated projection (Figs. 1B, D). Antenna positioned far from orbit (Fig. 1B). Eye short, almost completely protected inside depression on inner surface of postorbital tooth (Figs. 1B, D). Epistome rectangular, almost smooth (Fig. 1D). Third maxilliped relatively short; anterior margin of merus setose; proximal part of merus and most of ischium swollen, forming boss-like structure, glabrous; ischium with deep oblique submedian sulcus, inner margin strongly denticulated, outer margin with large, sharp

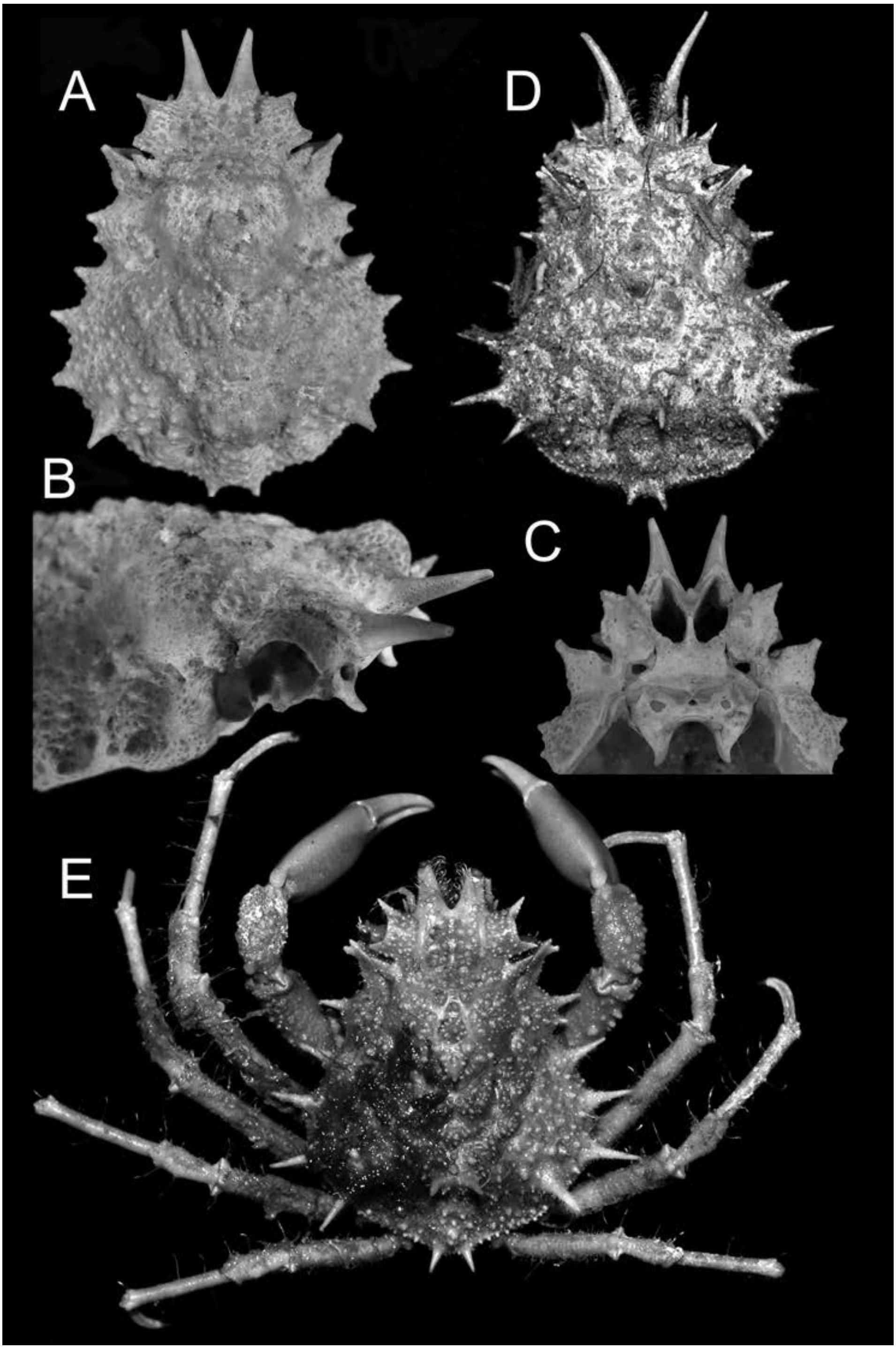

Fig. 3. General habitus. **A–C**, *Leptomithrax sinensis* Rathbun, 1916, holotype carapace (32.0 × 25.3 mm) (USNM 48219), Philippines; **D**, *Leptomithrax bifidus*, dried male (36.5 × 29.4 mm) (KPM NH4024), Japan [only carapace depicted]; **E**, *Leptomithrax bifidus*, male (32.5 × 27.5 mm) (NHM 1961.11.13.28), Japan. **A, D, E**, overall dorsal views of carapaces; **B**, fronto-lateral view of orbits and front showing position of antenna; **C**, ventral view of carapace showing antennae, antennulular fossa and epistome.

tooth (Fig. 1C). Anterior part of male sternum with deep depressions on sternites 3 and 4, medially separated by low raised ridge; sternites 5–7 with distinct median depression (Fig. 1E). Male abdomen subrectangular, all 6 somites and telson free; telson broadly triangular with convex lateral margins (Fig. 1E). G1 relatively thick, curved, distal part with lower margin slightly expanded, lined with short spines (Figs. 2A–C).

Etymology. We name this species in honour of Lucius G. Eldredge, a good friend, and close colleague, with whom we shared a long-time interest in majoid and homoloid crabs.

Remarks. *Leptomithrax eldredgei* sp. nov. is most similar to *L. sinensis* in the general shape of the carapace. It can easily be separated by having the margins of the pseudorostral spines straight in dorsal view (Fig. 1A) (versus concave on the outer margin in *L. sinensis*, Fig. 3A), the truncate intercalated spine (Fig. 1A) (versus acutely triangular in *L. sinensis*, Fig. 3A), and the broadly foliaceous postorbital spine that is divided into two lobes (Fig. 1A) (versus slender and acutely triangular with tip weakly bifid in *L. sinensis*, Fig. 3A). The regions of the carapace of *L. eldredgei* are more prominent and the granules proportionately larger (Fig. 1A) compared to *L. sinensis* (Figs. 3A, C) but this may be due to the fact that the type (and only known specimen) of *L. sinensis* is only an eroded carapace. The type locality of *L. sinensis* is in the South China Sea, near southern Luzon, which is not far from Hong Kong and from where *L. eldredgei* has been found. The differences observed between *L. eldredgei* and *L. sinensis*, however, support their distinctness as separate species. *Leptomithrax sinensis*, however, is very close to *L. bifidus* (Figs. 3D, E) from Japan, and most of the differences in the spine proportions can be explained by the erosion of the structures in *L. sinensis*. The two species may prove to be synonymous

Acknowledgments

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A New Mesophotic Branching Coral Species of *Psammocora* from the Mariana Islands Archipelago (Cnidaria: Scleractinia: Psammocoridae)

Richard H. Randall
Professor Emeritus, University of Guam Marine Laboratory, Mangilao, Guam 96932;
email: richardhrandall@gmail.com

Abstract. A new mesophotic zoozanthellate coral species, *Psammocora eldredgei,* **sp. nov**. (Scleractinia), is described as new to science. It has small 2 to 5 mm diameter branches arranged in an open arborescent manner. The calices are small, ranging from 1.40 to 2.41 mm in diameter with 6 to 9 thick closely spaced granulated septa that reach a central fossa and small styliform columella. The species is represented by 516 specimens collected from 16 stations between 33 and 200 m depth from deep banks and island forereef slope habitats along the fore-arc of the Mariana Island Archipelago. The species is named *Psammocora eldredgei* in honor of the late marine biologist Dr. Lucius. G. Eldredge, who was my thesis chairman in 1971, and a colleague during his long tenure at the University of Guam Marine Laboratory where we worked together on many research projects.

Introduction

On 9 August 1971, thirty-one living coral specimens were recovered from a dredge haul along a 89-meter depth contour adjacent to the southwest leeward coast of Guam (see Coll. Sta. RHR 226C-CS-2 below) that consisted of various sized small 2 to 4 mm diameter compound arborescent branch fragments that had corallite characteristics of *Psammocora*, but differed from any other known branching species of the genus. On 11 August 1971 an identical living compound branch cluster was recovered from a dredge haul along the 200 meter depth contour adjacent to the northeast windward coast of Guam (see Coll. Sta. RHR 226C-CS-1 below). Between Aug. 1971 and Feb. 1984, 506 specimens of this arborescent branching *Psammocora* have been collected from 16 dredge haul stations on deep banks and seaward reef slopes of islands along the north-south trending Mariana Island Archipelago between latitude 18°2.5’N near the south end of Pagan Island and latitude 12°42’N at an unnamed bank south-west of Santa Rosa Reef bank, a distance of approximately 600 kilometers (Fig. 1).

In Randall & Myers’s (1983) handbook of the corals of Guam this branching *Psammocora* was considered a deep-water coral and not listed, and in the Randall (2003) checklist it was listed as *Psammocora* sp. 3 (fine ramose). Here the branching specimens are referred to a new species named *Psammocora eldredgei* in honor of the late marine biologist Dr. Lucius. G. Eldredge, who was my thesis chairman in 1971, and a colleague during his long tenure at the University of Guam Marine Laboratory where we worked together on a many research projects. Also in 1973, Dr. Lucius. G. Eldredge along with Dr. Richard W. Grigg dredged 14 specimens of *Psammocora* (= *P. eldredgei*) from the leeward coast of Rota in the Southern Mariana Islands (see Coll. Stations RHR 1147-CS-6 and RHR 1147CS-7 below).

Following is a description of *Psammocora eldredgei* that includes a description of each of the 16 collecting stations, and a comparison of it to the other three branching *Psammocora* species that have been recognized from the Mariana Island Archipelago.

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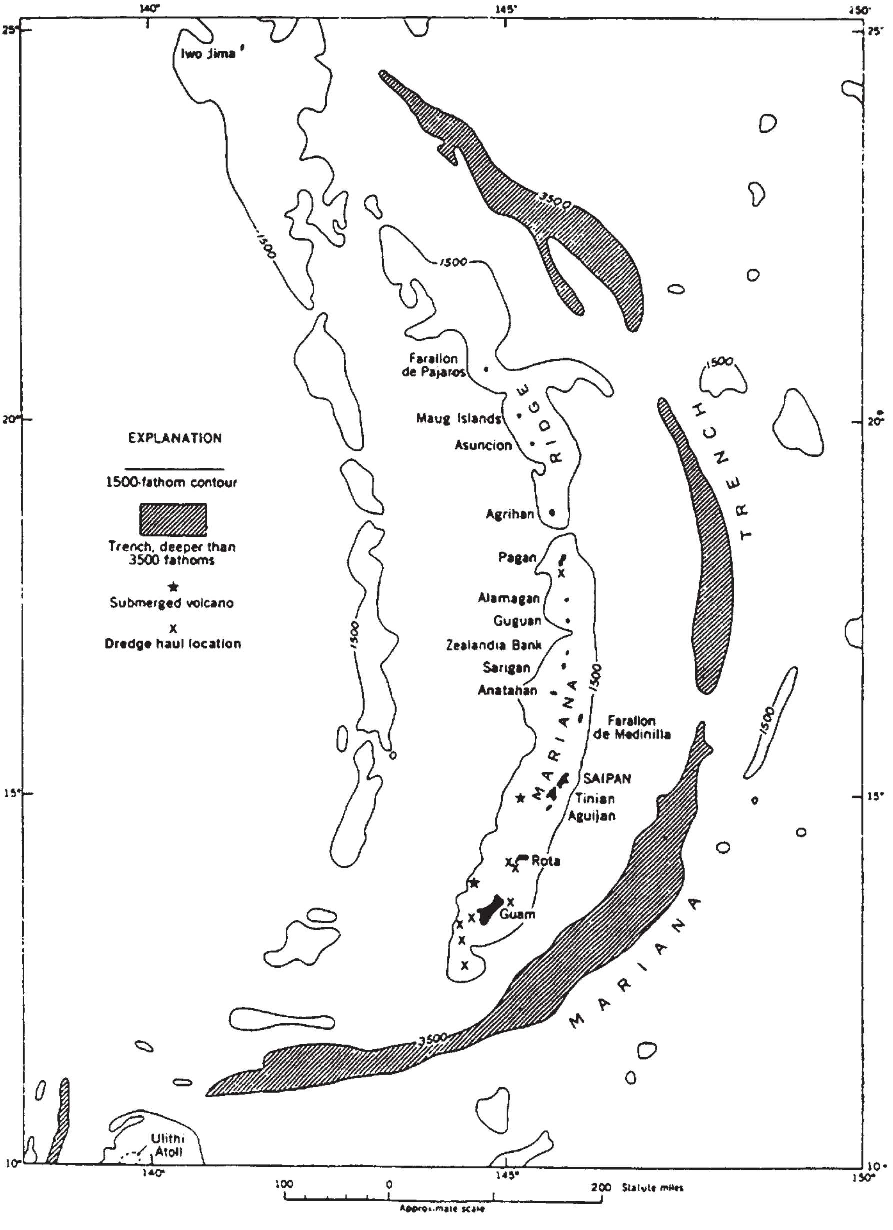

Fig. 1. Map of the Mariana Island Archipelago showing the locations of the 13 dredge and 3 scuba dive stations from which specimens of *Psammocora eldredgei* were collected. From top to bottom the number of dredge hauls at each station are Pagan 1 dredge haul, Rota 2 dredge hauls, Guam-two dredge hauls, and the three banks south of Guam are the Eleven Mile Bank 1dredge haul, Galvez Bank 6 dredge hauls and three scuba dives, and Santa Rosa Reef Bank 1 dredge haul. Map modified from Hess (1948).

Family Psammocoridae Chevalier & Beauvais, 1987

Genus *Psammocora* Dana, 1846

Psammocora eldredgei, sp. nov.

Figs. 2, 3A, 3B, 4

Synonymy:

Psammocora (undescribed sp.), Grigg & Eldredge, 1975: 10, Dredge Stations 6 &7.

Psammocora sp. 3 (fine ramose), Randall, 2003: 130 & Referenced Voucher Spec. 12505.

Material Studied:

A total of 516 specimens were studied that were collected from 16 dredge haul stations. Of these specimens 304 were living and 212 were dead specimens. Each of the following 16 dredge haul stations gives the collecting station number, specimen numbers of living and dead colonies collected, method of collection and date, geographic collection location and depth, and reef zone and habitat. See Fig. 1 for the dredge stations locations along the Mariana Island Archipelago.

Description of the Collecting Stations

***Guam Island*:**

COLLECTING STATION: RHR 226C-CS-2: Specimens**:** 31 living (3127 & 28918, USNM 1260054 & 2890 thru 28947); Collection Method: R.V. "*Tanguisson*" utilizing a biologic dredge, Date: 9 Aug. 1971; Geographic Location: Guam, southwest leeward coast, 200 meters offshore from the fringing reef margin at Facpi Point, from where the bottom was dredged 150 meters northward along the 89-meter contour; Depth: 89 meters; Reef Zone: A gently seaward dipping **s**ubmarine terrace that interrupts the general steeper seaward dipping reef slope; Habitat: Inner part of an unconsolidated terrace where it grades into a steeper shallower consolidated part of the seaward reef slope. Substrate: The dredge haul contained 20 kg of a mixture of mostly bioclastic sand and *Halimeda* segments intermixed with dead and living foraminifera tests and gravel- to pebble-sized bioclastic sediment.

COLLECTING STATION: RHR 227C-CS-1: Specimen: 1 living (3142); Collection Method: R. V. "*Tanguisson*" utilizing a biologic dredge. Date: 11 Aug. 1971; Geographic Location: Guam, northeast windward coast, midway between Pati Point and Janum Point, offshore from a supratidal bench; Depth: 200 meters; Reef Zone: Apron reef along the 200 meter depth contour of the seaward reef slope; Habitat: Probably a consolidated reef rock substrate as no sediment other than a few bioclastic pebbles and cobbles was present in the dredge haul. Notes: This is the deepest depth at which living or dead *Psammocora eldredgei* specimens were collected, but may have somewhat deeper as the as the dredge was initially emplaced at 220 meters depth and was brought upslope to the 200 meter contour depth.

***Rota Island*:**

COLLECTING STATION: RHR 1147-CS-6: Specimens: I living (23307) & 4 dead (23411& 30662 thru 30664); Collection Method: R.V. "*Panglau Oro*" utilizing a concrete breaker ball with attached coral tangle mops. Date: 25 Oct. 1973; Geographic Location: Rota Island along the leeward coast; Depth: 127 to 135 meters; Reef Zone: Seward reef slope; Habitat: Hard substrate veneered with bioclastic sand, pebbles, and cobbles.

COLLECTING STATION: RHR 1147-CS-7: Specimens: 2 living (23402 & 23403) & 7 dead (23404 thru 23410); Collection Method: R.V. "*Panglau Oro*" utilizing a concrete breaker ball with attached coral tangle mops Date: 25 Oct. 1973; Geographic Location: Rota Island along the leeward coast; Depth: 124 to 136 meters; Reef Zone: Offshore seaward reef slope; Habitat: Hard substrate veneered with bioclastic sand, pebbles, and cobbles.

***Pagan Island*:**

COLLECTING STATION: TC 84-02, STA. 12: Specimens: 21 living (24044 & 30665, USNM 1260052 & 30067 thru 30684); Collection Method: R. V. "*Townsend Cromwell*" utilizing bottom coral mop. Date: 21 Feb. 1984; Geographic Location: Pagan Island, Mariana Islands, at an offshore bank that extends off the south coast; Depth: 91 to 110 meters depth; Reef Zone: Upper peripheral seaward reef bank slope; Habitat: Hard reef rock substrate veneered with patches of bioclastic sand, pebbles, and cobbles.

***Eleven Mile Reef Bank off the SW coast of Guam*:**

COLLECTING STATION: TC 78-02 (72-79) Sta. 10, String 4: Specimens: 4 living (12505, 27932, 30686, and 30687); Collection Method: R.V. "*Townsend Cromwell*" utilizing bottom set lobster trap. Date: 28 May 1978; Geographic Location: Reef bank 11 miles off the southwest coast of Guam; Depth: 33 meters; Reef Zone: Reef bank platform: Habitat: Bioclastic sand and rubble with scattered coral patches (based upon previous scuba diving observations by the author). Note: This is the shallowest depth at which *Psammocora eldredgei* has been recovered on the 11-Mile Reef Bank.

***Galvez Bank*:**

COLLECTING STATION: RHR 541A-CS-1: Specimens: 3 living (10628, 10630, and 10631); Collection Method: Scuba diving; Date: 27 Oct. 1977; Geographic Location: Galvez Bank, Mariana Islands Archipelago; Depth: 38 to 41 meters; Reef Zone: A swale-like depression in the middle part of the upper bank platform; Habitat: Bioclastic sand and coral rubble with abundant scattered diverse coral patches.

COLLECTING STATION: RHR 541A-CS-2: Specimens: 3 living (10629, 30547, and 30548); Collection Method: Scuba diving; Date: 27 Oct. 1977; Geographic Location: Galvez Bank, Mariana Islands Archipelago; Depth: 33 meters; Reef Zone: Middle part of the upper bank platform; Habitat: Bioclastic sand and coral rubble with abundant scattered diverse coral patches. Note: This is the shallowest depth at which *Psammocora eldredgei* has been recovered on Galvez Bank

COLLECTING STATION: RHR 542A-CS-1: Specimens: 2 living (30539 & 30550); Collection Method: Scuba diving; Date: 27 Oct. 1977; Geographic Location: Galvez Bank, Mariana Islands Archipelago; Depth: 41 meters; Reef Zone: Upper steep region of the peripheral seaward slope of the bank platform; Habitat: Bioclastic sand and coral rubble with abundant scattered diverse corals.

COLLECTING STATION: RHR 1123A-CS-1: Specimens: 11 living (22703 & 29182, USNM 1260053 & 29184 thru 29191); Collection Method: R.V. "*Mom*", utilizing a biologic dredge bag. Date: 29 Nov. 1983; Geographic Location: Galvez Bank, Mariana Islands Archipelago; Depth: Upslope dredge haul from 366 to 146 meters; Reef Zone: Peripheral seaward reef bank slope; Habitat: Hard reef rock substrate veneered with patches of bioclastic sand, pebbles, and cobbles. Note: The specimens here are being listed at 146 meters depth, but they could also be from a deeper depth as well.

COLLECTING STATION: TC 78-02 (72-79) Sta.. 7, String 4, Trap 21: Specimens: 14 living (27975, 27976, USNM 1260051 & 27978 thru 27988) & 23 dead (27989 thru 28001 & 30650 thru 30659); Collection Method: R.V. "*Townsend Cromwell*" entrapped within a bottom set fish trap. Date: 27 May 1978; Geographic Location: Southern tip of Galvez Bank, Mariana Islands Archipelago; Depth: 143 m depth. Reef Zone: **U**pper region of a peripheral seaward reef bank slope; Habitat: Hard reef rock substrate veneered with patches of bioclastic sand, pebbles, and cobbles.

COLLECTING STATION: TC 78-02 (72-79) Sta. 7, String 9: Specimens: 3 living (12516, 27931 and 27932); Collection Method: R.V. "*Townsend Cromwell*" utilizing bottom set fish trap. Date: 27 May 1978; Geographic Location: Southern tip of Galvez Bank, Mariana Islands Archipelago; Depth: 143 meters; Reef Zone: Peripheral seaward reef bank slope; Habitat: Hard reef rock substrate veneered with patches of bioclastic sand, pebbles, and cobbles.

COLLECTING STATION: TC 78-02 (72-79) Sta. 7, String 7, Trap 30: Specimens: 12 living (12519 & 27945, USNM 1260050 & 27947 thru 27955) & 20 dead (12518 & 27956 thru 27974); Collection Method: R.V. "*Townsend Cromwell*" entrapped within a bottom set lobster trap. Date: 27 May 1978; Geographic Location: Southwestern part of Galvez Bank. Galvez Bank, Mariana Islands

Archipelago; Depth: 44 meters; Reef Zone: Bank platform; Habitat: Sand and coral rubble with scattered coral patches (based upon previous scuba diving by the author on this part of the bank platform).

COLLECTING STATION: TC-78-02 (72-79) Sta. 7 String 8, Trap 30: Specimens: 23 living (28010, 28011 & 28012 thru 28032) & 20 dead (28033 thru 28052); Collection Method: R.V. "*Townsend Cromwell*" utilizing bottom set fish net. Date: 25 May 1978; Geographic Location: Southern tip of Galvez Bank, Mariana Islands Archipelago; Depth: 44 meters; Reef Zone: Upper bank platform; Habitat: Bioclastic sand and rubble with scattered coral patches (based upon previous scuba diving observations by the author).

COLLECTING STATION: TC-78-02 (72-79) Sta. 7 String 6; Specimens: Lot 1- 22 living (28053 thru 28073 & USNM 1260044) & 26 dead (28075 thru 28100); Lot 2 – 27 living (USNM 1260046 & 28102 thru 28127) & 23 dead (28128 thru 28150); Lot 3 – 30 living (28151, USNM 1260043 Holotype & 28153 thru 28179 & USNM 1260045) & 21 dead (28181 thru 28201); Lot 4 – 28 living (28202 thru 28227 & USNM 1260047) & 22 dead (28230 thru 28251); Lot 5 – 27 living (USNM 1260048 & 28253 thru 28278) & 19 dead (28279 thru 28297); Lot 6 – 38 living (USNM 1260049 & 28299 thru 28335) & 19 dead (28336 thru 28354); Collection Method: R.V. "*Townsend Cromwell*" utilizing bottom set fish net. Date: 25 May 1978; Geographic Location: Southern tip of Galvez Bank, Mariana Islands Archipelago; Depth: 44 meters; Reef Zone: Upper bank platform; Habitat: Bioclastic sand and rubble with scattered coral patches (based upon previous scuba diving observations by the author).

***A large unnamed bank located SW of Santa Rosa Reef*:**

COLLECTING STATION: TC-78-02 (72-79) Sta. 2 North: Specimens: 1 living (12496) & 8 dead (27933 thru 27940); Collection Method: "R.V. *Townsend Cromwell*" utilizing bottom set fish net. Date: 25 May 1978; Geographic Location: A large unnamed bank located SW of Santa Rosa Reef. The tag accompanying the specimens indicate that they were collected at the north end of this bank; Depth: 91 meters; Reef Zone: Upper peripheral slope of the bank platform; Habitat: Bioclastic sand and rubble with scattered coral patches.

Associated Corals in the Dredge Hauls: From most of these 16 dredge hauls, as well as other hauls from similar depths, a diverse assemblage of both zooxanthellate and azooxanthellate coral species was present.

Description of the Specimens

To avoid confusion in terms used to describe the polyps and skeletal morphology the terminology established by Benzoni *et al.* (2007), Stefani *et al.* (2008a), Stefani *et al.* (2008b) & Benzoni *et al.* (2010) is used here, which in the authors opinion elegantly explains the complex morphological skeletal development expressed in the psammocorid corals. In addition to the above 516 specimens the Randall coral collection contains another 1031 specimens of *Psammocora* collected from numerous geographic and habitat locations of the Pacific Ocean.

Polyps: Living polyps could only be described from specimens collected by the author at Collecting Stations RHR 226C-CS-1 and RHR 226C-CS-2, where about half the dredged living specimens (including the specimen from 200 m depth) survived after being place in shaded running sea water aquaria. Upon immediately being recovered from the dredge haul their color ranged from an overall medium brown on what appeared to be the exposed branch surfaces to tan on the underside of the branch surfaces. In the aquaria the fully expanded polyps form concentric circles outward from directly around the polyp mouth that is typical of all *Psammocora* species. The first circle of tentacles are borne on the petaloid entosepta between the polyp mouth and first occurring ring of synapticulae that places them within the calice or inter-calicular in position. The remaining circles of tentacle are positioned outside the first occurring ring of synapticulae and thus are extra-calicular in position, or in the sense of Benzoni *et al.*(2007) are termed extrapolypal tentacles. In shape fully expanded tentacles are relatively long and thick at the base that taper upward to a slightly knobbed

Fig. 2. View of 12 selected paratype and holotype (USNM 1260043 top row, fifth specimen from left to right) specmens of *Psammocora eldredgei* that shows the general overall range of colony form and size, branch diameter, and arborescent branching pattern. Specimen numbers with a asterisk (*) display significant thickening of the basal branch regions by encrusting organisms. Top row left to right: Spec. 3127 Coll. Sta. RHR 226C-CS-2; 3142 Coll. Sta. RHR 227C-CS-1; 23307 Coll. Sta. RHR 1147-CS-6; 23402 Coll. Sta. RHR 1147-CS-7; USNM 1260043 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 3. Middle row left to right: 22703* Coll. Sta. RHR 1123A-CS-1; 24044 Coll. Sta. TC 84-02, Sta. 12; 27975* Coll. Sta. TC-78-02 (72-79) Sta. 7, String 4, Trap 21; 12519 Coll. Sta. TC-78-02 (72-79) sta. 7, string 7, trap 30. Bottom row left to right: 12516* Coll. Sta. TC 78-02 (72-79) Sta. 7, String 9; 12505* Coll. Sta. TC-78-02 (72-79) Sta. 10, String 4; 12496* Coll. Sta. TC-78-02 (72-79) Sta. 2 North; 28010* TC-78-02 (72-79) Sta. 7 String 8, Trap 30. For details of each of the above collecting stations (collection method and date, geographic collection location and depth, reef zone and habitat) see ”Description of the Collecting Stations” section. Scale bar is 5 cm.

tip. Their color is a pale translucent brown with pale tan to nearly white tips. Since the corallum surface topography is relatively flat and not raised into colline ridges in this species the boundary between tentacles from adjacent polyp mouths was not distinctive. Over time the aquaria specimens gradually acquired a darker brown color with slightly greenish tinged tentacles. At collecting stations 541-CS-1, 541-CS-2, and 542-CS-1 where eight specimens were collected by scuba diving, the colonies did not have their polyps expanded and displayed an overall tan color. At the remaining collecting stations the specimens were immediately preserved in 70 percent alcohol or 10 percent formalin solution in which their preserved color ranged from light brown to pale tan.

Colony Form, Colony and Branch Size, and Depth Range: All the collected specimens display an open arborescent branching form of crookedly diverging small branches that arise mostly from di- to tri-chotomous stem tip divisions as shown in Figs. 2 and 3A. The overall corallite surface is topographically rather smooth and even with no conspicuous colline ridges or excavated calices. The branches are terete to sub-terete in cross section that at their base mostly range from 3 to 5 mm in diameter from where they taper gradually to 2 to 3 mm in diameter one centimeter below the stem tip. Non-dividing stem tip shapes range from bluntly rounded to tapering to a small blunt point, and where undergoing division they may be somewhat compressed. The interval between branching nodes is irregular and short, generally less than a centimeter. Most of the specimens consist of single stems or compound branch clumps that display two to ten or more terminal and lateral branch-

Fig. 3A. View of the paratype (Spec. No. 28151) that displays the typical crooked arborescent branching pattern of *Psammocora eldredgei*, from Coll. Sta. TC-78-02 (72-79) Sta. 7, String 6, Lot 3 where the species was particularly abundant with 172 living and 135 dead specimens collected. Scale bar is 10 mm.

lets. Although dredge hauls with multiple specimens revealed a wide range in branch diameter, there was a slight general trend for branch diameter to decrease, have fewer secondary branchlets, and display an increase in the interval between branching nodes with increasing depth. Of the living specimens about three-fourths of the compound branch clumps display a freshly fractured face at their basal end that indicates they were broken from a larger branch clump or intact colony, and about one-fourth display a worn or encrusted basal end that indicates they were probably living unattached on the substrate. The preponderance of broken specimens is not surprising when considering their small branch diameter and that they were for the most part dredged and rather haphazardly collected by using breaker balls with attached mops of netting, bottom set nets designed to catch fish, and lobster traps. Even so, the eight colonies collected by scuba diving occurred in small aggregations of unattached branch clumps. Anastomosing of adjacent branch stems is rare, with only a few cases occurring where a broken living branch fragment became lodged and fused to another living branch. On approximately half of the living specimens the living tissue was restricted to the distal one to occasionally three centimeters of the branch tips (Fig. 3A), with the remaining proximal branch surfaces somewhat swollen and thickened by encrusting bryozoans, colonial foraminifera (mostly *Gypsina*), and crustose coralline algae (Fig. 2). The overall branch surfaces of most of the dead specimens were similarly encrusted. Freshly fractured surfaces of all the branch stems revealed that immediately below the septal surface the skeletal elements are secondarily thickened into a solid mass.

Overall colony size is difficult to determine as most specimens consist of broken compound branch clumps that range from 1 to 6.7 cm in length and 1 to 6.5 cm in width as shown in Fig. 2 of selected specimens from each of the 13 dredge locations. The largest intact specimen collected was a dead cespitose colony 6.7 cm long, 6.5 cm wide, and 4.8 cm in height that except for the branch tips was encrusted by bryozoans and colonial foraminifera. The smallest specimens collected were two newly settled single corallite spats less than a millimeter in diameter.

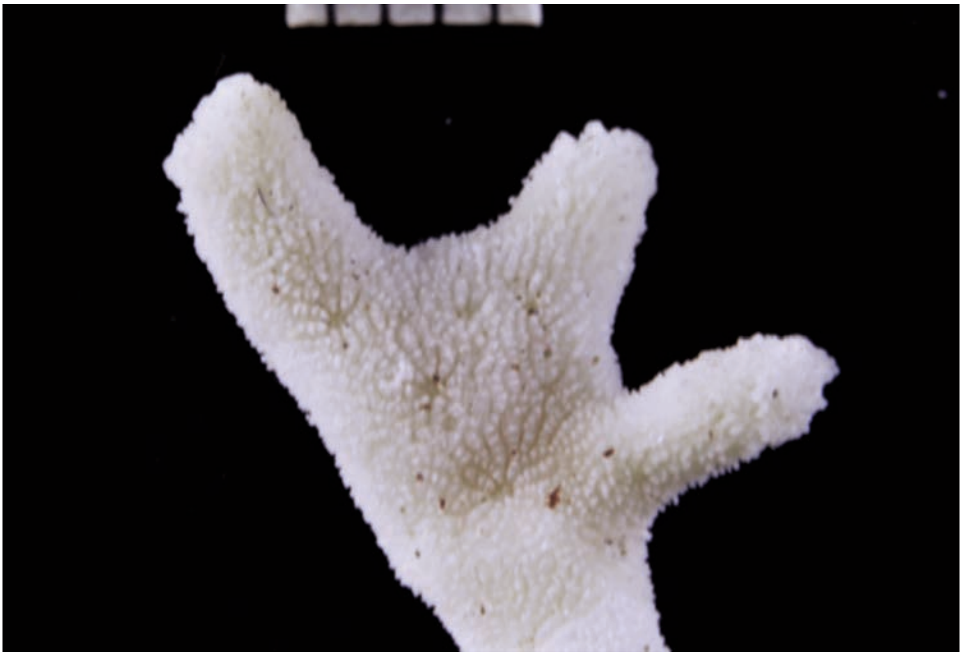

Fig. 3B. Detail of the upper side of a branch tip of the paratype (Spec. No. 28151 from Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 3) that shows the less robust corallites and septa from the branch tip of a specimen with relatively small diameter branches. Compare to Fig. 4 below. For a view of the entire specimen see Figure 3A above. Scale bar is 5 mm.

Depth range for the 304 living colonies ranged from 33 to 200 meters, of which 82 percent occurred between 33 and 91 meters depth and 18 percent between 91 and 200 meters depth. Depth range for the 212 dead colonies ranged from 44 to 143 meters, of which 87 percent occurred between 44 and 91 meters depth and 13 percent between 91 and 143 meters depth. To date no specimens have been observed or collected from habitats shallower than 33 meters. Because of the depth from which the living specimens were recovered, samples of their living and preserved tissues revealed under compound microscopic analysis abundant zooxanthellae throughout their depth range., including the specimen from 200 meters depth. No evidence of green or red endolithic algae was noted in the cleaned corolla.

Corallites: In general the corallites vary considerably in diameter, number of septa reaching the fossa, distance between calicular centers, and degree of secondary thickening of their septal and synapticular elements between the stem tips and their basal living regions as shown in Figs. 3B and 4. At the stem tips where most new divisions occur the corallites are smaller, more crowded, generally somewhat elongated and distorted, and have thinner septal elements. Proximally from the tips the corallites become larger, less crowded, more symmetrical in shape, and attain their characteristic number of very thick petaloid and non-petaloid septa and peripheral enclosed petaloid septa. As the thicker basal region of a branch is approached the septal and synapticular elements of the corallites are also secondarily thickened. Because of such corallite variation expressed along a branch the following corallite characteristics are those of the more representative middle living region of a branch, similar to those shown in Fig. 4. The following measurements of the corallite elements are derived from a suite of ten or more mature corallites that were not undergoing division. Because of the small corallite size such measurements are given to the nearest second decimal place.

The calice diameter (peripherally limited by the first row of synapticulae) ranges from 1.40 to 2.41 mm in diameter, with a central fossa that forms a small conspicuous circular pit 0.20 to 0.34

Fig. 4. Detail of the upper side of a branch tip of holotype (Spec. No. USNM 1260043 from Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 3) that shows the more typical robust corallites with thickened closely spaced septa of *P. eldredgei*. Compare to Figs. 3A & 3B above. For a view of the entire specimen see Fig. 2, top row, fifth specimen from left to right. Scale bar is 5 mm.

mm in diameter. A small slender styliform columella 0.10 to 0.12 mm in diameter rises up from the fossa floor that under magnification is minutely granulated and in height is lower than the upper margins of the surrounding circle of septa. Commonly the columella is no higher than the innermost septal dentitions. With magnification at the branch tips where the septa are not quite so crowded the structural arrangement of the calicular elements at the fossa can sometimes be revealed that shows small synapticulae uniting the septa around the columella and small short deeply set granulated rod-like processes positioned horizontally at the inner end of the septa that attach to the columella. A short distance proximally from the stem tip though, all the calicular fossa floor elements become obscured into a solid mass around the columella by secondary thickening and presence of irregularly scattered granulations. Without magnification these small granulations are not conspicuous. Both the petaloid (entosepta) and non-petaloid (exosepta) septa within the calice are conspicuously thickened, particularly the former, with the interseptal locular spaces between them reduced to mere slits

Fig. 5. *Psammocora contigua* (Specimen No. 4788): Dorsal-lateral view of an entire corallum with contorted compressed branches. Collection Location: Guam, Pago Bay fringing reef. Reef Zone and Habitat: Middle part of the inner fringing reef flat platform low tide moat at less than 50 cm depth. Scale bar is 5 cm.

0.03 to 0.04 mm wide which for the most part conceals their synapticular junctions. In vertical section a short distance below the corallite surface adjacent septa are juxtapositioned against each other and fused into a solid mass. Six to nine septa generally reach the fossa that are comprised of three to four petaloid entosepta, two to three exosepta, and one to three fused duplets and triplets that may consist of both entoseptal and exoseptal members. Occasionally as many as four septa were fused together in a group. The petaloid entosepta are distinctly club shaped with a rounded outer margin that range from 0.26 to 0.41 mm at their widest part and 0.65 to 0.90 mm in length. Non- petaloid exosepta, identified as those that bifurcate before reaching the first row of synapticulae, are only slightly narrower than the petaloid entosepta with their individual bifurcated limbs ranging from 0.15 to 0.25 mm in width. Sometimes these limbs undergo another bifurcation or a new petaloid entoseptum is inserted between them that becomes enclosed by subsequent bifurcation and fusion of the two exosepta limbs on each side of it. Because of the narrow separation of most corallites from one another the septa from adjacent calices are sometimes juxtapositioned against each other, or are separated by a narrow meshwork of exosepta and enclosed petaloid septa. Where enclosed petaloid septa are present between corallites they are generally small granulated low flattened round to ellipsoid mounds that are commonly incompletely distributed around the calice periphery with only a single row generally present between adjacent calices. Some of the larger ones measured ranged from 0.12 to 0.16 mm wide and 0.29 to 0.34 mm long. Near the basal stem regions where the corallite elements are somewhat secondarily thickened the enclosed petaloid septa and their associated surrounding non-petaloid septa were commonly more distinguishable.

Fig. 6. *Psammocora contigua*: Detail view of several branches from Specimen No. 4788 shown above. Scale bar is 10 mm.

Figure 7. *Psammocora stellata*: Detail view of several branches from Specimen No. 3498 shown below. Scale bar is 10 mm.

The upper septal margins of both the intercalicular and extracalicular septa bear conspicuous granulated dentitions that are compressed into paddle-shaped ridges oriented at right angles to the radial septal plane. These paddle-shaped ridges are very closely spaced, which sometimes are so close together they appear as a single continuum. Some of the larger longer petaloid septa can have up to eight of them aligned along the upper septal margin that individually can be up to 0.10 mm in thickness and 0.41 mm wide. In the wedge and club shaped septa the width of the paddle-shaped ridges decrease in width toward the fossa, with the innermost one reduced to a small granulated pillar. With magnification these paddle-shaped ridges bear numerous minute short spines and granule clusters (centers of calcification) that taper to point and are not arranged or oriented in any particular pattern. Such granulations extend downward on the lateral septal surfaces as well.

Because of the extremely close spacing of the septa the connecting synapticulae are difficult to discern, but with magnification they can be generally be distinguished, particularly the first circle of synapticulae that delimits the calice. The wall boundary between adjacent corallites is presumably synapticulate, but other than where the septa of adjacent calices are juxtapositioned against each

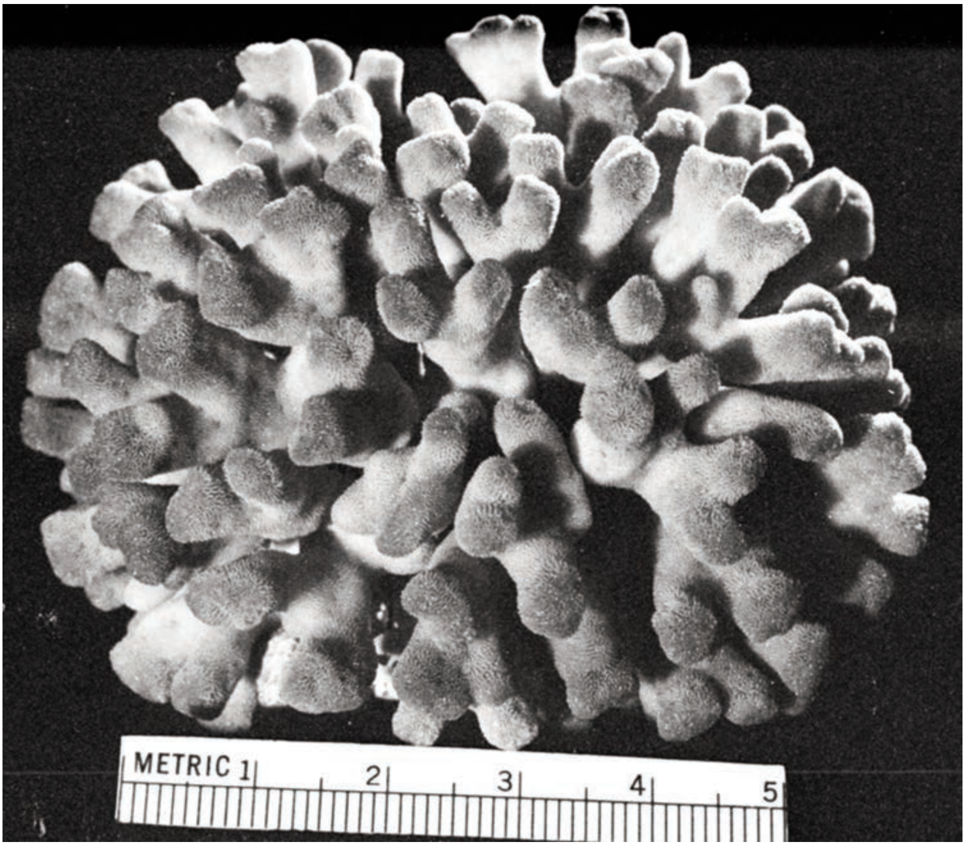

Fig. 8. *Psammocora stellata* (Specimen No. 3498): Dorsal view of an entire corallum. Collection Location: Guam, Tumon Bay fringing reef. Reef Zone and Habitat: Outer part of the inner fringing reef flat platform low tide moat at less than 50 cm depth. Scale bar is 5 cm.

other, it is difficult to distinguish, as the overall surface topography between the calices is relatively flat and not raised into a ridge crests united by a distinguishable row of synapticulae that is present in some other psammocorid species.

Etymology: This species is named in honor of the late Dr. Lucius. G Eldredge who was my thesis chairman (1971) and a colleague at the University of Guam Marine Laboratory until he retired and relocated to Hawai‘i.

Holotype:
Specimen No. USNM 1260043; Figs. 2, 4. **Dimensions:** Entire colony collected that measures 3.1 cm long, 3.1 cm wide, and 1.56 cm in height (before being broken into two pieces to facilitate photography; **Geographic Locality:** Southern tip of Galvez Bank, Mariana Islands Archipelago; **Depth:** 44 meters; **Collecting Station:** TC-78-02 (72-79) Sta. 7, String 6, Lot 3; **Collection Method:** "R.V. *Townsend Cromwell*" utilizing bottom set fish net. **Reef Zone:** Upper bank platform; **Habitat:** Bioclastic sand and rubble with scattered coral patches; **Collector:** R.V. "*Townsend Cromwell*" crew; **Date:** 25 May 1978; **Holotype Location:** U.S. National Museum, Washington, D.C.

Paratypes: Of the following 36 designated paratypes the specimen numbers with subscripts $_1$ are located in the Randall Collection, University of Guam, Marine Laboratory; those with subscripts $_2$

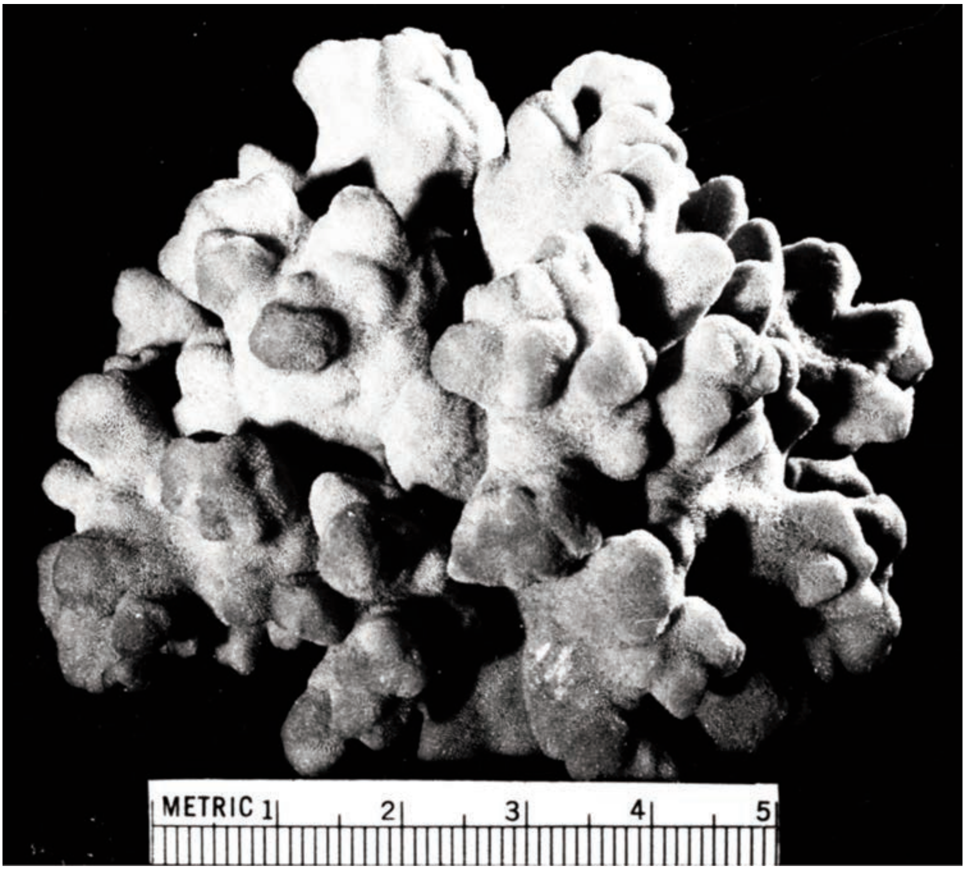

Fig. 9. *Psammocora* (Sp. A), (Specimen No. 78): Dorsal-lateral view of an entire corallum. Collection Location: Guam, Tumon Bay fringing reef. Reef Zone and Habitat: Outer part of the inner fringing reef flat platform low tide moat at less than 50 cm depth. Scale bar is 5 cm.

are located at the Bishop Museum, Honolulu, Hawai‘i; and those with subscripts $_3$ are located at the Smithsonian USNM, Washington D.C.

Specimens: 3127_1, 28918_2, & 28919_3 Coll. Sta. RHR226C-CS-2; 3142_1 Coll. Sta. RHR 227C-CS-1; 23307_1 & 23411_2 Coll. Sta. RHR 1147-CS-6; 23402_1 & 23403_2 Coll. Sta. RHR 1147-CS-7; 22703_1, 29182_2 & 29183_3 Coll. Sta. RHR 1123A-CS-1; 24044_1, 30665_2 & 30666_3 Coll. Sta. TC 84-02, Sta. 12; 27975_1, 27976_2 & 27977_3 Coll. Sta. TC 78-02 (72–79) Sta. 7, String 4, Trap 21; 12519_1, 27945_2 & 27946_3 Coll. Sta. TC 78-02 (72–79) Sta.7, String 7, Trap 30; 12516_1 & 27931_2 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 9; 12505_1 & 27932_2 Coll. Sta. TC 78-02 (72-79) Sta. 10, String 4; 12496_1 Coll. Sta. TC 78-02 (72-79) Sta. 2 North; 28010_1 & 28011_2 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 8, Trap 30; 28151_1 & 28180_3 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 3; 28202_2 & 28229_3 Coll. Sta. TC 78-02 (72-79) Sta.7, String 6, Lot 4; 28053_2 & 28074_3 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 1; 28252_3 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 5; 28101_3 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 2; 28298_3 Coll. Sta. TC 78-02 (72-79) Sta. 7, String 6, Lot 6.

Comparison of *Psammocora eldredgei* to Other Branching Species

A comparison of the characters of *P. eldredgei* with three other confirmed branching species of

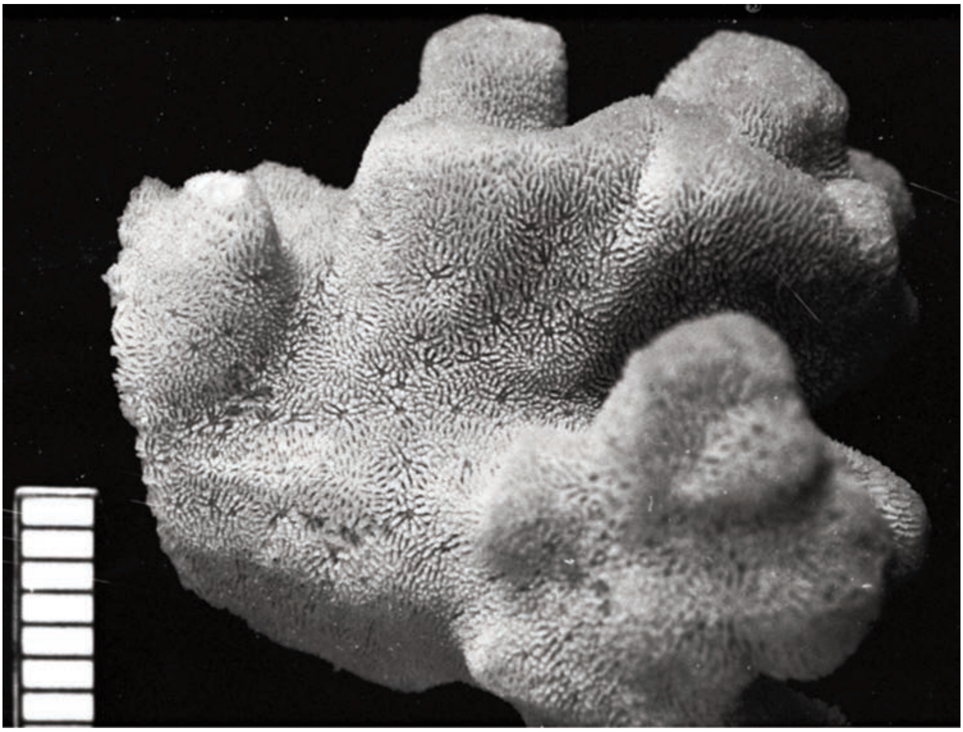

Fig. 10. *Psammocora* (Sp. A): Detail view of a nodular branch tip from Specimen No. 78 shown above. Scale bar is 10 mm.

Psammocora is given below. Within the Mariana Islands Archipelago there are now four branching *Psammocora* species that include *P. contigua* (Figs. 5 and 6), *P. stellata* (Figs. 7 and 8), and *P. obtusangula* = *Psammocora s*p. A (Figs. 9 and 10), and the present newly described *P. eldredgei* (Figs. 2, 3A, 3B, 4). Although Stefani *et al.* (2008) has convincingly synonomized *Psammocora obtusangula* (Lamarck, 1816) with *Psammocora contigua* (Esper, 1794), the specimens that we assigned to *Psammocora obtusangula* in Randall & Myers (1983) and Randall (2003) are quite different from *P. contigua,* and are presently in the process of being described in more detail as a new species in a monograph of the corals of the Mariana Island Archipelago, which for purposes of comparison are here being referred to as *Psammocora s*p. A. In comparing the characters of *P. contigua*, *P. stellata*, and *P. eldredgei* branches of similar size were used.

Polyps: Except for possible size and shape the expanded polyps of the four branching species are remarkable similar in shape and color with the only noticeable difference being the number of rows of tentacles associated with enclosed non-petaloid septa present between adjacent calices, and in *P. eldredgei* the polyps (observed in aquaria) are somewhat thicker at the base and slightly knobbed and pale tan to nearly white at the tip. The number of rows between calices ranges from one to eight rows in *P. contigua*, one to occasionally three rows in *P. stellata* and *Psammocora s*p. A, and generally one row to occasionally two or three in *P. eldredgei*.

Colony Form, Colony and Branch Size, Depth and Habitat Range, and Geographic Distribution: In respect to colony form, size, and branch diameter; in *P. eldredgei* the colonies range in size from sub-centimeter long stems to cespitose clumps 6.7 cm in diameter that display an open laxly branching arborescent form of crookedly diverging small terete branches 2 to 5 mm in diameter (Figs. 2–4); in *P. contigua* the colonies range from centimeter sized encrusting spats with a single stem to 50 cm in diameter that display a wide range of laxly to compactly arranged terete to variously compressed branches that mostly range from 4 to 10 mm diameter in terete to sub-terete branches and to 15 mm or more in width in compressed branches (Figs. 5 and 6); in *P. stellata* the colonies range from centimeter sized encrusting spats with a single stem to 20 cm in diameter that display closely spaced compact to slightly openly arranged terete branches that mostly range from 4 to 11 mm in diameter (Figs. 7 and 8); and in *Psammocora s*p. A the colonies range from centimeter sized encrusting spats with a single thick nodular stem to 20 cm in diameter that display a rounded clump of nodular tipped thick branches from 1 to 3 cm in diameter that are extensively anastomosed below the outer surface (Figs. 9 and 10).

Depth range for the four branching species of *Psammocora* ranged 33 to 200 meters for *P. eldredgei*, < 1 to 20 meters for *P. contigua*, < 1 to 5 meters for *P. stellata*, and < 1 to 25 meters for *Psammocora s*p. A. There appears to be a distinct hiatus between the depth range of *P. eldredgei* and the other three branching species of *Psammocora*, as none of the former have been collected or observed in habitats shallower than 33 meters. Although most of the collected specimens of *P. eldredgei* have been collected from banks where shallow habitats are absent, none have been collected from depths shallower than 89 meters from Guam, Rota, and Pagan where contiguous shallow to deepwater water habitats are present. Because of the depth from which *P. eldredgei* specimens were recovered, samples of their living and preserved tissues revealed abundant zooxanthellae throughout their depth range.

In respect to habitat *P. contigua*, *P. stellata*, and *Psammocora s*p. A are all common to locally abundant on shallow reef flat platforms where large moats of low tide perched water occur, and on shallow fringing reef and lagoon terraces in water generally less than five meters depth, where all three are commonly found growing beside each other and are quite easily discriminated from one another on the basis of colony form and septal characteristics. *Psammocora contigua*, and *Psammocora* sp. A are also common to widely scattered on fringing seaward reef slopes, embayment reefs, fringing reef channels, and lagoon slopes and terraces to 10 meters depth, and uncommon to absent in deep fringing seaward slope and lagoon habitats 20 to 25 meters depth. To date *P. eldredgei* is restricted to fringing seaward reef slopes and isolated bank platforms and their associated peripheral seaward slopes between 33 and 200 meters depth, or possibly deeper as in the deeper upslope dredge hauls the shallower depth has been assigned.

To date the geographical distribution of *P. eldredgei* is restricted to the north-south trending Mariana Island Archipelago between latitude 18°2.5'N near the south end of Pagan Island and latitude 12°42'N at an unnamed bank south-west of Santa Rosa Reef bank, a distance of approximately 600 kilometers (Fig. 1). Because of its restriction to habitats generally below scuba diving depths and its local abundance on bank habitats it is probably more widely distributed in similar habitats along the Mariana Island Archipelago than at the present 13 dredge and three scuba diving stations. *P. contigua* that occurs in snorkeling and scuba diving depths has been collected or recorded from all but Farallon de Medinilla in the five southernmost Mariana Islands. *Psammocora stellata* has been collected in Guam and Saipan in the southern Mariana Islands. In the nine northernmost Mariana Islands *P. contigua* and *P. stellata* were not reported by Randall (1995). To date *Psammocora s*p. A has only been reported or collected from Guam and Saipan.

Corallites: In *P. eldredgei* the calice (peripherally limited by the first occurring row of synapticulae) ranges from 1.40 to 2.41 mm in diameter, which is smaller than *P. stellata* that ranges from 1.72 to 2.50 mm in diameter, and larger than *P. contigua* that ranges from 0.53 to 1.10 mm in diameter and *Psammocora s*p. A that ranges from 0.42 to 0.85 mm in diameter.

In *P. eldredgei* the fossa ranges from 0.20 to 0.34 mm in diameter, which is smaller than *P. stellata* that ranges from 0.35 to 0.62 mm in diameter and larger than *P. contigua* that ranges from 0.11 to 0.17 mm in diameter and *Psammocora s*p. A that ranges from 0.18 to 0.25 mm in diameter.

In *P. eldredgei* and *P. contigua* the columella is a small slender granulated styliform process 0.10 to 0.12 mm in diameter, which is smaller than *P. stellata* that ranges from 0.22 to 0.41 mm in diameter and slightly larger than in *Psammocora s*p. A that ranges from 0.09 to 0.11 mm in diameter.

The number of calicular septa that reach the fossa ranges from 6 to 9 in *P. eldredgei* and *P. contigua*, 6 to 8 in *Psammocora s*p. A, and 7 to 11 in *P. stellata*. In *P. stellata* three to six small short deeply set innermost septal denticals (false paliform lobes) are commonly present, and sometimes one or more small granulated vertical rod-like processes are present on the fossa floor that are not associated with the innermost septa. In *P. eldredgei* such false paliform lobes are rarely developed, but occasionally one or more small granulated vertical rod-like processes are present on the fossa floor that are not associated with the innermost septa. False paliform lobes positioned at the inner end of the septa are generally absent in *P. contigua* and *Psammocora s*p. A.

The inter-locular space between the septa is very narrow in *P. eldredgei*, moderately separated in *P. contigua* and *P. stellata,* and widely separated (generally more than the septal width) in *Psammocora s*p. A.

In *P. eldredgei* the three to four wedge to club shaped petaloid entosepta are present that range from 0.26 to 0.41 mm at their widest part and 0.65 to 0.95 mm in length. In *P. contigua* three to four petaloid entosepta are present that are rice grain shaped and range from 0.15 to 0.25 mm at their widest part and 0.35 to 0.45 mm in length. In *P. stellata* three to four petaloid entosepta are present that are elongated rice grain to slightly wedge or club shaped and 0.18 to 0.35 mm wide, and 0.62 to 0.95 mm long at their widest point. In *Psammocora s*p. A generally two to three petaloid entosepta septa are present that that are thin, laminar, an rather uniform in width along their length and range from 0.10 to 0.16 in width and 0.29 to 0.34 in length.

In *P. eldredgei* three to four bifurcating non-petaloid exosepta septa are generally present within the calice that are wedge shaped before dividing and only slightly narrower than the petaloid entosepta with the individual outer bifurcated limbs narrower and ranging from 0.15 to 0.25 mm in width. In *P. contigua* three to four bifurcating non-petaloid exosepta septa are generally present within the calice that are wedge shaped before dividing and only slightly narrower than the petaloid entosepta with the individual outer bifurcated limbs ranging from 0.10 to 0.15 mm in width. In *P. stellata* three to four bifurcating non-petaloid exosepta septa are generally present within the calice that are wedge shaped before dividing and only slightly narrower than the petaloid entosepta with the individual outer bifurcated limbs ranging from 0.13 to 0.25 mm in width. In *Psammocora s*p. A two to three bifurcating non-petaloid exosepta septa are generally present in the calice that that are thin, lamina, and rather uniform in width along their length before dividing and only slightly narrower than the petaloid entosepta with the individual outer bifurcated limbs ranging from 0.11 to 0.15 mm in width.

The remaining calicular septa consist of one to three fused bi- and tri-branched forms with the inner undivided part and outer limbs that are similar in shape and width to the respective bifurcating non-petaloid septa in the four branching *Psammocora* species.

In *P. eldredgei* the extra-calicular enclosed petaloid and associated bifurcating non-petaloid septa are moderately distinct with the enclosed petaloid ones generally forming one encircling row between adjacent calices that range from 0.12 to 0.16 mm wide and 0.29 to 0.34 mm long. In *P. contigua* the extra-calicular enclosed petaloid septa and associated bifurcating non-petaloid are very distinct with the enclosed petaloid ones generally forming one to eight encircling rows between adjacent calices that range from 0.15 to 0.25 mm wide and 0.35 to 0.45 mm long. In *P. stellata* the extra-calicular enclosed petaloid septa and associated bifurcating non-petaloid are moderately distinct with the enclosed petaloid ones generally forming one to two or three encircling rows between adjacent calices that range from 0.18 to 0.36 mm wide and 0.62 to 0.91 mm long. In *Psammocora s*p. A extra-calicular enclosed petaloid septa and associated bifurcating non-petaloid are not very distinct from one another that commonly appear as a ramifying laminar meshwork with the enclosed petaloid ones varying from one to three encircling rows between adjacent calices that range from 0.10 to 0.16 mm wide and 0.29 to 0.34 mm long.

In *P. contigua* the calicular petaloid septa and extra-calicular enclosed petaloid septa are conspicuously raised above the level of the adjacent calicular and extra-calicular non-petaloid septa, whereas in the other three branching *Psammocora* species all the calicular and extra-calicular septa are rather even in height.

In *P. eldredgei* the upper septal margins of all the septa bear up to eight conspicuous but low granulated dentitions that are compressed into paddle-shaped ridges oriented at right angles to the radial septal plane. In *P. contigua* and *Psammocora s*p. A the upper septal margins bear two or three granulated dentitions, which are thin and elongated in the septal plane and not generally thickened into paddle-shaped ridges. In *P. stellata* the upper septal margins bear five to seven conspicuous granulated dentitions, which on thickened septa can be moderately compressed into paddle-shaped ridges oriented at right angles to the septal plane. Septal dentitions of *P. stellata* are more extant with a more open less compactly arranged granulation pattern than in *P. eldredgei*.

The septal dentitions of all four branching *Psammocora* species bear short spines and granule clusters (centers of calcification) that taper to point and are not arranged or oriented in any particular pattern. Such granulations extend downward on the lateral septal surfaces as well, which in *P. eldredgei* are less conspicuous and shorter than in the other three species because of the narrow interlocular space between the septal elements.

Discussion

From the above comparison of the four branching *Psammocora* species it is apparent that *P. eldredgei* is morphologically more similar to *P. stellata* than to *P. contigua* and *Psammocora s*p. A. A remaining question is whether *P. eldredgei* represents a deep-water ecomorph of *P. stellata* and not a new species, given that, for example, thin ecomorphs are typical among many scleractinian species at greater depths (Bert Hoeksema, personal communication, June 2014). The data and analyses presented here argue for a previously unrecognized species in the contigua-stellata clade, and predict that molecular genetic data will demonstrate that *P. eldredgei* represents a unique branch in that clade. *Psammocora stellata* occupies very shallow water (typically less than 5 m depth), and if it had a habitat range from shallow to mesophotic depths, populations would be found (but are not) in intermediate depths, as is typical of scleractinians that range continuously from shallow to mesophotic depths. To substantiate this the author has collected corals from over 3,000 collecting stations in the Mariana Archipelago and has yet to find a living colony of *P. stellata* deeper than five meters, whereas it is commonplace to find it at five meters or less where it is particularly abundant on shallow reef flat platforms in less than one meter depth. Furthermore, small unattached finely branched *P. stellata* specimens with the same branch diameter size range as *P. eldredgei* are commonly found intermixed in the same microhabitat with robust more compactly thick-branched *P. stellata* specimens, which is likely the result of most *P. stellata* colonies being found as loose branches intermixed with larger rounded compact coralliths with the smaller thinner-branched ones being frequently overturned by wave action. Upon growing to a larger size the colonies gain a refuge in size and mass, and are less likely to be overturned, and with their upper surface being more constantly exposed to direct light thus develop into typical compact thicker branched rounded coralliths. Also in respect to ecomorphic differences between species that span a continuous depth range from shallow to mesophotic depths is that with increasing depth their skeletal elements become less calcified and thinner, which is not case with *P. eldredgei* that is restricted to mesophotic depths and has relatively thicker calcified skeletal characteristics than *P. stellata*, particularly in the nature of its thick compactly arranged calicular septa. Other morphological differences between *P. eldredgei* and *P. stellata* are noted in the above description of the former and comparison of P. *eldredgei* to other *Psammocora* branching species found in the Mariana Island Archipelago.

Acknowledgements

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The Diet of *Diodon hystrix* (Teleostei: Tetraodontiformes): Shell-crushing on Guam's Reefs

Geerat J. Vermeij & Edith Zipser
Department of Earth & Planetary Sciences, University of California, One Shields Avenue,
Davis, California 95616, USA; email: gjvermeij@ucdavis.edu

Abstract. The spiny puffer *Diodon hystrix* is one of the most powerful shell-crushing predators on tropical coral reefs. We counted, measured, and identified molluscan and hermit crab prey remains in the digestive tracts of twelve spiny puffers collected on Guam between 1975 and 1981. Individual fish contained up to 142 prey belonging to a total of 27 gastropod and 8 hermit-crab species. Recovered shell fragments ranged up to 31.5 mm in length and up to 3.5 mm in wall thickness. *D. hystrix* is a voracious consumer of well-armored shell-bearing reef animals.

Introduction

The spiny puffer or porcupinefish *Diodon hystrix* (Linnaeus, 1758) (Diodontidae) stands out as one of the most powerful shell-crushing predators of molluscs on the world's tropical coasts (Vermeij 1978, Palmer 1979, Bertness *et al*. 1981). At a purported maximum length of 90 cm, *D. hystrix* is the largest member of the Diodontidae and, like its smaller congener *D. holocanthus* (Linnaeus, 1758), is found throughout the tropics except in West Africa (Leis 1974). In common with most other Diodontidae and Tetraodontidae, *D. hystrix* crushes its prey between upper and lower plates (each composed of fused teeth) in a vise-like jaw (Fig. 1) (Tyler 1980, Ralston & Wainwright 1997, Wainwright & Bellwood 2002, Korff & Wainwright 2004). Along with the digestible parts, skeletal fragments are ingested, whose diagnostic features make species-level identification possible.

Few of the hundreds of studies of diets of reef fishes report species identifications of prey consumed in the wild. Ingested molluscan prey have been documented at the species level for the bonefish *Albula vulpes* (Linnaeus, 1758) in Puerto Rico (Warmke & Erdman 1963), the labrid wrasses *Lachnolaimus maximus* (Walbaum, 1792) in the Caribbean (Randall & Warmke 1967, Wainwright 1987) and *Cheilinus undulatus* (Ruppel, 1835) in the Indo-West Pacific (Randall *et al*. 1978), tetraodontid puffers of the genus *Sphoeroides* in Florida and the Pacific coast of Costa Rica (Targett 1978, Duncan & Szelistowski 1998), and numerous species including *D. hystrix* in the West Indies (Randall 1964, 1964, 1967). The only records of prey molluscs identified to species in *D. hystrix* from the Indo-West Pacific are those of Rehder & Randall (1975) at Ducie Atoll in southeast Polynesia.

Here we report the diet composition of *Diodon hystrix* in Guam. We dedicate this paper to the memory of Lucius G. Eldredge, who first introduced one of us (GJV) to the importance of shell-breaking predation of molluscs in 1970. Lu was not only a most generous host, along with his wife Jo and four daughters, but also freely shared his laboratory and extraordinary library of reprints during seven productive stays at the University of Guam Marine Laboratory from 1968 to 1984. Further personal details of our friendship with Lu and his family, and the influence Lu had on GJV's scientific development, are given in Vermeij (1997, 2010).

Materials and Methods

During extensive research on shell-breaking predation on molluscs in the field and laboratory in Guam in 1974, 1975, 1979, and 1981, we obtained 12 specimens of *Diodon hystrix*. These were caught from early morning to early afternoon on both the windward and leeward sides of the island by students and staff at the University of Guam Marine Laboratory in Mangilao. One of the 12 specimens was caught by an unidentified fisherman who participated in a spearfishing contest held at

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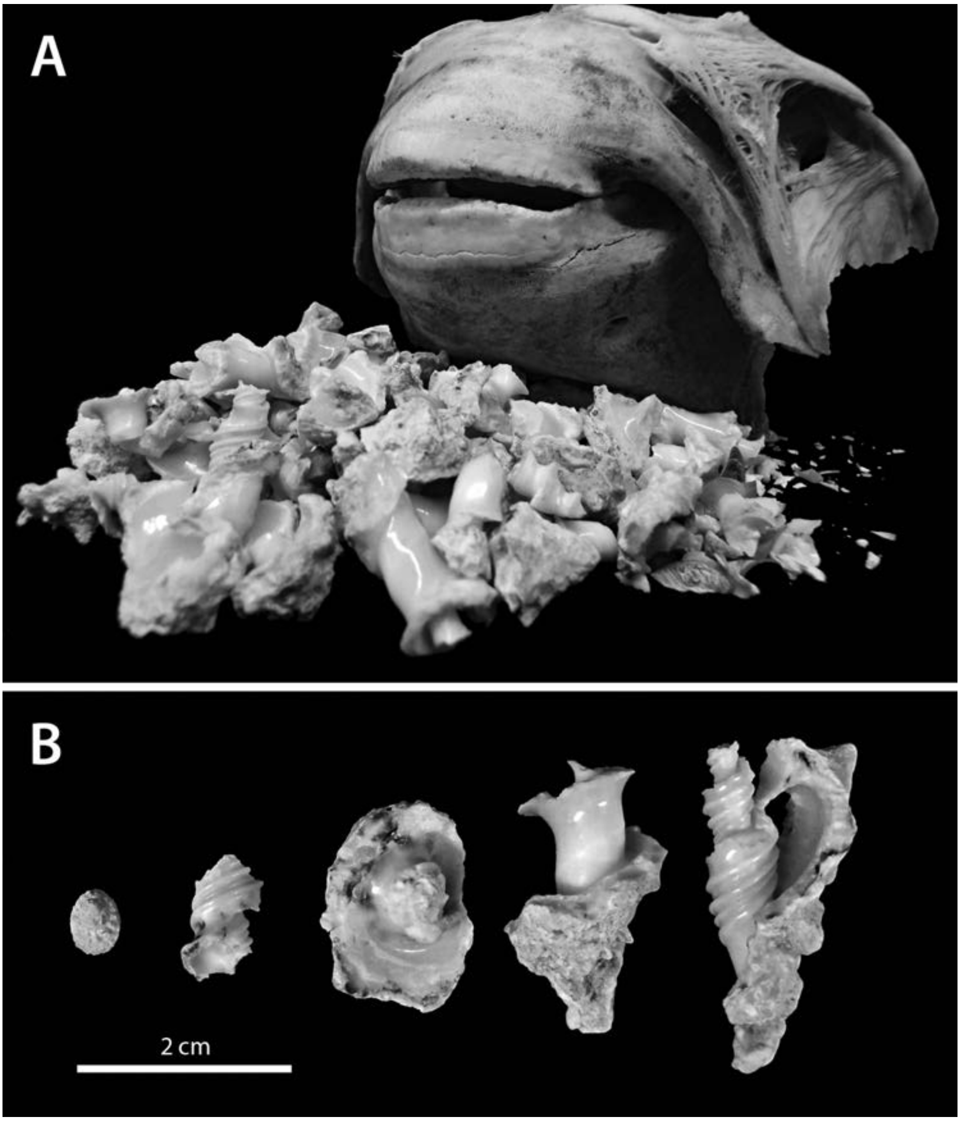

Fig. 1. A. Upper and lower jaw of a 47 cm long *Diodon hystrix*, together with the skeletal fragments in its digestive tract. **B**. Close-ups of five fragments, including a whole individual of the limpet-like *Sabia conica* (left) and a fragment of the columella of *Vasum turbinellus* (right); in between are fragments of *Drupa* spp.

Umatac on 5 and 6 August 1975. This specimen was examined with his permission and with prior agreement with the village commissioner of Umatac. Several other molluscivorous fish species were also examined for gut contents at Umatac.

We recorded the standard length (cm) and, where possible, the gape (mm) of the jaws for each specimen. All skeletal fragments in the digestive tract of each fish were recovered, counted, and identified when possible; and some of the larger fragments were measured. The number of prey per fish was estimated first by counting gastropod shell apices, opercula, and undamaged shells. The minimum number of hermit crab individuals was estimated by counting pairs of chelae. Apices with a glossy inner surface were considered to belong to prey gastropods that were alive when ingested.

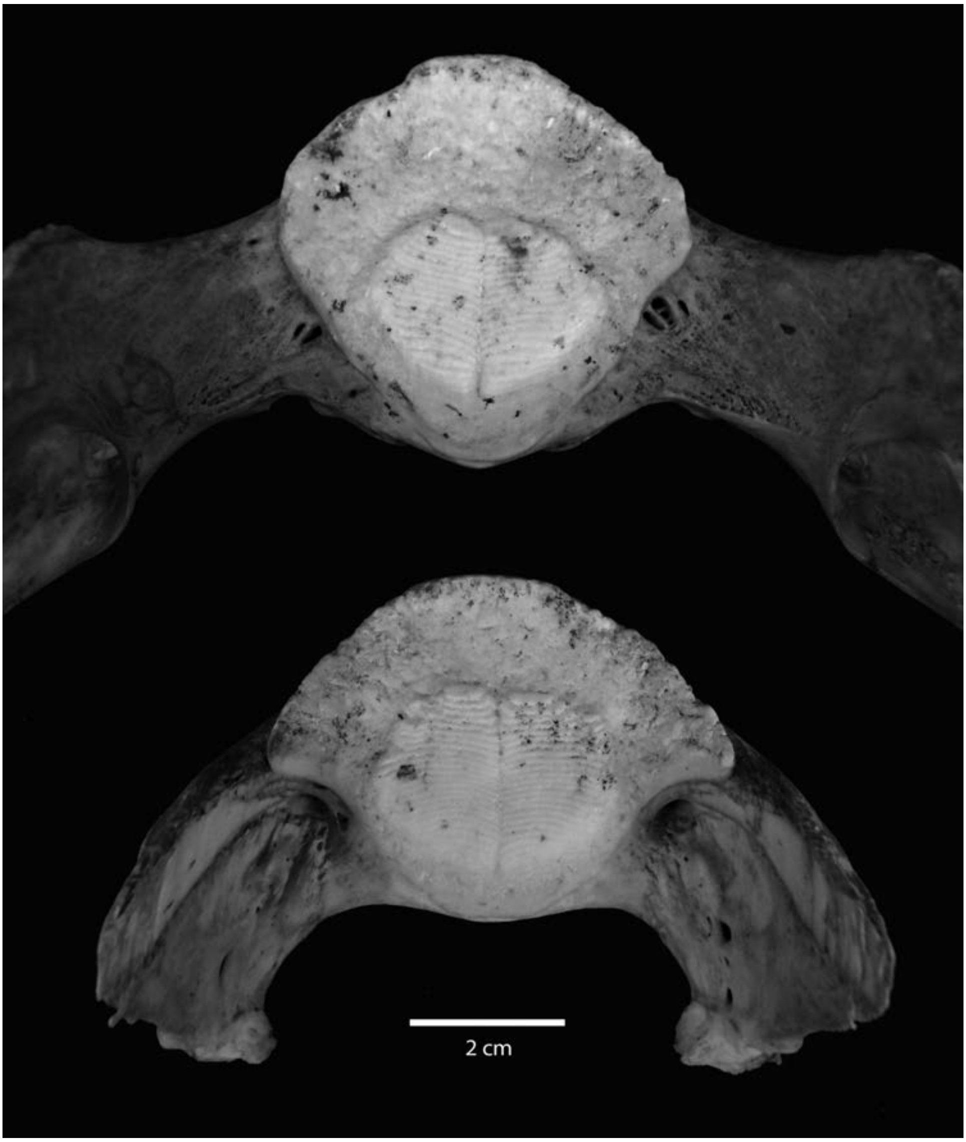

Fig. 2. Close-up of the crushing surfaces of the jaws of a 47 cm *Diodon hystrix*.

Where opercula were available, their number indicated the minimum number of living gastropod taken by the fish. The total number of ingested prey included items that could not be identified to species.

Results

The 12 puffer specimens we examined ranged in length from 23 cm (close to the lower limit of size at which individuals begin to feed in the benthos; see Leis 1974) to 56 cm (Table 1). The gape at the front of the mouth ranged from 15 mm in a 27 cm long specimen to 32 mm in a 47 cm puffer (Table 1).

Of the digestive tracts we examined, 11 (92%) contained skeletal remains of prey. All ingested fragments consisted of either gastropods or hermit crabs. Estimated numbers of prey per fish, includ-

Table 1. Length (cm), gape (mm), and number of prey ingested in individual *Diodon hystrix*.

Length	gape	prey
23	-	16
25.5	-	95
25.5	-	142
27	19	19
27	15	0
34	25	6
34.5	-	134
37	-	38
45	-	33
46	23	52
47	32	14
56	-	49

ing unidentified prey individuals, ranged from 0 to 142 (Table 1), with a mean and standard deviation of 50 +/- 48.5. All fish were caught during daylight hours, indicating that *Diodon hystrix* is a voracious shell-crushing predator, which likely feeds at night or near dawn (see also Hobson 1974).

We identified 27 species of living gastropod and 8 species of hermit crab in the digestive tracts of *D. hystrix* (Table 2). All prey species are common inhabitants of reef flats and the reef margin. No bivalves, barnacles, or sea urchins were found in any of the gut contents. Given that the remains of these other groups are common in the digestive tracts of other shell-crushing fishes, it is likely that *D. hystrix* in Guam is specialized to feed on shell-bearing gastropods and hermit crabs.

Nearly all skeletal material in the digestive tracts was highly fragmented, consisting of shell apices and columellas (Fig. 1). Among these fragments, outer lips of gastropod shells were never recovered and were likely spit out before ingestion. The only intact shells found were a few very small naticids, three individuals of the small cerithiid *Semivertagus nesioticus*, and the limpet-like hipponicid *Sabia conica* (Fig. 1). The last-named species excavates a pit on the exterior of host gastropods (Vermeij 1998) and was ingested together with host specimens of the genera *Drupa* and *Vasum*.

Two of the larger puffers ingested and crushed impressively large and thick-shelled prey. The 56 cm puffer contained 5 apices of *Virgiconus flavidus*, one of which was associated with a fragment 29.9 mm long and 1.8 mm thick at a broken edge. This same individual ingested 32 individuals of *Drupa* spp. (represented by opercula) including *D. morum*; one of the fragments was 25 mm in length and 2.1 mm thick. It also contained two individuals of *Menathais intermedia*, one of which had a diameter of 21.4 mm and a thickness of 2.6 mm at a broken edge. A 46 cm puffer ingested 27 *Drupa* individuals as represented by opercula, of which at least 15 belong to *D. rubusidaeus* (Fig. 2). Some fragments of *D. rubusidaeus* were 25.5 mm long and 3.5 mm thick. Of the 8 *Vasum turbinellus* individuals (as represented by opercula) ingested by this puffer, one fragment was a 31.4 mm long segment of the columella.

Discussion

Our data show that the puffer *Diodon hystrix* is a highly specialized shell-crushing predator on gastropods and hermit crabs. Within this category, however, the fish feeds on a wide variety of species, and shows little discrimination with respect to either shell architecture or occupancy by a living snail or a hermit crab. Other diodontid or tetraodontid puffers whose diets have been studied are smaller and have more generalized feeding habits. For example, we found molluscs, hermit crabs, and sea urchins (*Echinometra* sp.) spines in the digestive tracts of two specimens of *Diodon holocanthus*

Table 2. Prey species in the digestive tracts of *Diodon hystrix* in Guam.

Taxon **Hermit crabs**	N_f	N_{pmax}
Aniculus aniculus (Frabricius, 1787)	1	1
Aniculus sp.	1	1
Calcinus elegans H. Milne Edwards, 1836	1	1
C. laevimanus Randall, 1840	1	1
C. latens Randall, 1840	5	120
C. morgani Rahayu and Forest, 1999	5	8
Ciliopagurus strigatus (Herbst, 1804)	2	1
Clibanarius humilis (Dana, 1851)	1	18
Gastropods		
Turbinidae		
Astralium rhodostoma (Lamarck, 1822) s.l.	1	3
Neritidae		
“Puperita” bensoni (Récluz, 1850)	2	1
Theliostyla albicilla (Linnaeus, 1758)	2	1
Cerithiidae		
Cerithium columna Sowerby, 1855	3	16
“C.” punctatum Bruguiére, 1792	1	30
Clypeomorus nympha Houbrick, 1985	1	17
Semivertagus nesioticus (Pilsbry and Vanatta, 1906)	1	3
Strombidae		
Canarium mutabile Swainson, 1821	2	16
Gibberulus gibbosus (Röding, 1798)	2	12
Hipponicidae		
Sabia conica (Schumacher, 1817)	2	6
Naticidae		
Notocochlis gualteriana (Récluz, 1844)	3	4
Tectonatica bougei (Sowerby, 1908)	1	1
Cypraeidae		
Mauritia maculifera (Schilder, 1832)	1	3
Ranellidae		
Monoplex nicobaricus (Gmelin, 1791)	1	1
Muricidae		
Drupa morum Röding, 1798	3	24
D. ricinus (Linnaeus, 1758)	2	1
D. rubusidaeus Röding, 1798	1	27
Drupina grossularia (Röding, 1798)	1	1
Ergalatax fiscella (Gmelin, 1791)	1	1
Menathais intermedia (Kiener, 1835)	1	2
Nassa serta (Bruguiére, 1789)	1	1
Tenguella granulata (Duclos, 1832)	1	1
Buccinidae		
Pollia fumosa (Dillwyn, 1817)	1	1
P. undosa (Linnaeus, 1758)	1	1
Vasidae		
Vasum turbinellus (Linnaeus, 1758)	5	8
Costellariidae		
Costellaria semifasciata (Lamarck, 1811)	1	1
Conidae		
Rhizoconus rattus (Hwass in Bruguiére, 1792)	2	2
Virgiconus flavidus (Lamarck, 1810)	2	5

N_f	Number of fish containing the species
N_{pmax}	Maximum number of prey in one fish

from New Guinea (pers. observ.); and studies of American *Sphoeroides* spp. show these puffers to consume a wide range of invertebrate prey (Targett 1978, Ralston & Wainwright 1997, Duncan & Szelistowski 1998, Korff & Wainwright 2004).

Many other species of reef fish consume gastropods, bivalves, and hermit crabs by crushing these prey either in the oral jaws or with the pharyngeal bones. In Guam, perhaps the most powerful of these is the wrasse *Coris aygula* Linnaeus, 1758 which, at a maximum length of 36 cm, consumes relatively small prey including young individuals of *Astralium rhodostoma*, *Trochus ochroleucus* Gmelin, 1791, small conids, and the hermit crabs *Calcinus guamensis* Wooster, 1984, *C. lineopropodus* Morgan & Forest, 1991, *C. minutus* Buitendijk, 1937, *C. morgani*, *C. pulcher* Forest, 1958, and *Ciliopagurus strigatus* (pers. observ. on 4 individuals from Guam ranging in length from 23.5 to 36 cm). Neither this wrasse nor any other mollusk-eating fish in Guam matches the size and power of *Diodon hystrix*.

Together with reef-dwelling carpiid and parthenopid crabs (see Zipser & Vermeij 1978), *Diodon hystrix* is able to crush exceptionally strong shells. Specimens of *Drupa morum* comparable in size to those crushed by *Diodon hystrix* were estimated to break under a load of up to 5000 N (Vermeij & Currey 1980). Experiments with relatively small (29 cm) individuals of *Diodon hystrix* in Panama indicated that the presence of large knobs on the shell surface increased the effective size of prey and prevented the puffers from successfully crushing gastropods near the upper limit of size that could fit in the puffer's jaws (Palmer 1979). We have seen specimens of *Drupa morum, D. ricinus*, and *Vasum turbinellus* in the field in Guam with broken knobs or spines, potentially indicating the role of these protrusions in defense against shell-crushers like *Diodon*. As a relatively common and voracious predator, *Diodon hystrix* is likely to be an important selective agent for reef-dwelling shell-bearing animals.

In the modern fauna, *Diodon hystrix* has a nearly circumtropical distribution, in part owing to an exceptionally long pelagic phase (Leis 1974). It would be interesting to know where this most powerful diodontid evolved. The genus *Diodon* is known from the Early Eocene onward in Europe and the Indo-West Pacific (Bellwood 1996, Tiwari & Ralte 2012) and from the Middle Eocene to the present in Florida in the western Atlantic (Hulbert 2001), but the sparse fossil record of this genus has not yet revealed where and when *D. hystrix* arose.

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New Species Named for Lucius G. Eldredge in this Volume

Crustacea	
Isopoda	
Avada eldredgei Boyko, 2015	Parasitic isopod
Decapoda: Anomura	
Porcellanopagurus eldredgei Kropp, 2015	Hermit crab
Decapoda: Brachyura	
Leptomithrax eldredgei Richer de Forges and Ng, 2015	Spider crab
Forestiana lucius Ng, 2015	Xanthid crab
Cnidaria	
Anthozoa: Scleractinia	
Psammocora eldredgei Randall, 2015	Coral