Cah. Biol. Mar. (2013) 54 : 531-540

The littoral sea cucumbers (Echinodermata: Holothuroidea) of Guam re-assessed – a diversity curve that still does not asymptote

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Abstract: The Micronesian island of Guam has been an important site for the study of littoral tropical holothurian taxonomy for almost 200 years. Despite substantial attention by both expeditions and resident taxonomists, new records are still regularly added to the fauna, demonstrating the challenge of documenting even such large and well-known animals in a small hyper-diverse area. Guam is the type locality of species described by Quoy & Gaimard (1833) and Brandt (1835). A survey of the sea cucumber fauna by Rowe & Doty (1977) led to one of the most used guides for the identification of tropical Pacific sea cucumbers because of the color illustrations of living animals it presented. Focus on echinoderms including holothurians continued with numerous new records added in the following decades. Paulay (2003a) summarized the fauna last, recording 46-47 species. At this stage the fauna was thought to be well documented. A week-long workshop on holothurian systematics sponsored by the National Science Foundation PEET (Partnerships for Enhancing Expertise in Taxonomy) project in 2010 included a substantial field work component, sampling both during the day and night, with snorkeling and SCUBA, across a variety of habitats. This survey yielded 40 species, including numerous new records and even species. Further sampling by Kerr's lab since the workshop has added additional records. The littoral holothuroid fauna of Guam now comprises 65 species in 17 genera and 7 families. Half of the 19 newly recorded species are the result of unravelling cryptic species in complexes, the other half are based on new collections. Eleven species are known from single specimens, suggesting that much still remains to be learned about the fauna.

Résumé : *les concombres de mer (Echinodermata : Holothuroidea) littoraux de Guam réévalués - Une courbe de diversité qui n'atteint pas d'asymptote.* L'île micronésienne de Guam a été un site d'étude important pour la taxonomie des holothuries littorales tropicales pour presque 200 ans. Malgré les efforts d'expéditions et de taxonomistes résidant sur place, des espèces sont encore recensées pour la première fois, démontrant les difficultés associées au recensement d'une faune comprenant des animaux pourtant de grande taille et bien connus dans une zone aussi restreinte et diverse. Guam est la localité type d'espèces décrites par Quoy & Gaimard (1833) et Brandt (1835). Le recensement de la faune des concombres de mer par Rowe & Doty (1977) a généré un des guides d'identification les plus utilisés pour l'Indo-Pacifique du fait des illustrations en couleur des animaux vivants qu'il incluait. L'attention portée aux échinodermes a continué avec de nombreuses espèces recensées pour la première fois dans les décennies qui ont suivi. Paulay (2003a) a récapitulé la liste faunistique incluant 46-47 espèces. A ce stade, la faune était présumée être bien connue. En 2010, un groupe de travail d'une semaine sur la taxonomie des holothuries, organisé grâce aux subsides du projet NSF PEET a permis un travail de terrain significatif, avec des échantillonnages de jour comme de nuit, en plongée libre et en scaphandre, et ce dans de nombreux types d'habitats. Cet effort a conduit au recensement de 40 espèces, y compris des espèces vues pour la première fois à Guam, et des espèces nouvelles. Des échantillonnages supplémentaires supervisés par Kerr depuis cet atelier ont encore complété la liste d'espèces recensées. La faune des holothuries littorales de Guam comprend maintenant 65 espèces réparties dans 17 genres et 7 familles. La moitié des 19 espèces recensées pour la première fois sont le résultat de la découverte de complexes d'espèces, l'autre moitié est basée sur de nouvelles récoltes. Onze des espèces recensées ne sont connues que d'un exemplaire indiquant que beaucoup reste à apprendre de cette faune.

Keywords: Holothuroids • Biodiversity • Micronesia • Echinoderms

Introduction

One of the great challenges of our age is to document the biosphere as well as possible before it deteriorates further under the impact of human activities. Recent large-scale biodiversity surveys have demonstrated that our knowledge of biodiversity is surprisingly limited. In many systems we cannot even reliably estimate the order of magnitude of species diversity, let alone describe and name the species present or their biology (e.g., Bouchet et al., 2002; Appeltans et al., 2012; Samyn & Declerck, 2012). The marine realm is particularly challenging, because it is less accessible to direct observation and has received substantially less biological attention than terrestrial systems. Nevertheless we are beginning to have a fairly good knowledge at least of the diversity of larger marine organisms, such as fishes, marine tetrapods, macroalgae, and some groups of macroinvertebrates. Being large-bodied, conspicuous, and charismatic, echinoderms rank among the best-studied macroinvertebrates. The objective of this paper is to review how much we know, how our knowledge has increased, and consider how much remains to be learned about the holothurian fauna of the Micronesian island of Guam.

The holothurian fauna of Guam is among the best documented of any tropical area as a result of a long history of study, visits by major workers, and resident specialist taxonomists. The first written record is by Quoy & Gaimard (1834), who described *Holothuria guamensis* Quoy & Gaimard, 1834 and noted (but did not name) that they encountered five holothurian species on the island. Brandt (1835) described *Holothuria maculata* Brandt, 1835 and *Stichopus chloronotus* Brandt, 1835 from Guam soon after. A few echinoderms were recorded from Guam early in the 20th century, after Guam passed into US hands (Fisher, 1919, Clark, 1920). Following World War II, Cloud (1959) reported on a number of species from Guam and neighboring Saipan. Numerous studies followed after the establishment of the University of Guam and the Marine Laboratory, especially in the wake of a large outbreak of crown-of-thorns sea stars that devastated Guam's reefs in 1967. Echinoderms in general were studied by several faculty and students, including Masashi Yamaguchi and Chuck Birkeland. Holothurian specialist Frank Rowe visited Guam in the 1970's and worked through the fauna with graduate student Jim Doty. Their review of the island's sea cucumbers (Rowe & Doty, 1977) became a popular introduction to holothurian taxonomy in the Pacific for years because of the numerous color plates it offered. The echinoderms of Guam were reviewed in "A working list of marine organisms from Guam" (UOGML, 1981), and numerous new records added subsequently by Kerr et al. (1992). The latest published checklist for holothurians (Paulay, 2003a), was prepared for the *Micronesica* volumes "Marine biodiversity of Guam and the Marianas", recording 47 species (including *H. scabra* Jaeger, 1833, a

doubtful record (see Paulay, 2003a), and here no longer considered) with 10 new records. Gustav Paulay was on the faculty of the University of Guam Marine Lab through the 1990's, while Alex Kerr was a graduate student during part of that time, and returned as faculty in 2005.

In June 2010, a week-long workshop on holothurian systematics sponsored by the NSF PEET holothurian project (Paulay & Kerr, PIs) included a substantial field work component, sampling with snorkeling and SCUBA, during the day and at night, across a variety of habitats, and led to the collection of 40 species. Integrative taxonomic studies also resolved a number of species complexes and thus improved our knowledge of the taxonomy of several species on Guam. Here we review how these efforts have changed our understanding of this fauna.

Materials & Methods

We used Paulay (2003a) as the starting point of this survey, as it critically reviewed the holothurians of Guam known to that date. Field work since then included collections by Kerr's lab at the University of Guam Marine Laboratory, as well as other local naturalists, who brought specimens to Kerr's lab, and collections by Paulay during a visit in 2003 and by Michonneau during a visit in 2008. In 2010 all of us collected sea cucumbers during a two-week workshop. Collections were by snorkel and SCUBA across all types of reef habitats represented on the island, and included searching in the reef matrix (mostly under rocks) and at night. Two species were collected in 2010 by technical diver Jim Pinson, on the deep reef slope below SCUBA-accessible depths (> 60 m). A set of voucher specimens were deposited in the Florida Museum of Natural History, University of Florida (UF), with sets of duplicates in the collections of the "Colección Nacional de Equinodermos, Instituto de Ciencias del Mar y Limnología Universidad Nacional Aútónoma de México" in Mexico City, Mexico, and the Royal Belgian Institute of Natural Sciences in Brussels, Belgium. Some specimens from previous collections have been deposited at the US National Museum of Natural History (USNM).

Revisionary efforts, particularly of members of the Holothuriidae have also clarified species limits and diversity in a number of clades since 2003. Thus morphological revision of *Labidodemas* (Massin et al., 2004) increased the recognized species of that group from 4 to 8. Studies of animals in the field (color patterns, behavior, ecology, etc) and DNA sequence data have allowed us to better understand species limits in a number of complexes, including *Actinopyga, Bohadschia* (Kim et al., 2013), *Holothuria,* and *Euapta*. We provide a brief summary of some of these results as they pertain to the species diversity on Guam.

Results

Approximately 65 species of sea cucumbers are now recorded from Guam (Table 1). New records and nomenclatural updates are presented in systematic order below.

Order Apodida

Family Synaptidae

Euapta tahitiensis Cherbonnier, 1955

UF 10327: Guam, Tanguisson, powerplant inflow channel, 0-5 m, 11.VI.2010, Fig. 1A.

A single *Euapta* species, *E. godeffroyi* , has been generally recognized across the Indo-West Pacific, although two other species have been proposed: *E. magna* Heding, 1928 and *E. tahitiensis*. Our work indicates that *E. tahitiensis* is valid; the status of *E. magna* remains to be evaluated. *Euapta tahitiensis* is widespread in the Pacific and is here recorded from Guam for the first time. Examination of previous *Euapta* collections from Guam revealed that the species was also collected, but not recognized in the past.

Order Aspidochirotida

Family Stichopodidae

Stichopus herrmanni Semper, 1868

UF 1683: Guam, Apra Harbor: SW end of Glass Breakwater, sand slope, 18 m. 10.VII.2003.

Definitively recorded from Guam based on the single specimen above. *Stichopus herrmanni* is one of the largest and most conspicuous stichopodids on reefs, thus lack of other records suggests that the sole individual collected was a vagrant. *Stichopus herrmanni* was in the past confused with other species of the *S. variegatus* complex (see below).

***Stichopus* sp. 1**

= *Stichopus ?monotuberculatus*, Paulay 2003a, non Quoy & Gaimard 1834.

Two other specimens of the *Stichopus variegatus* complex have been recorded from Guam, one collected early in the 1900's (USNM E24500) with no indication as to provenance other than "Guam" and not readily identifiable to species within the complex. The second specimen was collected and released ca. 1990, but observed by Kerr. It was the color morph illustrated by Chao & Chang (1989: plate I) as *S. variegatus*, not *S. herrmanni*. These were tentatively identified by Paulay (2003a) as *S. monotuberculatus*, a species since found to be restricted to the Indian Ocean (Starmer & Paulay, unpublished; Conand

Table 1. Records of holothurians on Guam. Liste des holothuries recensées à Guam. Q&G: Quoy & Gaimard (1834); R&D: Rowe & Doty (1977), Kerr: Kerr et al. (1992 & 1993).

Species	Q&G 1834	Brandt 1835	R&D 1977	Kerr 1992-3	Paulay 2003a	This study
Apodida: Synaptidae						
Euapta godeffroyi (Semper, 1868)			1	1	1	1
Euapta tahitiensis Cherbonnier, 1955						1
Opheodesoma grisea (Semper, 1868)			1	1	1	1
Patinapta sp. 1					1	1
Polyplectana sp. 2			1	1	1	1
Polyplectana galatheae Heding, 1928					1	1
Synapta maculata (Chamisso & Eysenhardt, 1821)			1	1	1	1
Synaptula sp. 1					1	1
Apodida: Chiridotidae						
Chiridota hawaiiensis Fisher, 1907			1	1	1	1
Chiridota violacea Müller, 1850					1	1
Aspidochirotida: Stichopodidae						
Stichopus chloronotus Brandt, 1835		1	1	1	1	1
Stichopus herrmanni Semper, 1868						1
Stichopus sp. 1				1	1	1
Stichopus horrens Selenka, 1867			1	1	1	1
Stichopus noctivagus Cherbonnier, 1980				1	1	1
Thelenota ananas (Jaeger, 1833)			1	1	1	1
Thelenota anax H. L. Clark, 1921			1	1	1	1
Thelenota rubralineata Massin & Lane, 1991					1	1
Aspidochirotida: Holothuriidae						
Actinopyga echinites (Jaeger, 1833)			1	1	1	1
Actinopyga varians (Selenka, 1867)	1	1	1	1	1	1
Actinopyga sp. 1						1
Actinopyga palauensis Panning, 1944				1	1	1
Bohadschia argus Jaeger, 1833			1	1	1	1
Bohadschia marmorata Jaeger, 1833			1	1	1	1
Bohadschia koellikeri (Semper, 1868)						1
Bohadschia vitiensis (Semper, 1868)						1
Bohadschia ocellata Jaeger, 1833						1
Holothuria (Thymiosycia) arenicola Semper, 1868			1	1	1	1
Holothuria (Halodeima) atra Jaeger, 1833			1	1	1	1
Holothuria (Semperothuria) cinerascens (Brandt, 1835)			1	1	1	1
Holothuria (Mertensiothuria) coronopertusa Cherbonnier, 1980						1
Holothuria (Platyperona) difficilis Semper, 1868			1	1	1	1
Holothuria (Stauropora) discrepans Semper, 1868						1
Holothuria (Halodeima) edulis Lesson, 1830			1	1	1	1
Holothuria (Halodeima) aff. *edulis* Lesson, 1830						1
Holothuria (Platyperona) excellens (Ludwig, 1875)				1	1	1
Holothuria (Semperothuria) flavomaculata Semper, 1868				1	1	1
Holothuria (Stauropora) fuscocinerea Jaeger, 1833				1	1	1
Holothuria (Microthele) fuscopunctata Jaeger, 1833			1	1	1	1
Holothuria (Lessonothuria) hawaiiensis Fisher, 1907					1	1
Holothuria (Thymiosycia) hilla Lesson, 1830			1	1	1	1
Holothuria (Thymiosycia) impatiens ESU1 (Forsskål, 1775)			1	1	1	1
Holothuria (Thymiosycia) impatiens ESU2 (Forsskål, 1775)						1
Holothuria (Thymiosycia) impatiens ESU4 (Forsskål, 1775)						1
Holothuria (Cystipus) inhabilis Selenka, 1867			1	1	1	1
Holothuria (Mertensiothuria) leucospilota Brandt, 1867			1	1	1	1
Holothuria (Lessonothuria) lineata Ludwig, 1875			1	1	1	1
Holothuria (Microthele) fuscogilva Cherbonnier, 1980		1		1	1	1
Holothuria (Stauropora) olivacea Ludwig, 1888						1
Holothuria (Lessonothuria) pardalis Selenka, 1867						1
Holothuria (Stauropora) pervicax Selenka, 1867			1	1	1	1
Holothuria (Cystipus) rigida (Selenka, 1867)						1

Holothuria (Metriatyla) scabra Jaeger, 1833			1	0
Holothuria (Halodeima) signata Ludwig, 1875			1	1
Holothuria (Lessonothuria) verrucosa Selenka, 1867			1	1
Holothuria (Theelothuria) turriscelsa Cherbonnier, 1980		1	1	1
Holothuria (Microthele) whitmaei Bell, 1887	1	1	1	1
Holothuria ("Thymiosycia") n. sp.				1
Labidodemas semperianum Selenka, 1867	1	1	1	1
Labidodemas pseudosemperianum Massin, Samyn & Thandar, 2004				1
Labidodemas pertinax (Ludwig, 1875)				1
Labidodemas rugosum (Ludwig, 1875)				1
Pearsonothuria graeffei (Semper, 1868)	1	1	1	1
Dendrochirotida: Cucumariidae				
Thyone okeni Bell, 1884	1	1	1	1
Dendrochirotida: Phyllophoridae				
Phyrella n. sp.				1
Dendrochirotida: Sclerodactylidae				
Afrocucumis africana (Semper, 1868)	1	1	1	1

et al., 2010). Thus at least two species of the *S. variegatus* complex have now been recorded from Guam.

Order Aspidochirotida

Family Holothuriidae

***Actinopyga* sp. 1**

UF 237: Guam, Anae Islet, NS side, in sand patch, 5-7 m. 14.X.1994.

Study of specimens of black *Actinopyga* taken on Guam revealed that a second species is present in addition to *A. palauensis* (= *A. obesa,* in Kerr et al., 1992). Ossicles of this species somewhat resemble those of *A. spinea*, but it differs from that as well as other species studied to date in its COI sequence. This species also occurs in the Philippines.

Actinopyga varians (Selenka, 1867)

= *Actinopyga mauritiana*, Rowe & Doty, 1977; Paulay, 2003a; non Quoy & Gaimard, 1834.

Netchy & Paulay (in prep) separate the Pacific form of the widespread *Actinopyga mauritiana* species complex as *A. varians.*

Bohadschia marmorata Jaeger, 1833, species complex

Bohadschia marmorata Jaeger, 1833

UF 4748: Guam, Piti Bombholes, in and near inshore seagrass bed 1 m. 28.VI.2003.

Bohadschia vitiensis (Semper, 1868)

UF 4701: Guam, Piti Bombholes lagoon on sand, out in day 5-7 m. 20.VII.2003.

Bohadschia koellikeri (Semper, 1868)

UF 4705: Guam, Piti Bombholes moat, 0-2 m. 19.VII.2003.

Bohadschia ocellata Jaeger, 1833

UF 7143: Guam, Tumon sand flat, 1-1.5 m. IV.2008.

Bohadschia is one of the most challenging genera among holothurians for species delineation, as the group has very simple ossicles, with substantial intraspecific variation and limited interspecific differentiation both in ossicles as well as in color pattern (Kim et al., 2013). Rowe & Doty (1977) showed the great variability of their color patterns and considered all forms on Guam, other than the distinctive *B. argus*, to represent a single species, *B. marmorata*. Paulay (2003a) noted at least two distinguishable species in this complex but did not separate them; these two forms were then distinguished with mtDNA sequences by Clouse et al. (2005). Subsequent work focusing on color patterns and mtDNA sequences demonstrate that four species are involved, and all four occur on Guam (Kim et al., 2013).

Holothuria (Cystipus) inhabilis Selenka, 1867

= *Holothuria (Cystipus) rigida* Rowe & Doty, 1977; Paulay, 2003a, non Selenka, 1867.

Holothuria rigida is confused in much of the literature with *H. inhabilis*. Previous records of *H. rigida* from Guam all appear to pertain to *H. inhabilis*.

Holothuria (Cystipus) rigida (Selenka, 1867)

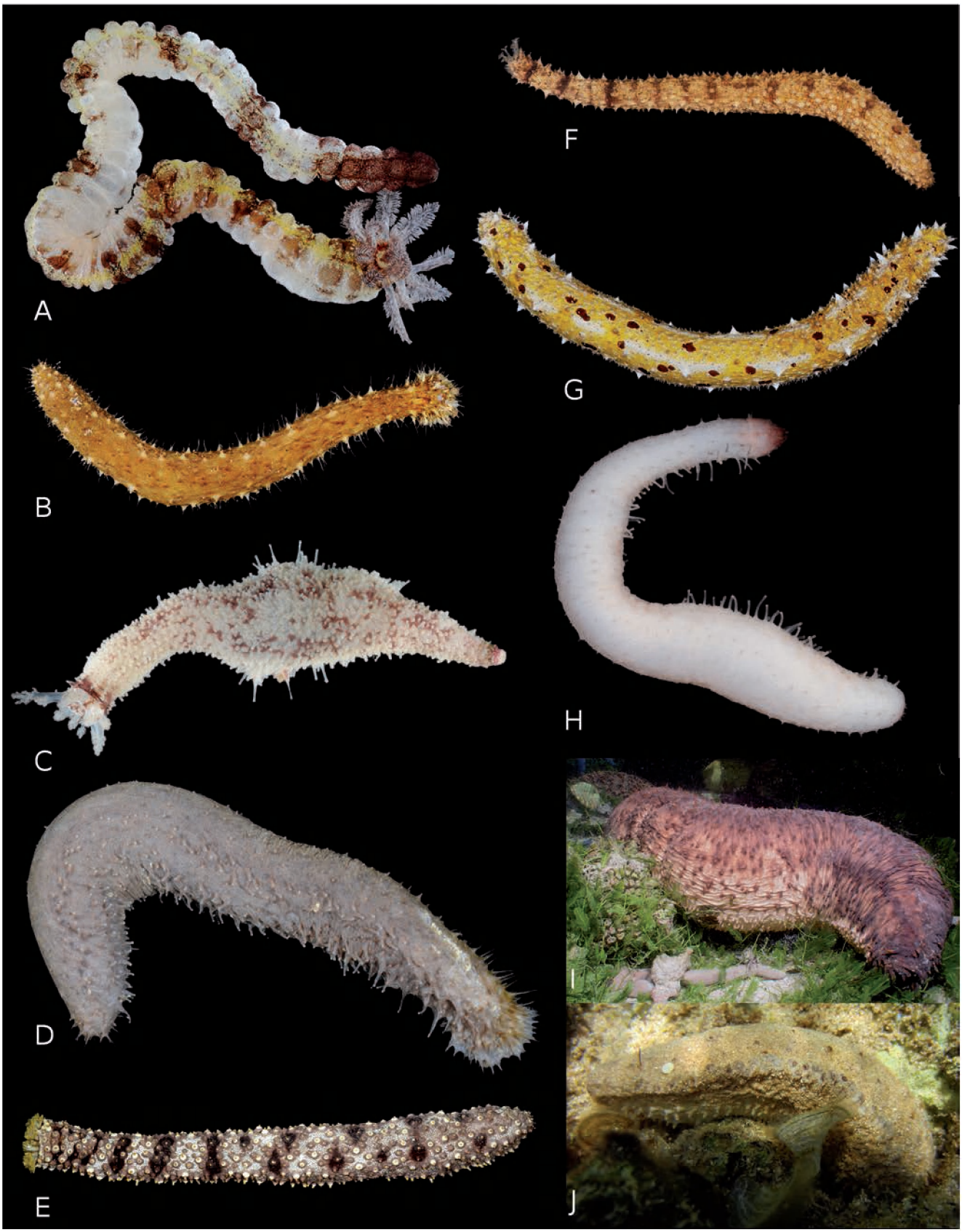
UF 12507: Guam: Ylig Bay ("Turtle Cove"), inner reef flat, 1 m, under coralline rubble. 24.IV.2012, Fig. 1J.

While *H. inhabilis* is fairly common on Guam, *H. rigida* proper has not been recorded until recently and is known from the single specimen cited above.

Holothuria (Halodeima)* aff. *edulis Lesson, 1830

UF 11292: Guam, Tumon Bay, deep reef slope, 100 m. 2011.

This gray colored, reef-dwelling variant of *H. edulis* is suspected to be a distinct species, and is known sporadically across the Pacific (O'Loughlin et al., 2007). A single specimen was collected in deep water by technical diver Jim Pinson on Guam recently. Jim saw several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animals at this location, but has otherwise not seen the species elsewhere in deep water on Guam.

Holothuria (Lessonothuria) verrucosa Selenka, 1867

= *Holothuria (Lessonothuria)* sp. 1 in Paulay, 2003a.

This species, first recorded by Paulay (2003a), has now been identified as *H. verrucosa*.

Holothuria (Mertensiothuria) coronopertusa Cherbonnier, 1980

UF 11543: Guam, on coralline sand, 100 m. 22.XI.2010, Fig. 1I.

This striking holothurian described from New Caledonia has turned up in recent years across much of the Indo-West Pacific in deep water. A single specimen was collected on Guam, 100 m deep, by technical diver Jim Pinson.

Holothuria (Microthele) fuscogilva Cherbonnier, 1980

= *H. (Microthele) nobilis* Paulay, 2003a; non Selenka, 1867.

See Paulay (2003a) for discussion of the history of identification in this complex on Guam. Uthicke et al. (2004) have reassessed the group based on broad sampling and sequence data and showed that the appropriate name for the dark and light mottled Pacific form is *H. fuscogilva*.

Holothuria (Stauropora) discrepans Semper, 1868

UF 10319: Guam, Double Reef, deep under rock, 1-2 m. 11.VI.2010, Fig. 1D.

This rather inconspicuous and relatively small *Stauropora* is easy to overlook and uncommon, but appears to be rather widespread in the western and central Pacific. A single specimen was collected on Guam in 2010.

Holothuria (Stauropora) olivacea Ludwig, 1888

UF 10760: Guam, Apra Harbor, Kilo Wharf wharf wall and lagoon slope, 0-15 m. 23.VI.2010, Fig. 1B.

Another inconspicuous and small *Stauropora*, known from many locations, but not previously recorded from Guam.

Holothuria (Thymiosycia) impatiens (Forsskål, 1775), species complex

***Holothuria (Thymiosycia) impatiens* ESU1**

UF 10341: Guam, Apra Harbor, Glass Breakwater, near sunken barges, 1-15 m. 15.VI.2010, Fig. 1F.

***Holothuria (Thymiosycia) impatiens* ESU2**

UF 6729: Guam, Hagatna, S of Adalupe Island. 0-1 m. 6.II.2008, Fig. 1E.

***Holothuria (Thymiosycia) impatiens* ESU4**

UF 4709: Guam, Pago Bay reef flat to crest channel, under rocks 0-2 m. 2003.

Michonneau's dissertation research is demonstrating that *H. impatiens* is a large species complex that includes at least 12 ESUs (Evolutionarily Significant Units, or phylogenetic species, see Malay & Paulay, 2010 for definition), species which can be differentiated based on subtle morphological and clear genetic characters. Three of these have now been recorded from Guam.

Holothuria ("Thymiosycia") sp. nov.

UF 10317: Guam, Tanguisson outer reef slope under rock on sand 22-25 m. 11.VI.2010, Fig. 1G.

A single specimen of a distinctive, fairly large *Holothuria*, with *Thymiosycia*-type ossicles was collected in 2010, and appears to represent an undescribed species. Phylogenetic analysis of DNA sequences indicates the species is not related to other *Thymiosycia*, and represents a deeply divergent lineage.

Labidodemas pseudosemperianum Massin, Samyn & Thandar, 2004

Labidodemas was not studied in detail on Guam in the past. Massin et al. (2004) revised the genus, doubling the number of species known, and recorded *L. pseudosemperianum* from Guam based on a specimen (USNM E 53083) collected in Tumon Bay by Kerr.

Labidodemas pertinax (Ludwig, 1875)

UF 10329: Guam, Tepungan Channel tunnel, under road, 0-2 m. 12.VI.2010, Fig. 1H.

In 2010, we encountered two species of *Labidodemas* on

Figure 1. Live photographs of newly recorded species. Photographies d'espèces recensées pour la première fois. **A.** *Euapta tahitiensis* (UF 10327). **B.** *H. olivacea* (UF 10760). **C.** *Phyrella* sp. nov. (UF 10336). **D.** *H. discrepans* (UF 10319). **E.** *H. impatiens* ESU2 (UF 6729). **F.** *H. impatiens* ESU1 (UF 10341). **G.** *Holothuria* sp. nov. (UF 10317). **H.** *Labidodemas pertinax* (UF 10329). **I.** *Holothuria coronopertusa* (UF 11543). **J.** *H. rigida* (UF 12507).

Guam, both fairly common, *L. semperianum* and *L. pertinax*. The latter represents a new record.

Labidodemas rugosum (Ludwig, 1875)

UF 6721: Guam, Hagatna, S. of Adalupe Island, 0-1 m. 9.II.2008.

This species known from a single individual is otherwise widespread in the Indo-West Pacific. It can be differentiated from other *Labidodemas* by its uniform gray-pinkish body wall, the cream colored tentacles, and a yellow circle around the suckers of the ventral tube feet. It represents a new record and fourth *Labidodemas* species in Guam's fauna.

Order Dendrochirotida
Family Phyllophoridae
Phyrella sp. nov.

UF 10336: Guam, Gun Beach, N end of Tumon Bay reef flat and reef front, 0-2 m. 12.VI.2010, Fig. 1C.

Since 2003, three specimens of an undescribed *Phyrella* have been collected on Guam (Michonneau & Paulay, in press). The species is densely covered with podia and has relatively few ossicles. Only two dendrochirotids have been recorded from Guam previously, the common sclerodactylid *Afrocucumis africana*, and *Thyone okeni*, (considered a synonym of *Thyone venusta* Selenka, 1868 by Thandar (1990)) recorded by Rowe & Doty (1977) based on a small specimen (described as 5 mm long in the text, and 2 cm long in the plate legend). The latter species was not described, the illustration presented of the live animal is of too limited resolution to evaluate. The specimen has now been located at the Australian Museum (AM J.9328), but not yet reexamined. It is possible that this specimen represents a juvenile of the *Phyrella* species here recorded. *Thyone okeni* is noted to lack ossicles (Bell, 1884), but the presence/absence of ossicles is not discussed for the Guam specimen. Ossicles are often uncommon in juvenile species of *Phyrella*. *Thyone okeni* is presumed to have 10 tentacles like other members of the genus, while *Phyrella* n. sp. has 17-18, but likely several are added during ontogeny.

Discussion

The 65 species of sea cucumbers recorded from Guam represent a greater diversity than known from almost any other comparable-sized area (541 km^2). It is comparable to the recorded fauna of the Spermonde archipelago in Indonesia (56 species: Massin, 1999) near the global center of marine diversity (Hoeksema, 2007; Renema et al., 2008). The high richness reflects both the proximity of Guam to the diversity center and the intense scrutiny the fauna has received over the years by both resident and visiting holothurian specialists.

The large increase in recorded diversity (from 46 to 65 species) in the past decade is remarkable, given the long history of research on holothurians in Guam, and the fact that sea cucumbers are among the largest and most conspicuous mobile invertebrates on reefs. The diversity *vs.* time curve on Guam shows no sign of reaching an asymptote (Fig. 2). This trend underscores how little we know about marine diversity (e.g., Bouchet et al., 2002; Paulay, 2003b). Three species appear to be undescribed, while another four remain unidentified.

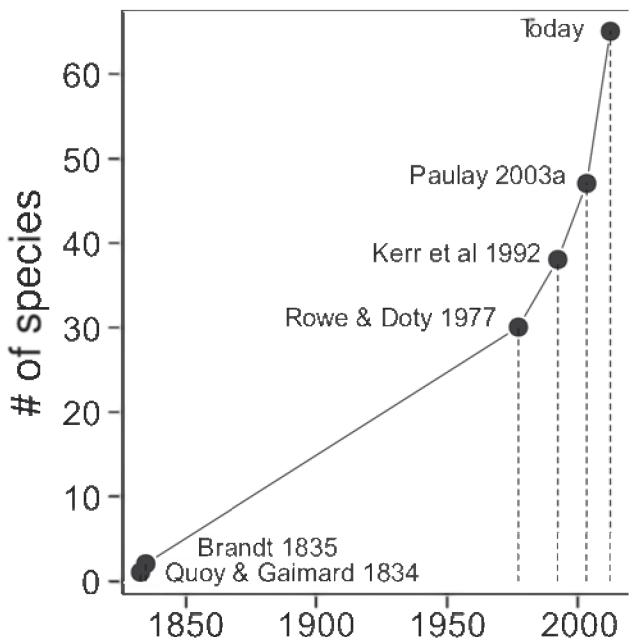

Figure 2. Increase of known diversity of holothurians on Guam over time. Augmentation au cours du temps de la diversité connue des holothuries de Guam.

Half of the new records (8 of 19) are genuinely new, meaning they were not encountered and recorded previously. Remarkably, 7 of these, together with 4-5 others (previously recorded or part of species complexes) are known from single specimens on Guam (*Synaptula* sp. 1, *Stichopus herrmanni, Thelenota rubralineata, Holothuria coronopertusa, H. discrepans, H.* aff. *edulis*, *H. olivacea, H. rigida, Holothuria* n. sp., *Labidodemas pseudosemperianum*, *L. rugosum*, and possibly "*Thyone okeni*"). Three of these species represented by singletons are known only from deep water on Guam (*T. rubralineata, H.*

coronopertusa, H. aff. *edulis*), and their rarity likely reflects the difficulty of accessing this habitat. Six are parts of species complexes or are fairly non-descript, and may have been missed by less focused past surveys (*Euapta tahitiensis, H. discrepans, H. olivacea, H. pardalis, H. rigida, Labidodemas pseudosemperianum*). Two are minute and cryptic (*Synaptula* sp. 1, "*Thyone okeni*"). Increased sampling efforts, in particular below SCUBA-accessible depths, will likely lead to additional records.

The other half of new records emerged from differentiation of species complexes. Molecular and morphological examination of fresh material and collaborative integrative revisions of the reef-associated holothurians pursued partly through the NSF PEET holothurian project has revealed high levels of cryptic diversity in several species complexes. About one third (~ 15 of 46) of the species recorded from Guam in the past are now known to be species complexes. Many of these complexes include or are comprised of a geographic mosaic of allopatric species, of which only a single species is known to occur on Guam. For these, revisions have changed or may change the name of the Guam form. However five of the species include multiple sympatric cryptic species not previously differentiated on Guam, adding substantially to the diversity of the fauna: *Euapta godeffroyi, Bohadschia marmorata, Holothuria edulis, H. impatiens,* and *Labidodemas semperianum*. Integrative taxonomic studies have revealed species lost in synonymies (e.g., 4 species in the *Bohadschia marmorata* complex), not recognized since their description (e.g., distinction of *Euapta tahitiensis* and *E. godeffroyi*), and species that were missed because characters traditionally used in species delimitation do not vary among related forms (e.g., the three species in the *H. impatiens* complex).

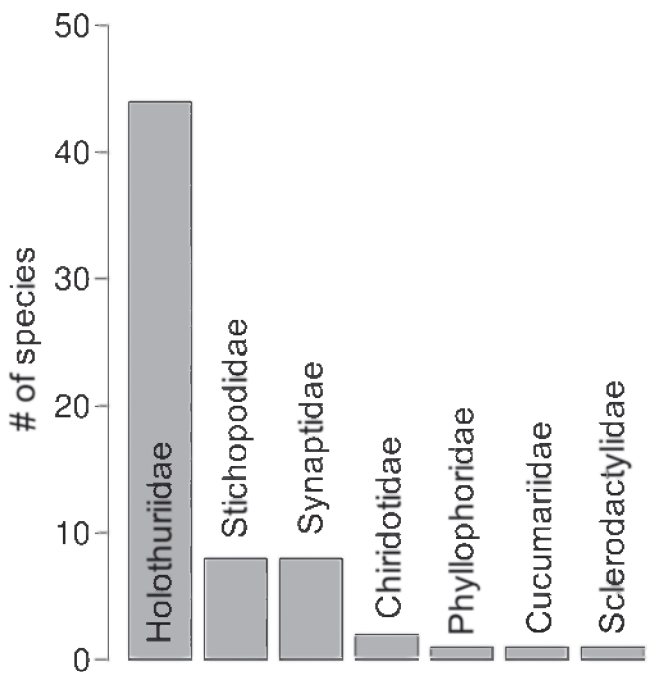

Figure 3. Species richness for each sea cucumber family represented in Guam.

The fauna is dominated by the Holothuriidae (44 species: 70%), followed by the Synaptidae and the Stichopodidae (both 8 species: 13%); two species of Chiridotidae, and one each of Cucumariidae, Sclerodactylidae, and Phyllophoridae, round out the fauna (Fig. 3). The dominance of aspidochirotids (81%) and poor representation of dendrochirotids (5%) is typical of oligotrophic environments such as oceanic islands in the tropics. Similarly dendrochirotids comprise 5% (2 of 37 species) of the holothurians of the oceanic island La Réunion (Conand et al., 2010) and 2.1% of the fauna off the oligotrophic coast of Kenya (Samyn, 2003; Samyn & Tallon, 2005), while they represent 34% (42 of 122 species) of the fauna on Madagascar (Cherbonnier, 1988), a neighboring microcontinent. Oligotrophic waters and isolation likely both contribute to the underrepresentation of this suspension feeding group with lecithotrophic development.

Acknowledgements

We thank the staff of the University of Guam Marine Laboratory for hosting and helping with the workshop that produced this study. Funding by NSF PEET (DEB 0529724) is gratefully acknowledged. The authors would like to thank Chantal Conand and Claude Massin for constructive remarks that improved this manuscript.

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