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On the Coexistence in Spain of *Prosopigastra kohli* Mercet, 1907 and *Prosopigastra bulgarica* Pulawski, 1958 (Hymenoptera: Crabronidae)

Wojciech J. Pulawski [1] **and Fernando Fresno López** [2]

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Prosopigastra bulgarica **Pulawski is first recorded from Spain and compared with** ***Prosopigastra kohli*** **Mercet. A lectotype is designated for the latter species.**

Four species of *Prosopigastra* (*P. handlirschi* Morice, *P. kohli* Mercet, *P. punctatissima* A. Costa, and *P. zalinda* de Beaumont) have been known from Spain until now. In 1985, however, F. Sanza collected there a fifth species, *P. bulgarica*, although he did not recognize it as such. Many more specimens were subsequently taken and recognized as *P. bulgarica* by F. Fresno López. This discovery makes it necessary to designate a lectotype for *P. kohli*, as it is closely similar to *P. bulgarica*.

Prosopigastra bulgarica Pulawski

This species was described from Bulgaria (Pulawski 1958), and in the following years it was found in Turkey (de Beaumont 1967), Iran and Kazakhstan (Pulawski 1979), and the European part of Russia (Shkuratov 1998). In Spain, specimens were collected in the Burgos and Segovia provinces. Below is a detailed list of the Spanish specimens known to us (CAS: California Academy of Sciences; FFL: Fernando Fresno López personal collection). All the specimens were collected by F. Fresno López except those from Fuentelcésped that were taken by F. Sanza.

Burgos Province: Fuentelcésped, 20 July 1985 (1 ♂, CAS), 3 Aug 1985 (1 ♀, CAS); Fuentespina, 6 July 2002 (7 ♀, 7 ♂, FFL), 21 June 2003 (1 ♀, 1 ♂, CAS; 3 ♀, 5 ♂, FFL), 21 June 2004 (3 ♂, FFL), 6 July 2009 (1 ♀, CAS; 1 ♀, 3 ♂, FFL), 23 June 2014 (1 ♂, CAS).

Segovia Province: Aldealengua de Santa Maria, 26 July 2014 (1 ♂, FFL), Maderuelo (4 July 2011, 1 ♂, FFL).

Prosopigastra kohli Mercet

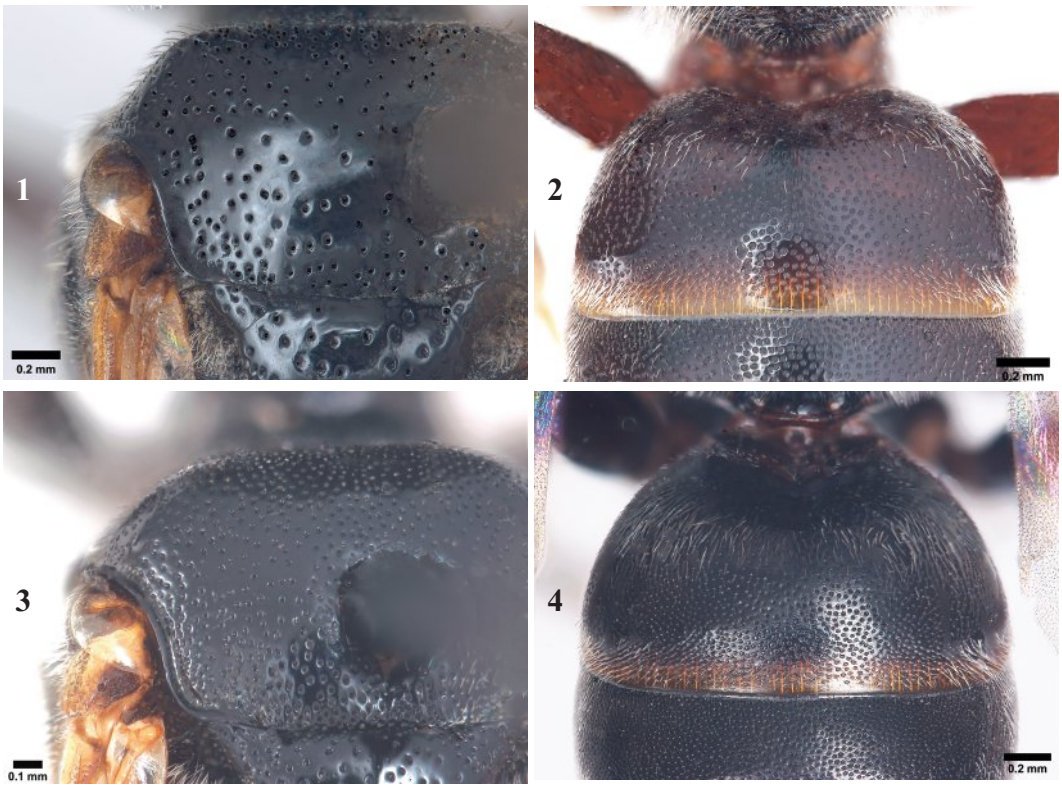
Described from Madrid area in Spain (Mercet 1907), the species was subsequently found in Portugal (de Andrade 1949). In Spain, it has been recorded from the Alicante, Cádiz, Ciudad Real, Madrid, Salamanca, Soria, Valladolid, and Zamora provinces, mainly by Gayubo and his co-authors (Gayubo 1982, among other papers).

In order to designate a lectotype for this species, we tried to locate Mercet's syntypes in the Museo Nacional de Ciencias Naturales, Madrid, Spain. Unfortunately, no such specimens could be found there. On the other hand, four specimens, all determined as *Prosopigastra kohli* by Mercet, are in The Natural History Museum in London, United Kingdom (according to David G. Notton,

they were all acquired with the E. Saunders collection in 1910). Two of them were collected in 1908, i.e., after the publication of the species description, whereas the other two (one female and one male) are apparently syntypes. The female, labeled Madrid but with no date, is hereby selected as the lectotype by W.J. Pulawski. The specimen was previously examined by Pulawski in 1978; it was the basis of his interpretation of *P. kohli* in his 1979 revision of the world *Prosopigastra*.

Recognition

The two species differ by the sculpture of the scutum and gaster which is markedly coarser in *P. bulgarica* than in *P. kohli* (Figs. 1–4). Pulawski (1979) thought that the males differ by the clypeal lamella, expanded mesally in the first species and not expanded in the second. This opinion, however, is inaccurate, as the clypeal lamella of *P. bulgarica* is expanded only in some, but not all specimens.



FIGURES 1–2. *Prosopigastra bulgarica* Pulawski, female. (1) Scutum; (2) Tergum I.
FIGURES 3–4. *Prosopigastra kohli* Mercet, female. (3) Scutum; (4) Tergum I.

FIGURE 5. Collecting localities of *Prosopigastra bulgarica* (red circles) and *P. kohli* (green triangles) in the Iberian Peninsula. Abbreviations used: A: Alicante Province, BU: Burgos Province, CA: Cádiz Province, CR: Ciudad Real Province, M: Madrid Province, SA: Salamanca Province, SO: Soria Province, SG: Segovia Province, VA: Valladolid Province, ZA: Zamora Province.

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LITERATURE CITED

DE ANDRADE, N.F. 1949. Esfecídeos de Portugal (Hym. Sphecidae). *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra* No. 194:1–27.

DE BEAUMONT, J. 1967. Hymenoptera from Turkey. Sphecidae, I. With Appendix. *Sphex* Linné, Subgenus *Palmodes* Kohl par P. Roth. *Bulletin of the British Museum* (*Natural History*). *Entomology* 19:253–382.

GAYUBO, S.F. 1982 [1981]. Himenópteros superiores de la Sierra de Béjar: Sphecidae. III. Astatinae y Larrinae (Hym.). *Boletín de la Asociación Española de Entomología* 5:93–115.

Mercet, R.G. 1907. El género «*Prosopigastra*». *Boletín de la Real Sociedad Española de Historia Natural* 7:292–304.

Pulawski, W.J. 1958 [1957]. Grzebacze (Hymenoptera, Sphecidae) zebrane w czasie podróży do Bułgarii – Sphecidae (Hymenoptera) récoltés pendant un voyage en Bulgarie. *Polskie Pismo Entomologiczne* 27:161–192.

——. 1979. A revision of the World *Prosopigastra* Costa (Hymenoptera, Sphecidae) – Rewizja rodzaju *Prosopigastra* (Hymenoptera, Sphecidae). *Polskie Pismo Entomologiczne* 49:3–134.

Shkuratov, A.V. [А.В. Шкуратов] 1998. Дополнения к фауне роющих ос (Hymenoptera, Sphecidae) Ростовской области [= Dopolneniya k faune royushchikh os (Hymenoptera, Sphecidae) Rostovskoy oblasti = Additions to the sphecid fauna of the Rostov Oblast', Russia]. [*Izvestiya Vysshikh Uchebnykh Zavedeniy. Severo-Kavkazskiy Regyon.*] *Estestvennyie Nauki* 3:97–99.

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A New Species of Gorgonian Octocoral from the Mesophotic Zone off the Central Coast of California, Eastern Pacific with a Key to Related Regional Taxa (Anthozoa, Octocorallia, Alcyonacea)

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Recent offshore benthic surveys utilizing Remotely Operated Vehicles in the National Marine Sanctuaries along the California coastline under the auspices of the National Oceanic and Atmospheric Administration and the Ocean Exploration Trust, have yielded newly collected material and imagery of octocoral cnidarians from mesophotic and deep-sea habitats. As part of this effort, a new species of gorgonian coral is here described that was first observed at Cordell Bank, approximately 112 km WNW of San Francisco. The species is allocated to the gorgonian genus *Chromoplexaura* based on morphological considerations, and has since been collected or observed from four localities in central and southern California, 86–107 m in depth.

KEYWORDS: Corals, sea fans, gorgonian octocorals, Central California, Cordell Bank, mesophotic zone, taxonomic key to the genus and related taxa.

Chromoplexaura is currently regarded as a monotypic octocoral genus (Cordeiro et al. 2018c), represented by *C. marki* (Kükenthal, 1913), and is distributed from central Oregon to southern California on the west coast of North America. Bathymetric distribution of this species varies from nine to at least 90 m (Williams 2013). The new species described here represents a second species of the genus and is known from central to southern California with a depth range of 86 to 106 m.

The two species currently share several morphological similarities. Herein we describe a new species that was first observed, but not collected in 2007 by ROV imagery at Cortes Bank in southern California, near the border between California and Mexico. In 2017, colonies were observed (also not collected) by ROV in the Cordell Bank National Marine Sanctuary in central California. In 2018, four specimens were collected by ROV and one was recorded by benthic ROV imagery on board the National Oceanic and Atmospheric Administration (NOAA) ship FSV *Bell M. Shimada*, at three locations in central and southern California: Cordell Bank NMS, Monterey Bay NMS, and Channel Islands NMS.

Materials and Methods

The type material was collected during the benthic surveys of Cordell Bank and Greater Farallones National Marine Sanctuaries on board the NOAA ship FSV *Bell M. Shimada* (Fig. 1), between 28 July and 11 August 2018. The holotype and paratypes of the new species are deposited in the marine invertebrate collections of the Department of Invertebrate Zoology and Geology at the California Academy of Sciences in San Francisco, California. Underwater video and still imagery were taken on board the ship by NOAA and MARE staff. Images of preserved material and scanning electron micrographs were taken by the first author at the California Academy of Sciences in 2018.

Abbreviations used in the text are as follows: FSV – Fisheries Survey Vessel, MARE – Marine Applied Research and Education; CASIZ – California Academy of Sciences Invertebrate Zoology; CBNMS – Cordell Bank National Marine Sanctuary; MBNMS – Monterey Bay National Marine Sanctuary; CINMS – Channel Islands National Marine Sanctuary; NMS – National Marine Sanctuary; NOAA – National Oceanic and Atmospheric Administration; ROV – Remotely Operated Vehicle.

Depths used in the text include: Shallow-water (0–40 m); Mesophotic (40–150 m); Deep-Sea (>150 m).

Material used for comparative purposes: *Chromoplexaura marki*; CASIZ 190436; NOAA Sample S-17; Gulf of the Farallones National Marine Sanctuary, Rittenburg Bank (37.88°N 123.32°W); 89.4 m depth; 08 October 2012; ROV Beagle (MARE) from R/V Fulmar (NOAA); three terminal branches, wet-preserved in 95% ethanol. *Euplexaura* sp.; CASIZ 220608; Western Pacific Ocean, Caroline Islands, Palau (7.54°N 134.47°E); 7-31 m depth; 08 December 2016; cool G.C. Williams; one partial colony, wet-preserved in 95% ethanol. *Swiftia torreyi*; CASIZ 220958; Cordell Bank National Marine Sanctuary (37.98°N 123.49°W); 948.82 m depth; 10 August 2017; ROV Hercules/Argus from E/V Nautilus; one whole colony, wet-preserved in 95% ethanol.

Figure 1. The National Oceanic and Atmospheric Administration (NOAA) Fisheries Survey Vessel, FSV *Bell M. Shimada*, conducts fisheries and oceanographic research throughout the Pacific coast of the United States. All type specimens of the new coral species described herein were collected by Remote Operational Vehicle (ROV) on board this ship in 2018. Photo by Gary C. Williams.

Systematic Account

Subclass Octocorallia Haeckel, 1866
Order Alcyonacea Lamouroux, 1812
Family Plexauridae Gray, 1859

Chromoplexaura Williams, 2013

Euplexaura Kükenthal, 1913:266; 1924:93.
Chromoplexaura Williams, 2013:17.

Generic diagnosis.— Growth form planar and sparse, branching lateral. Retracted polyps form low rounded protuberances, mound-like to hemispherical in shape. Polyps are present on all sides of the branches, but can be arranged biserially on some narrow terminal branches. Coenenchymal sclerites are primarily robust warty spindles, somewhat ovoid in shape or approaching girdled spindles. Other sclerite types that may be present include radiates, crosses, and spindles with a median waist that approach capstans. Anthocodial sclerites are rods that are straight or curved to sinuous. Colony color red or yellow due to conspicuous color of the sclerites.

Type species.— *Euplexaura marki* Kükenthal, 1913.

Chromoplexaura cordellbankensis Williams and Breedy, sp. nov.

Figures 2–10.

Holotype.— CASIZ 228195; NOAA Sample SH-18-09-017; Cordell Bank, Cordell Bank National Marine Sanctuary, CBNMS Transect-127; ca. 51 km W. of Point Reyes Peninsula (38°03′ 15.465″N 123°28′48.072″W); 100.5 m depth; 08 August 2018; ROV Beagle (MARE) from FSV *Bell M. Shimada* (NOAA); one partial specimen (missing holdfast), wet–preserved in 95% ethanol.

Paratypes.— CASIZ 228194. NOAA Sample SH-18-09-016; Cordell Bank, Cordell Bank National Marine Sanctuary, CBNMS Transect-127; ca. 51 km W. of Point Reyes Peninsula, California, USA (38°03′15.915″N 123°28′49.874″W); 101.6 m depth; 08 August 2018; ROV Beagle (MARE) from FSV *Bell M. Shimada* (NOAA); one partial specimen (14 mm long branch fragment), wet-preserved in 95% ethanol. CASIZ 207519; La Cruz Canyon, Monterey Bay National Marine Sanctuary; California, USA (35.7694°N 121.4475°W); 106.8 m depth; 28 October 2018; coll. by ROV on board FSV *Bell M. Shimada* (NOAA); one whole specimen. CASIZ 207520; Anacapa Island, Channel Islands National Marine Sanctuary; California, USA (33.992°N 119.3722°W); 86 m depth; 31 October 2018; coll. by ROV on board FSV *Bell M. Shimada* (NOAA); one specimen in two pieces.

Habitat and distribution.— Found on rugose, rocky substrata often with conspicuous vertical relief, or on rounded boulders in boulder fields (Fig. 3). Distributed off the central and southern coasts of California, between 38.2° and 32.5°N latitude (Figs. 8–9); at mesophotic depths between 86 and 107 m. The type locality is Cordell Bank in the Cordell Bank National Marine Sanctuary, ca. 70 miles WNW of San Francisco, California, 100 m depth.

Etymology.— The specific epithet is derived from Cordell Bank and the Latin suffix – *ensis* (belonging to); referring to the region of discovery of the new species and collection of the holotype – Cordell Bank National Marine Sanctuary.

Description of the Holotype

External Morphology.— The holotype is part of a colony, 35 mm in length. The holdfast

and basal portion of the colony are missing. Branching is sparse and lateral. The main stem gives rise to two lateral side branches, about 9 mm apart and 2–2.5 mm in diameter (including polyp mounds). The longest branch is 3.4 mm in length (Fig. 2). The retracted polyps form low-rounded to hemispherical polyp mounds, each < 1 mm in length. The polyps are largely distributed biserially on the thinner distal-most portions of branches (Fig. 2B), but occur all around the stouter and more basal parts of the lateral branches and main stem (Fig. 2E). There are approximately ten mounds per cm of branch length. Finger-shaped portions of the coenenchyme-covered internal axis extend from the apical tips of some branches (Fig. 2B).

Anthocodiae.— Most of the anthocodiae are preserved totally retracted into the polyp mounds, while a few are partially exserted. The walls of the anthocodiae and bases of the tentacles are relatively densely set with narrow rods that have conspicuous tuberculation (Fig. 7). Due the retracted condition of the polyps, an *en chevron* arrangement of sclerites was not observed or easily apparent. The sclerites of the anthocodiae are lighter in color than the coenenchymal sclerites, many appearing virtually colorless, thus resulting in a white coloration of the polyps.

The polyp mounds are represented by conspicuous rounded protuberances along the branches, usually expanded at the base while some are hemispherical in shape. Adjacent polyp mounds are generally separated by about 1.0–1.5 mm of bare rachis, and vary in width from 1.5–2.0 mm at the base, and are usually less than 1.0 mm in height (Fig. 2).

Sclerites.— Coenenchymal sclerites vary from 0.06 to 0.22 mm in length (Figs. 4–6, 10A). They are predominantly wide, warty spindles with heavily warted tubercles, while some are narrower with less ornamentation (Figs. 4–5, 10A). Radiates and various immature forms are also present (Fig. 6).

Polyp sclerites are elongate rods (Fig. 7), often slightly curved or sinuous with variable tuberculation, while some are weakly club-shaped (Fig. 7, left). Small, flat rods (Fig. 7, center) are also present and could possibly be from the tentacles. Polyps sclerites vary in length from 0.08–0.24 mm in length.

Color.— Coenenchyme color is uniform lemon yellow throughout (Figs. 2–3), due to the conspicuous yellow coloration of the sclerites (Fig. 2F). The anthocodiae are colorless (Fig. 2E).

Remarks

Variation: Although the holotype specimen exhibits only three branches including the main stem, the paratypes as well as additional colonies observed in underwater still images taken by ROV, all exhibit relatively sparse branching, but may possess as many as ten branches including the main stem. One of the paratype colonies (CASIZ 207519), branches up to four times and produces seven lateral branchlets.

Discussion and Conclusion

Key to species of *Chromoplexaura* and related taxa in California

1a. Colonies planar and sparsely branched. Coenenchymal sclerites are broad to ovoid spindles with densely set tubercles, capstans, girdled spindles, elongated radiates, and/or tuberculated crosses 2

1b. Colonies unbranched to copiously branched or bushy. Coenenchymal sclerites may include elongate to needlelike spindles, compact radiates, double discs, and/or disc spindles 3

2a. Colonies red. Coenenchymal sclerites include ovoid spindles and girdled spindles . . . . . *Chromoplexaura marki* (Kükenthal, 1913)

2b. Colonies yellow. Coenenchymal sclerites include capstans, elongated radiates, and crosses . . . . . ***Chromoplexaura cordellbankensis*** sp. nov.

3a. Colonies unbranched or Y-shaped 4
3b. Colonies branched – copiously branched or bushy 5

4a. Colonies white; polyp mounds low-rounded. . *Swiftia farallonesica* Williams & Breedy, 2016
4b. Colonies coral red to dark red. Polyp mounds prominent – conical to low cylindrical. . . . . *Swiftia simplex* (Nutting, 1909)

5a. Branching bushy, polyp mounds prominent – conical to cylindrical 6
5b. Branching sparse, polyp mounds low-rounded. Colonies coral red with white polyps . . . . . *Swiftia spauldingi* (Nutting, 1909)

6a. Polyp mounds truncated conical; sclerites are radiates and elongate spindles with rounded tubercles . . . . . *Swiftia torreyi* (Nutting, 1909)
6b. Polyp mounds stout, conical to cylindrical; sclerites are primarily elongate spiny spindles, often needle-like and curved . . . . . *Swiftia kofoidi* (Nutting, 1909)

Taxonomic Assessment

The genus *Chromoplexaura* is superficially similar to several Pacific coast *Swiftia* species. The latter is currently regarded as a gorgonian genus of twenty species (Cordeiro et al. 2018b). The type species of *Swiftia* is *Swiftia exserta* (Ellis and Solander, 1786) from the western Atlantic Ocean. Several species from the Pacific coast of the Americas have been allocated to the genus *Swiftia*, and it is not clear at present whether the Atlantic vs. Pacific species represent the same genus or separate genera (Williams 2013:17). In addition, there appears to be two distinguishable groups of eastern Pacific species of *Swiftia* based on morphological characteristics. Preliminary molecular analyses (Everett and Park 2018; Everett, personal communication) have shown that the two groups (*Chromoplexaura* and *Swiftia*) have not exhibited a conspicuous differentiation, but from the morphological point of view are different (Fig. 10A, B, D). An overall detailed molecular analysis and morphological comparison are necessary to provide a cogent taxonomic assessment of the relevant taxa.

Chromoplexaura cordellbankensis sp. nov. shares superficial morphological similarities with some species of Eastern Pacific *Swiftia* regarding external morphology – such as branching pattern, low-rounded to hemispherical polyp mounds, and elongate-tubercated anthocodial sclerites. However, the coenenchymal sclerites differ markedly from those of *Swiftia*, while most closely resembling the sclerite complement of *Chromoplexaura marki* (Williams, 2013:20–21) – i.e. the presence of robust to ovoid, highly warty spindles in the coenenchyme, which are not found in species of *Swiftia* (Fig. 10A, B, D).

Chromoplexaura marki was originally placed in the Indo-Pacific genus *Euplexaura* by Kukenthal, 1913. However, the coenenchymal sclerites of *Euplexaura* species differ markedly from the two California species of *Chromoplexaura*, by the possession of tuberculate spheroids, subspheroids, double heads, and plump ovoid to irregular spindles (Fig. 10C; Fabricius and Alderslade 2001:190; Williams 2013:21, 24).

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Literature cited

Bayer, F.M. 1956. Octocorallia. Page 206 *in* R.C. Moore, ed., *Treatise on Invertebrate Paleontology Part F. Coelenterata*. The University of Kansas Press and the Geological Society of America. University of Kansas Press, Lawrence, Kansas, U.S.A. 498 pp.

Bayer, F.M. 1961. *The Shallow-water Octocorallia of the West Indian Region. A Manual for Marine Biologists*. Marinus Nijhoff, The Hague, Netherlands. 373 pp. + 27 plates.

Bayer, F.M. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata, Anthozoa), with diagnoses of new taxa. *Proceedings of the Biological Society of Washington* 94(3):902–947.

Breedy, O., and H.M. Guzman. 2014. A new species of alcyonacean octocoral from the Peruvian zoogeographic region. *Journal of the Marine Biological Association of the United Kingdom* 2014:1–6.

Breedy, O., S.D. Cairns, and V. Häussermann. 2015. A new alcyonacean octocoral (Cnidaria, Anthozoa, Octocorallia) from Chilean fjords. *Zootaxa* 3919(2):327–334.

Cordeiro, R., L. Van Ofwegen, and G. Williams. 2018b. World List of Octocorallia. *Swiftia* Duchassaing & Michelotti, 1864. Accessed through: World Register of Marine Species at: *http://www.marinespecies.org/aphia.php?p=taxdetails&id=125314* on 2018-11-01.

Cordeiro, R., L. Van Ofwegen, and G. Williams. 2018c. World List of Octocorallia. *Chromoplexaura* Williams, 2013. Accessed through: World Register of Marine Species at: *http://www.marinespecies.org/aphia.php?p=taxdetails&id=724230* on 2019-01-03.

Deichmann, E. 1936. The Alcyonaria of the western part of the Atlantic Ocean. *Memoirs of the Museum of Comparative Zoology at Harvard College* 53:1-317.

Duchassaing, P., and J. Michelotti. 1864. Supplément au mèmoire sur les coralliaires des Antilles. *Mémoires de l'Academie des Sciences de Turin*, Series 2(23):97–206.

Everett, M.V., and L.K. Park. 2018. From genomes to populations to communities: using genomic techniques to study deep-sea coral diversity. 15th *Deep-Sea Biology Symposium, Abstract* 159:64.

Fabricius, K., and P. Alderslade. 2001. *Soft Corals and Sea Fans – A Comprehensive Guide to the Tropical Shallow-Water Genera of the Central-West Pacific, the Indian Ocean and the Red Sea*. Australian Institute of Marine Science, Townsville, Australia. 264 pp.

Goldberg, W.M. 2001. The sclerites and geographic distribution of the gorgonian *Swiftia exserta* (Coelenterata: Octocorallia: Holaxonia). *Bulletin of the Biological Society of Washington* 10:100–109.

Harden, D.G. 1979. *Intuitive and numerical classification of east Pacific Gorgonacea* (*Octocorallia*). PhD thesis, Illinois State University, USA. Unpublished [page number unkown].

Kükenthal, W. 1913. Über die Alcyonarienfauna Californiens und ihre tiergeographischen Beziehungen. *Zoologische Jahrbücher* (*Systematik*) 35(2):219–270.

Kükenthal, W. 1924. *Gorgonaria*. Das Tierreich 47. Walter de Gruyter & Company, Berlin & Leipzig, Germany. 478 pp.

Nutting, C.C. 1909. Alcyonaria of the Californian coast. *Proceedings of the U.S. National Museum* 35(1658):681–727.

Verrill, A.E. 1883. Report on the Anthozoa, and some additional species dredged by the "Blake" in 1877–1879, and by the U.S. Fish Steamer "Fish Hawk" in 1880–82. *Bulletin of the Comparative Museum of Zoology, Harvard* 11:1–72.

Verrill, A.E..1928. Hawaiian shallow-water Anthozoa. *Bernice P. Bishop Museum Bulletin* 49:1–30.

Williams, G.C. 2013. New taxa and revisionary systematics of alcyonacean octocorals from the Pacific coast of North America (Cnidaria, Anthozoa). *ZooKeys* 283:15–42.

Williams, G.C., and O. Breedy. 2016. A new species of whip-like gorgonian coral in the genus *Swiftia* from

the Gulf of the Farallones in Central California, with a key to eastern Pacific species in California (Cnidaria, Octocorallia, Plexauridae). P*roceedings of the California Academy of Sciences*, ser. 4, 63(1): 1–13.

WRIGHT, E.P., AND T. STUDER. 1889. Report on the Alcyonaria collected by H.M.S. Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage Challenger, During the Years 1873–1876. Zoology* 31:1–314.

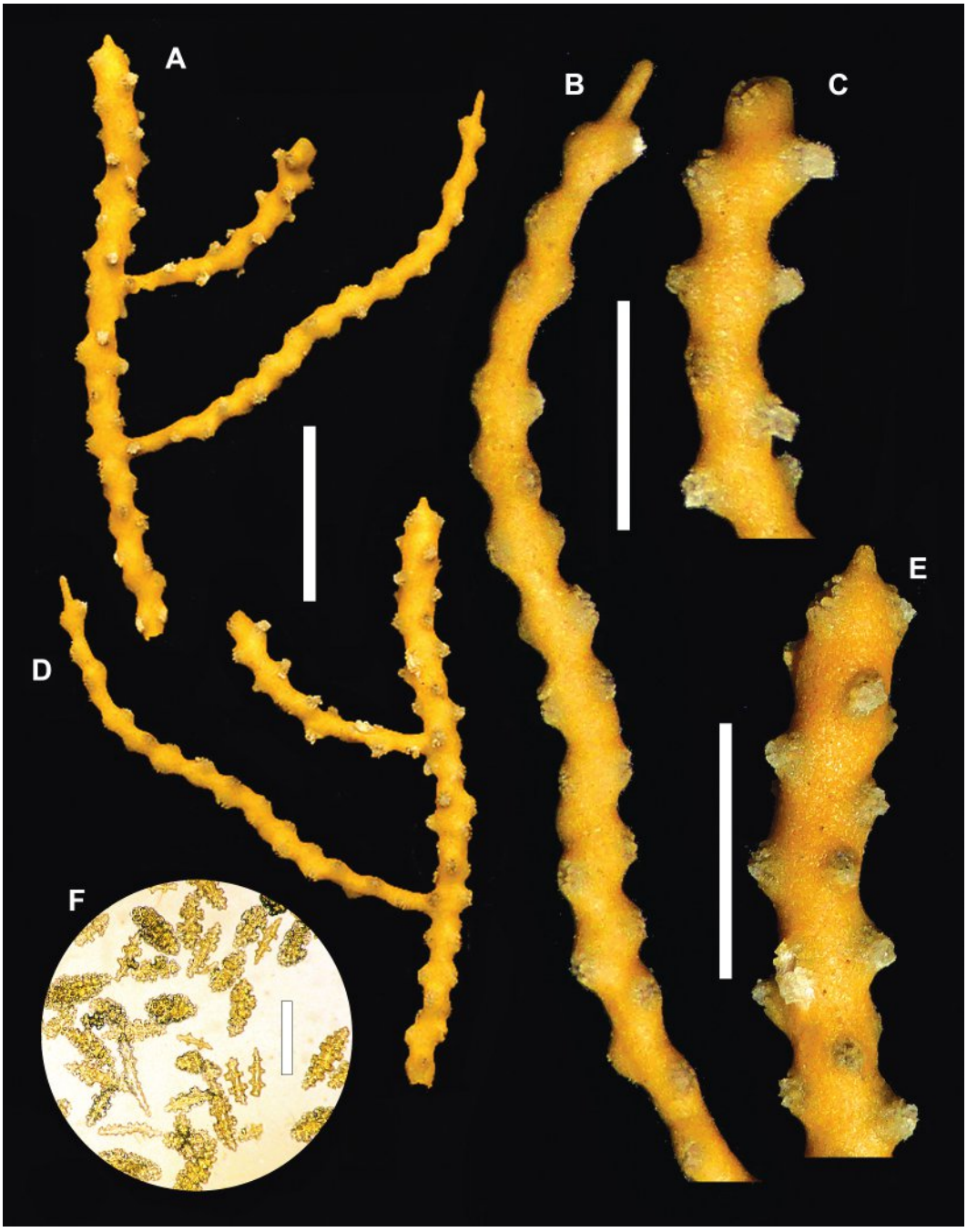

FIGURE 2. *Chromoplexaura cordellbankensis* sp. nov. Wet-preserved holotype, external morphology. A, D. Partial colony, scale bar = 10 mm. B. Detail of the proximal branch, scale bar = 5 mm. C. Distal apex region of the middle branch, scale bar = 5 mm. E. Apex region of the main stem, scale bar = 5 mm. F. Compound microscope view of sclerites at 100x magnification, showing yellow coloration, scale bar = 0.2 mm.

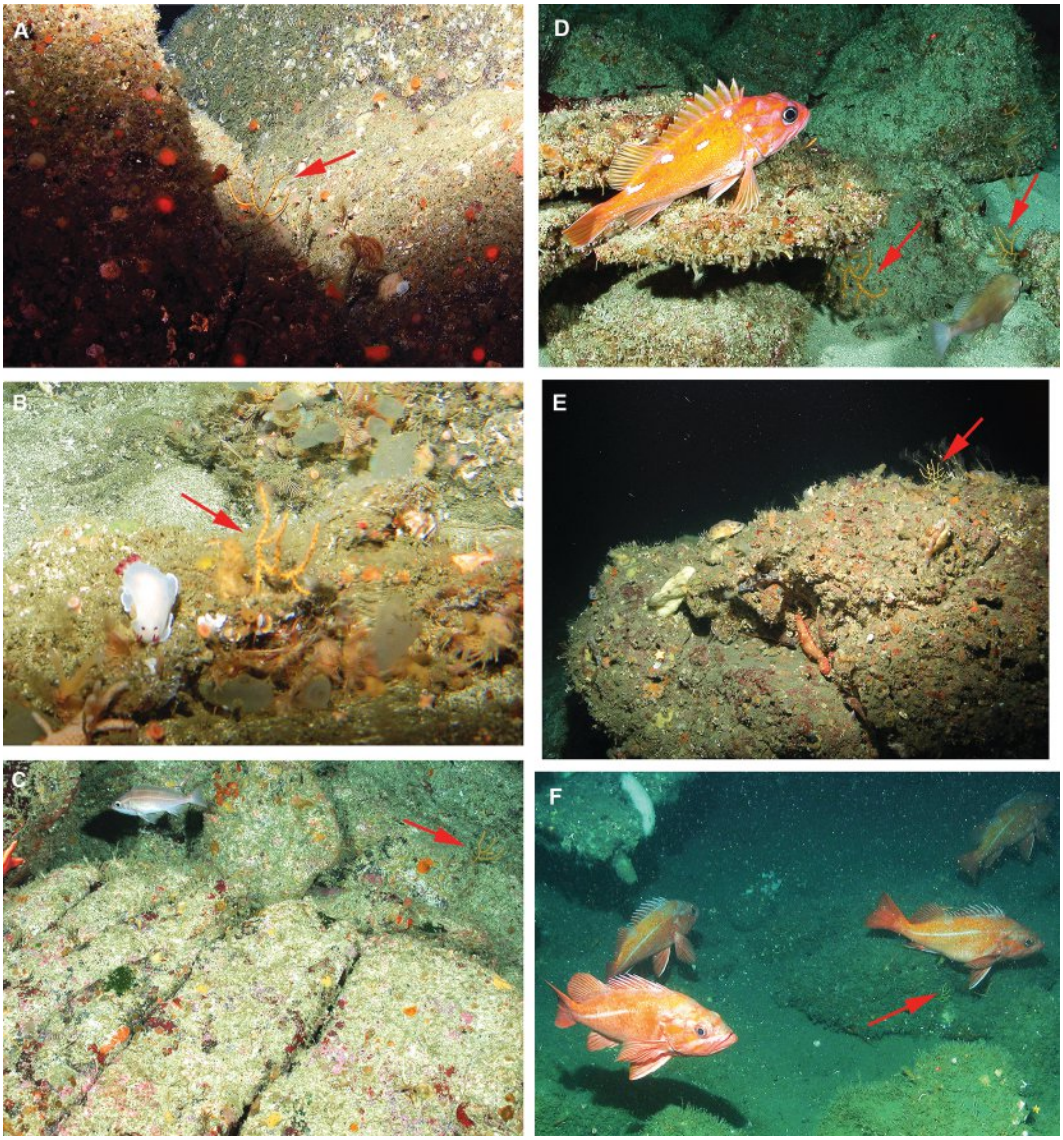

FIGURE 3. *Chromoplexaura cordellbankensis* sp. nov. Underwater photographs taken *in situ* by Remotely Operated Vehicles (ROVs), showing individual colonies of the new species (red arrows) with surrounding habitat. A. Image taken at Cordell Bank National Marine Sanctuary near the type locality, ca. 100 m depth, 8 August 2018. B. Image taken at Cordell Bank National Marine Sanctuary near the type locality, 102 m depth, 8 August 2018, with a nudibranch mollusk (*Dendrodoris azineae*) to the immediate left. C. Image taken at Cortes Bank, ca. 166 km west of Point Loma San Diego, 70 m in depth, 7 September 2007. D. Image taken at Cortes Bank, ca. 166 km west of Point Loma San Diego, 70 m depth, 8 September 2007. E. Image taken at La Cruz Canyon, Monterey Bay National Marine Sanctuary, 106.8 m depth, 28 October 2018. F. Image taken at Anacapa Island, Channel Islands National Marine Sanctuary, 86 m depth, 31 October 2018. Photographs courtesy of National Oceanic and Atmospheric Administration.

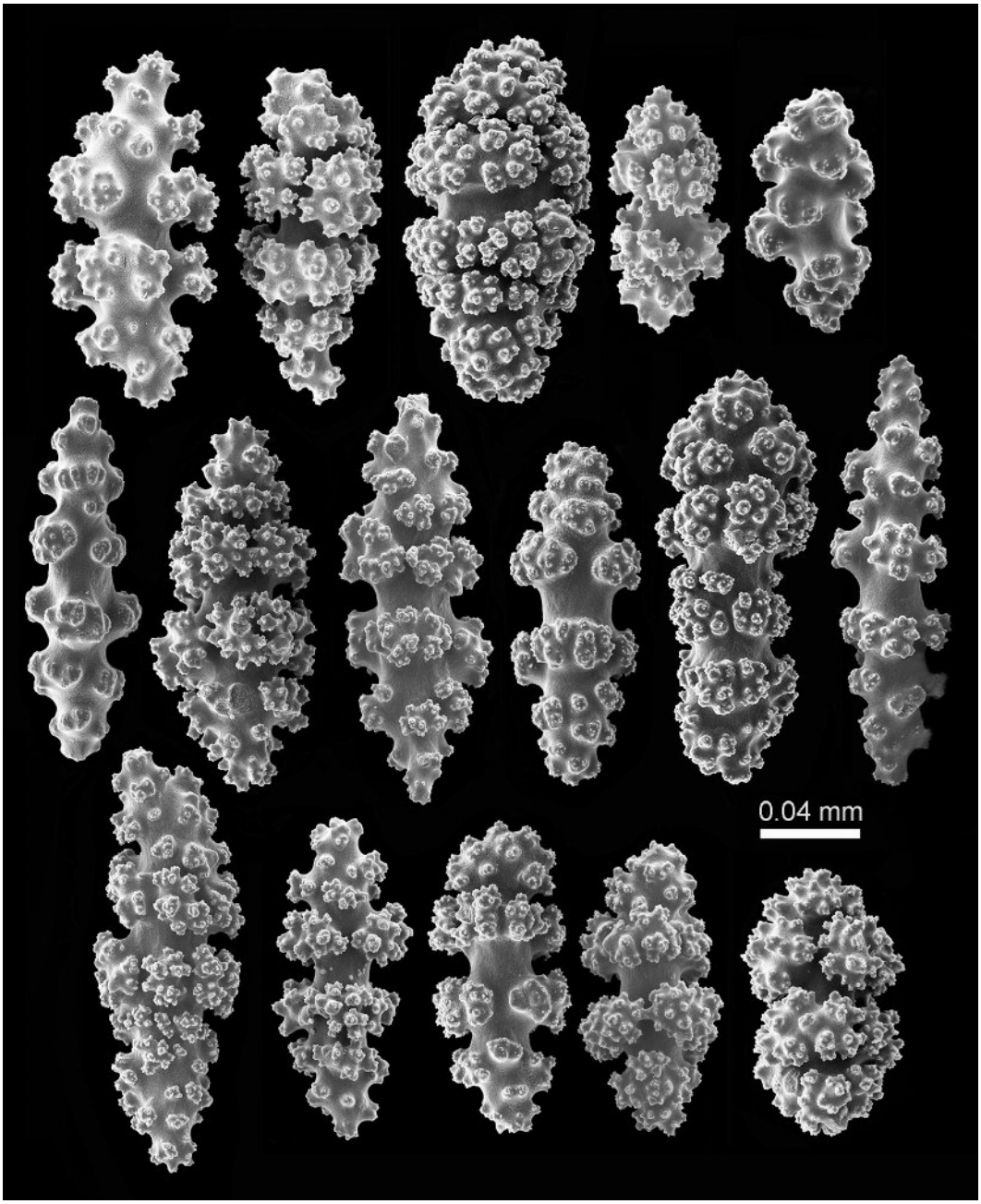

FIGURE 4. *Chromoplexaura cordellbankensis* sp. nov. Scanning electron micrographs of coenenchymal sclerites – warty spindles. Scale bar = 0.04 mm.

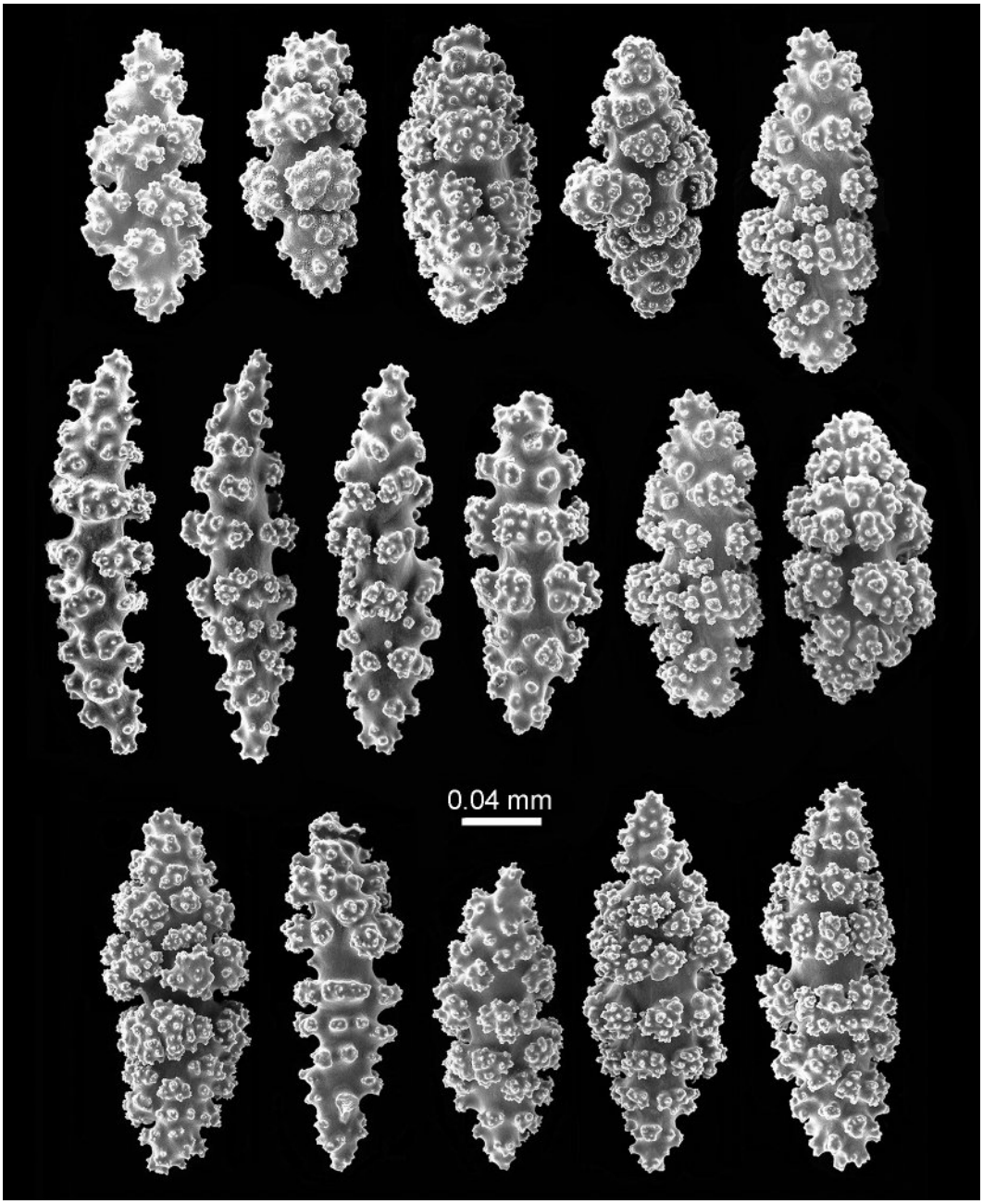

FIGURE 5. *Chromoplexaura cordellbankensis* sp. nov. Scanning electron micrographs of coenenchymal sclerites – warty spindles. Scale bar = 0.04 mm.

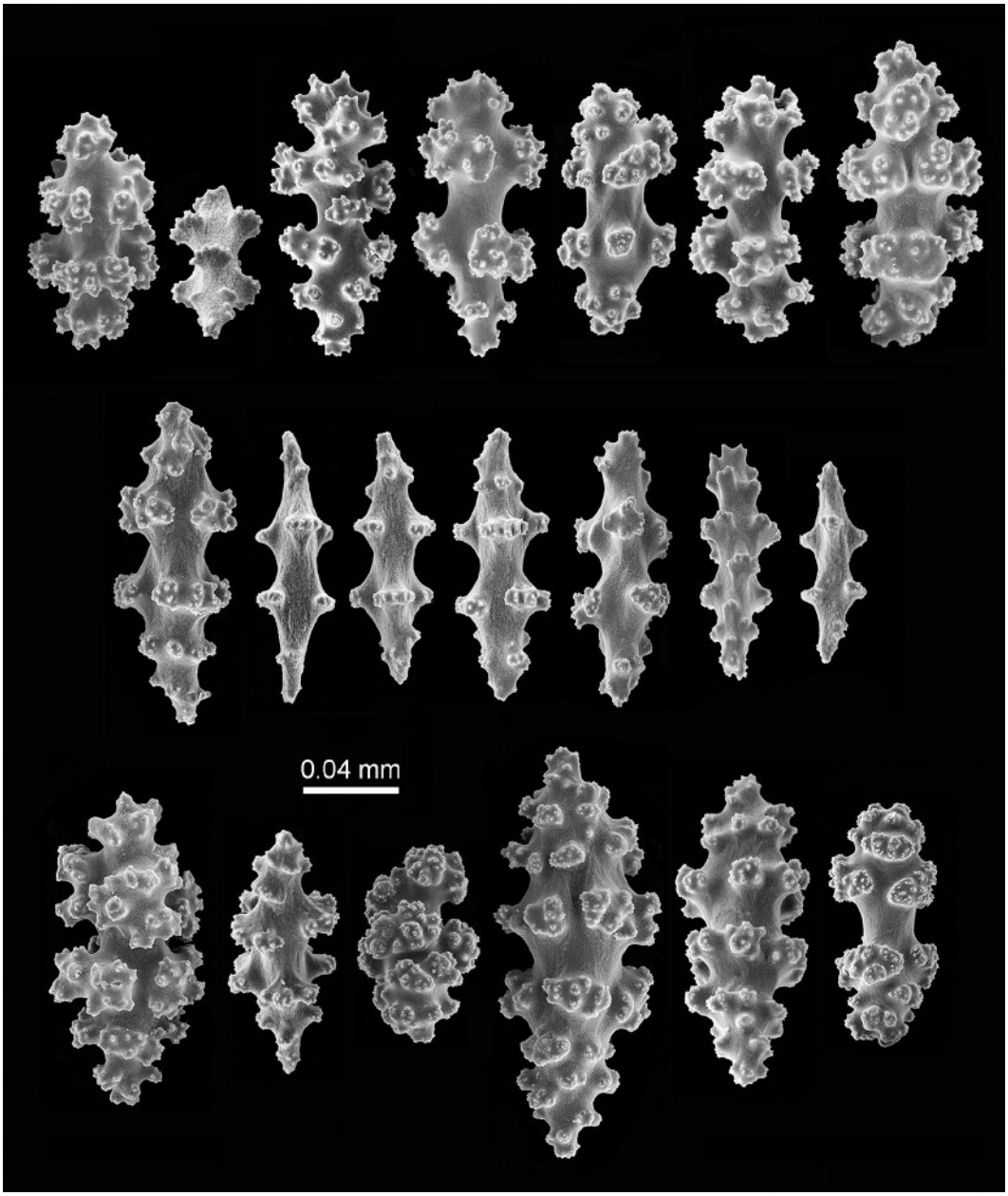

Figure 6. *Chromoplexaura cordellbankensis* sp. nov. Scanning electron micrographs of coenenchymal sclerites – radiates (top row) and various immature sclerites (middle and bottom rows). Scale bar = 0.04 mm.

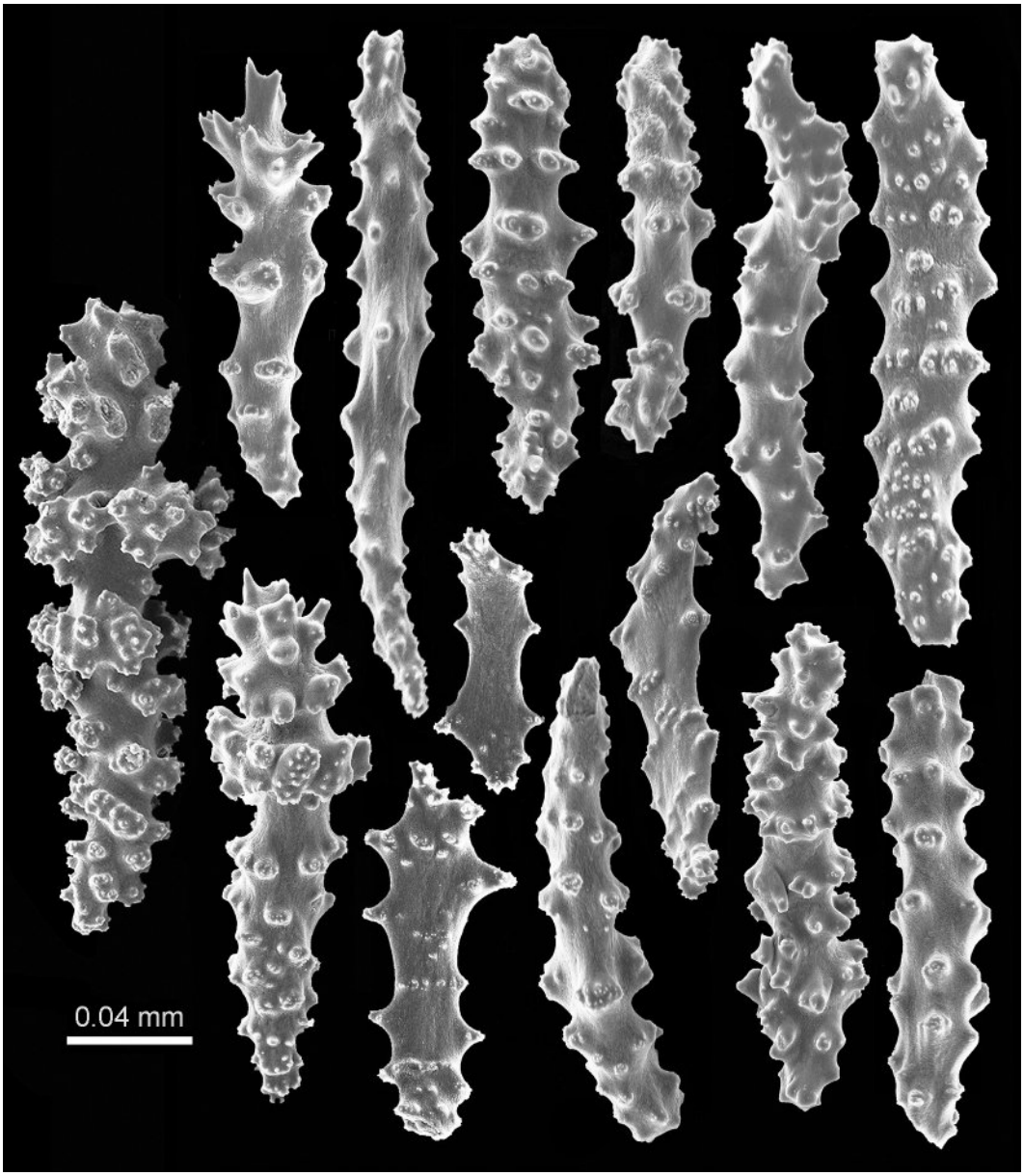

FIGURE 7. *Chromoplexaura cordellbankensis* sp. nov. Scanning electron micrographs of polyp sclerites. Scale bar = 0.04 mm.

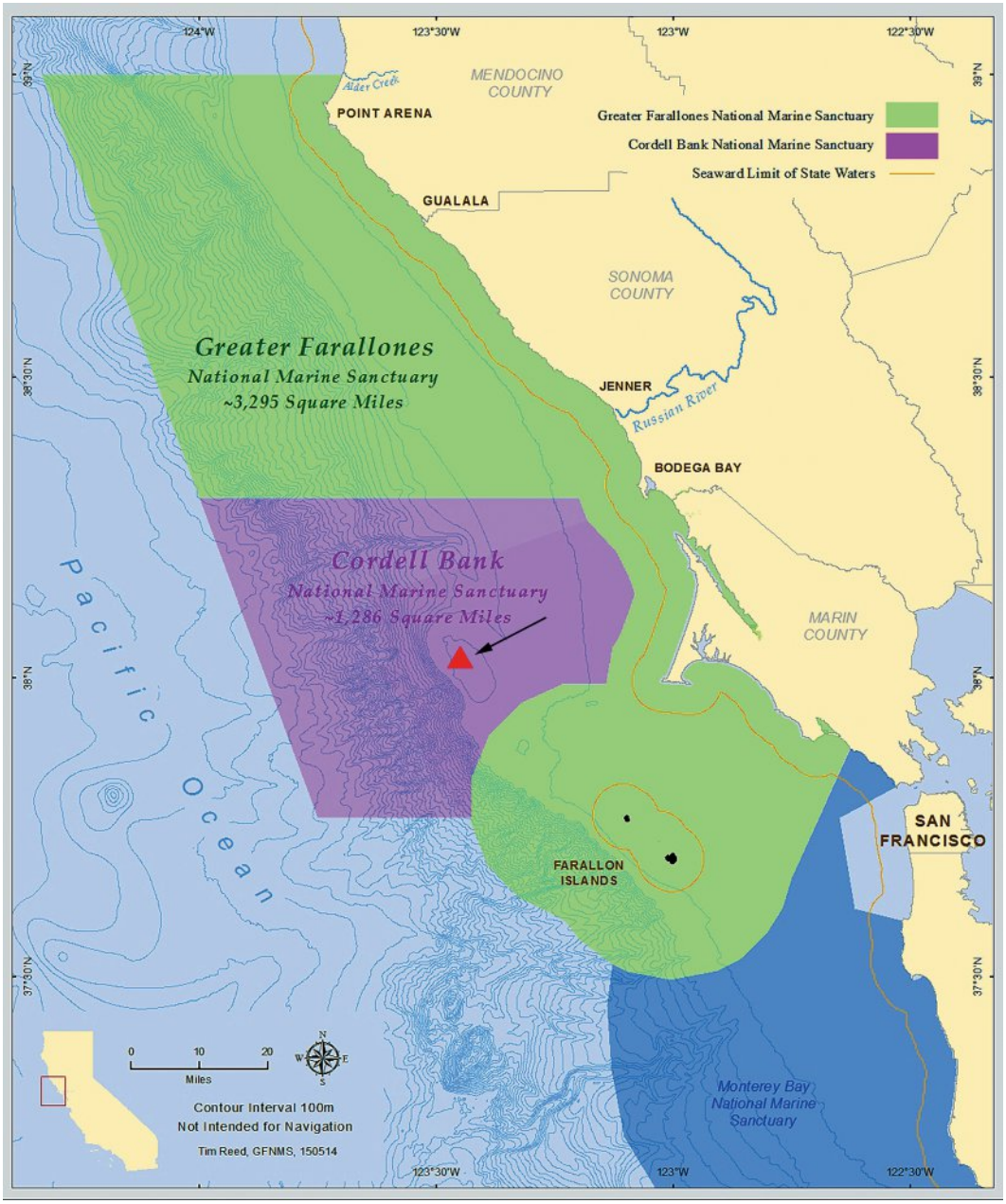

FIGURE 8. Map of Cordell Bank National Marine Sanctuary (central California); type locality of *Chromoplexaura cordellbankensis* sp. nov. (red triangle). Map adapted from National Oceanic and Atmospheric Administration (2014).

FIGURE 9. Map of the Pacific coast of the United States showing the geographical ranges of *Chromoplexaura marki* (●) and *Chromoplexaura cordellbankensis* sp. nov. (●); arrow denotes type locality.

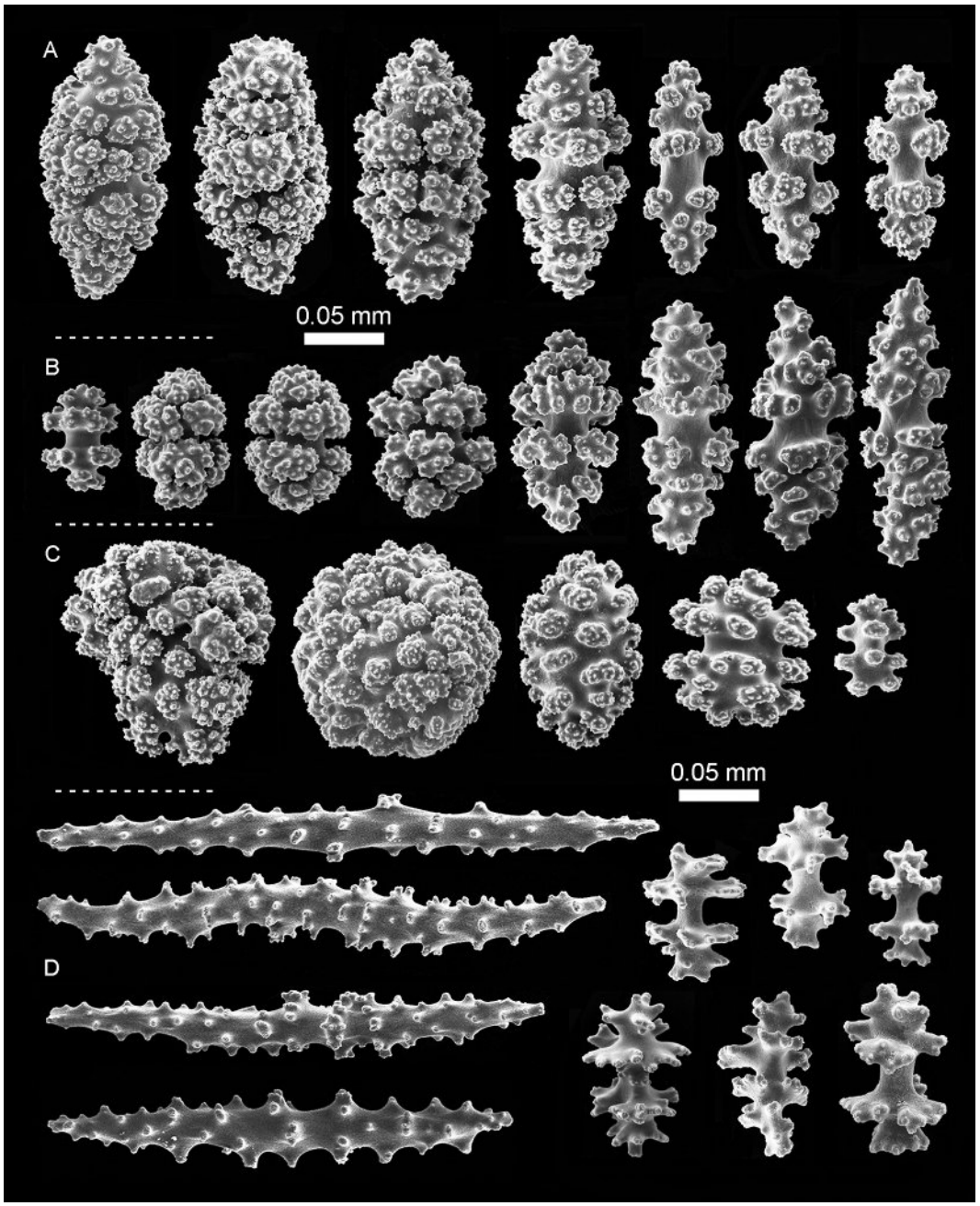

FIGURE 10. Scanning electron micrographs of coenenchymal sclerites. A. *Chromoplexaura cordellbankensis* sp. nov. (CASIZ 228194). B. *Chromoplexaura marki* (CASIZ 190436). C. *Euplexaura* sp. (CASIZ 220608). D. *Swiftia torreyi* (CASIZ 220958). Scale bars = 0.05 mm.

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Rollo H. Beck's Visits to Isla Guadalupe, Mexico, with Additions and Corrections to the Island's Avifauna

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Several summaries of the avifauna of Isla Guadalupe have been published in the last 60 years (Howell and Cade 1954, Jehl and Everett 1985, Luna-Mendoza et al. 2005, and Quintana-Barrios et al. 2006). During this period, the advent of Internet accessible information about the island has increased dramatically. Examination of now more readily available information, including unpublished field notes held in museums, has shed light on questions unanswered for decades and allows for additions to the record as well as correction of assumptions repeated for nearly 100 years.

Chief among the unanswered questions regarding now extinct endemic birds of the island are details regarding the collecting trips to the island by Rollo H. Beck in 1900 and 1912. This paper examines new information regarding Beck's visits and updates the island bird records based on Beck's field notes and a variety of other sources.

Rollo Howard Beck (1870–1950) was one of the most prolific bird collectors of all time. He was most noted for his collections in the Galapagos Islands and during the Whitney South Seas Expeditions of the 1920s (Murphy 1936, Pitelka 1986, Dumbacher and West 2010). Beck is also known for his December 1900 collection of nine Guadalupe Caracaras, *Caracara lutosa*, which may have been the last of the species seen before it was ultimately declared extinct (Abbott 1933).

The only published reference to Beck's 1912 visit to Isla Guadalupe was his August collection of two downy young Guadalupe Storm-Petrels, *Oceanodroma macrodactyla*, believed to be the last record of this now extinct species (Davidson 1928).

In 1985, Joseph R. Jehl, Jr. and I published a summary of all that we could find on the history of the avifauna of the island and included our own observations from several visits in the 1970s, as well as the observations of several others including many visits by Carl L. Hubbs of the Scripps Institution of Oceanography (Jehl and Everett 1985). For historic literature we relied heavily on information contained in Nelson (1921) as well as the incredibly detailed Summation of the Ornithology of Lower California published by Joseph Grinnell (1928).

Between 1985 and 2000 several brief notes were published adding species to the list of birds occurring on the island (Oberbauer et al. 1989, Mellink and Palacios 1990, Howell and Webb 1992, Pyle et al. 1994.) as well as the revelation that the Laysan Albatross, *Phobastria immutablis*, had begun to breed there (Dunlap 1988).

In June 2000, I co-led the Millennial Bi-National Multi-disciplinary Isla Guadalupe Expedition, which was sponsored by the San Diego Natural History Museum and funded by the National Science Foundation. With the aid of a helicopter aboard our ship, the *Shogun,* the expedition team had unprecedented ability to visit and examine areas of the island heretofore unexplored or not visited at length in nearly 100 years. With this mobility and a crew of nearly 15 scientists, the island was scoured, including the first ever visit (by helicopter) atop the precipitous Islote Adentro, just

off the south end of the island. The expedition led to further investigations into the bird-life and the eventual eradication of the goats that were responsible for destruction of not only bird habitat (and birds) but also many endemic plant species (Moran 1996; Sweet et al. 2001; Barton et al. 2004; Keitt et al. 2005; Quintana-Barrios et al. 2006).

Methods

This paper examines the now more readily available records of specimens taken in 1900 and 1912 by Beck (and by others in various years), as well as Beck's catalog and field notes for the 1912 visit (available on-line and held at the California Academy of Sciences in San Francisco). In addition, unreported visits of other collectors are described and the historic literature is reexamined in light of recent findings. Recent literature is corrected based on these new findings. The implications of the various historic spellings of the island's name are examined. Definitive information provided by Jehl and Everett (1985) or more recent accounts is not repeated here unless it is pertinent or based on new information.

Symbolic codes (acronyms) used for museum collections are: AMNH, American Museum of Natural History; CAS, California Academy of Sciences; CMNH, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; LACM, Los Angeles County Museum; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; SDNHM, San Diego Natural History Museum; USNM, National Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; WFVZ, Western Foundation of Vertebrate Zoology; YPM, Yale Peabody Museum; NHMUK, Natural History Museum United Kingdom; UABC, Universidad Autonoma de Baja California.

Results

Beck's 1900 Visit

In late November 1900, Beck was at the start of his second trip to the Galapagos Islands, this time aboard the schooner *Mary Sachs*, when it stopped at Isla Guadalupe for several days. He was sent on the expedition by Lord Walter Rothschild. In addition to the nine aforementioned caracaras, Beck also collected specimens of other endemic birds, including the Guadalupe Flicker, *Colaptes auratus rufipileus*, the Guadalupe Junco, *Junco hyemalis insularis*, and the Guadalupe Ruby-crowned Kinglet, *Regulus calendula obscurus*.

The only published information referring to Beck's visit in 1900 to Guadalupe is provided by Thayer and Bangs (1908), who reported "When Beck visited Guadaloupe [sic] in 1900-1901 the Caracara still occurred in the island, though probably in small numbers." [Beck did not visit the island in 1901], Clinton G. Abbott (1933), who cited correspondence with Beck wherein Beck reported that on 1 December 1900 he had collected the nine Guadalupe Caracaras (see below), and in an obscure reference on the fauna of the Galapagos (Rothschild and Hartert 1902) where the authors reported that Beck also collected an Eared Grebe, *Podiceps nigricollis*, and Burrowing Owl, *Athene cunicularia*, on Guadalupe on the same day. Why Rothschild and Hartert did not mention the other species Beck had collected is something of a mystery. Data from specimens, available on-line, indicate that the ship arrived at Guadalupe on 29 November and departed on 2 (or 3) December.

Beck's 1903 Visit?

The California Academy of Sciences sponsored a collecting trip to islands off the west coast of Mexico in 1903 with the primary focus on Los Islas Revillagigedos. Rollo Beck was in charge

of the expedition again aboard the *Mary Sachs*. The crew included four students from the University of California, Berkeley; A.S. Bunnell (ornithology), F.E. Barklin (botany), C.H. Marks (anthropology) and the teenager Edward Winslow Gifford (conchology). Gifford apparently developed a keen interest in birds during the voyage, as he was appointed as an assistant curator of Ornithology at CAS after later graduating from high school (he would eventually become renowned as the distinguished Curator of Anthropology at U.C. Berkeley, a position he held for most of his professional career).

The expedition set sail from San Francisco on 25 April and arrived in Ensenada to clear customs on 30 April (Beck field notes, CAS). On 1 May they set sail under light winds and arrived at Isla San Martin on 3 May. Their next stop, on 5 May, was at Islas San Benito. Isla Natividad was next on the itinerary, arriving on 9 May. As 10 May was a Sunday, the crew rested as was the custom established by Leverett M. Loomis, the Director of the Academy. Members of the expedition collected numerous specimens during their visits to these coastal islands off Baja California.

The expedition arrived at Isla San Benedicto in the Revillagigedos on 14 May, where they apparently remained until 26 May when they departed for and then arrived at Isla Socorro on 5 June. For the next month or so the expedition explored Socorro, visited Los Islas Tres Marias, Cabo Corrientes (near Puerta Vallarta), returned to Socorro, then sailed for Isla Clarion. Beck's field notes oddly end abruptly on 8 July. The *San Francisco Call* newspaper reported the return of the *Mary Sachs* on 13 August, 35 days after Beck's last journal entry, with cargo of over 1,000 specimens. Beck was known to collect many specimens while at sea, so why his field notes ended when they did is a mystery. However, the 35 days appears to have left ample opportunity for the expedition to visit Isla Guadalupe, especially since the island was well within the course the schooner would have taken on her return voyage. (Interestingly, Beck's field notes in the same volume resume on 24 August with a collecting trip to Watsonville and Moss Landing, on the central California coast).

There can be no doubt that Beck was keenly aware of the endemic birds of Isla Guadalupe. As noted above, his stop there in late November 1900 was both brief and during the non-breeding season for most birds. On the Revillagigedos Expedition, he collected birds on the voyage south from Ensenada, so it seems reasonable that he would have wanted to stop and collect birds on the return voyage (unfortunately, all the expedition's collections were destroyed in the 1906 San Francisco earthquake and firestorm). Beck rarely published on his collections, and after returning from the expedition he and others were likely preoccupied with preparations for their upcoming 17 month CAS expedition to the Galapagos Islands, which departed San Francisco on 28 June 1905.

Apparently, the only published references to the 1903 CAS Revillagigedo Islands Expedition are those by Richards and Brattstrom (1959) who in tabulating known historic visits to the islands noted "Except for a diary in the possession of E.W. Gifford all records and specimens [from the expedition] were lost in the San Francisco fire of 1906 (Joseph R. Slevin, personnel communication)", and Kaeding (1905, see Guadalupe Caracara account below). Clearly, Gifford's diary should answer the question of whether or not a stop was made at Isla Guadalupe but given the absence of specimens or other detailed records, the stop, if made, would likely only be of historic interest. The whereabouts of Gifford's diary remains a mystery for the time being. It is possible that an examination of Beck's archives and correspondence in the CAS and MVZ could shed light on the question of the 1903 visit.

As noted below in the Species Accounts, Howell and Cade (1954) listed three formerly breeding species of birds "last reported seen" in 1903. They offered no reference for such observations. A year later, in a brief note (Howell and Cade 1955), they corrected their reporting that the last encounter with the Guadalupe Storm-Petrel was not in 1919, but rather in 1912. They made no

mention in the *corrigenda* of the 1903 sightings. Grinnell (1928) provided no reference to any 1903 Isla Guadalupe visits.

Beck's 1912 Visit

The American Museum of Natural History sent Rollo Beck on a collecting trip to Isla Guadalupe from 22 July to 29 August 1912. During those five weeks he collected at least 195 specimens of 13 species. Notable among these were 16 Guadalupe Flickers and 25 Guadalupe Ruby-crowned Kinglets.

In Table 1 of our 1985 paper (Jehl and Everett 1985), which shows chronology of early ornithological research at Guadalupe, Jehl and I show only a question mark regarding Beck's 1912 visit, and the reference for that information was given as being from Abbott (1933), but it should have been cited as being from Davidson (1928).

Other Poorly Documented Early Visits

As shown in Table 1 of Jehl and Everett (1985), it was apparent that Walter E. Bryant visited the island in January 1885, nearly a year before his significant stay from 16 December 1885 to 1 April 1886. The evidence of this earlier visit can be found in his publication (1887a) describing his January 1885 collections. He noted several specimens that he had collected including a Guadalupe Caracara. The details of that visit were clarified in his August 1886 semi-scientific account (Bryant 1886) in *Forest and Stream* magazine, arguably the most popular magazine for outdoor enthusiasts at the time. The story was principally an account of his passage on a vessel (the steamer *Edith*) prospecting for the possibility of increasing and exploiting the goat population of "Cerros" [= Cedros] Island off the west coast of central Baja California. His entertaining account describes the vessel's stops at San Pedro (in California) then Ensenada, Baja California (to clear customs). On 6 January the ship arrived at Cedros. After exploring and collecting specimens, the ship left to resupply the apparently prosperous goat ranch on Isla Guadalupe. They spent two days there (Bryant 1886), 14 and 15 January, before leaving to return to California.

That Henry H. Kimball visited Guadalupe from 10–12 October 1913 is known only from a brief list of observations and specimens collected on the island (Kimball 1922). Kimball had collected quite a few Guadalupe endemics (Guadalupe Ruby-crowned Kinglets, Guadalupe Dark-Eyed Juncos, Guadalupe House Finches, *Haemorhous mexicanus amplus*; specimens LACM), but apparently, he only published his collection there of a White-throated Sparrow, *Zonotrichia albicollis*, and Summer Tanager, *Piranga rubra*, presumably because they had not been previously documented at the island. Table 1 provides details on additional visits to Isla Guadalupe between 1907 and 1962.

Island Name

The early avian literature about Isla Guadalupe contains a variety of different spellings of the island's name. As a result, there have been important specimens of endemic birds assigned by various collection managers to locations other than the Baja California island. The following traces the history of these various spellings and discusses the consequences thereof.

The first sighting of Isla Guadalupe (then known as Isla de los Pajaros — Island of the Birds) was likely made in 1565 by Andrés de Urdaneta, an Augustinian Friar who was a navigator aboard the *Capitana*. He pioneered the route for the Spanish galleons crossing from the Philippines to Acapulco in the latter half of the 16th century. The name Parajos was used in a 1648 map by Joannes Blaew and in 1700 by Guillaume Delisle. A 1748 map by Anson called the island Guadaloupe, followed with the same spelling on a map in 1771. That spelling persisted until 1791, when Juan Francisco de la Bodega y Quadra produced a map with the spelling Guadalupe (*fide* Wagner 1968).

TABLE 1. Additional unreported or poorly reported collecting visits to Isla Guadalupe. Information from Vertnet and as noted.

Year	Collector*	Dates	Additional References
1889	Charles H. Townsend	28 February 1889	Townsend 1890
1907	Charles M. Harris	29 May-13 June	Harris 1909, Specimens AMNH
1929	A.W. Anthony, Lawrence M. Huey	28-Sep	Huey 1930, Specimens SDNHM
1930	John G. Tyler, Steve A. Glassell, John R. Pemberton, Dudley S. DeGroot, Sidney B. Peyton	25-27 March	Specimens WFVZ
			Tyler and Pemberton Field Notes, WFVZ
1931	L.H. Cook, L.M. Huey	10-11 August	Specimens SDNHM
	C. Templeton Crocker	15-Nov	Specimens CAS
1933	John. S. Garth	29-31 May	Specimens LACM
1937	J. Elton Green	13-Jul	Specimens WFVZ, Green and Arnold 1939
1938	Ed N. Harrison, William H. Burt, and John R. Pemberton	6-8 April	Specimens SDNHM,
			WFVZ, UMMZ
1941	D. Feathers	25-Apr	Specimen USNM
1950	John R. Hendrickson and Carl L. Hubbs	27 January-3 February	Howell and Cade 1954, Specimens MVZ
1952	Ward C. Russell	8-Aug	Specimen MVZ
1962	Kenneth E. Stager	22-25 October	Jehl and Everett 1985, Specimens LACM

* In some cases it is unknown whether some of these individuals actually visited Isla Guadalupe or somehow got their names and the location on specimen labels, which was not an uncommon practice at the time.

The first appearance of the spelling "Guadalupe" Island in the scientific literature comes from specimens collected by Edward Palmer in 1875. Watson (1876), Greene (1885), Vasey and Rose (1890), and Francheschi (1893), in writing about Palmer's botanical collections, all spelled the name as we know it today. However, a junco specimen (#1601) in the SDNHM, collected in February 1875, bears a label with the island spelled Guadaloupe. Ridgeway (1876) writing about avian specimens collected by Palmer at first used the spelling "Guadeloupe" but quickly reverted to the current spelling a year later (Ridgeway 1877). However, in his 1876 publication he described the Guadalupe Rock Wren as *Salpinctes obsoletus guadeloupensis*, which has remained unchanged to this day.

Bryant used two spellings — Guadeloupe and Guadalupe. The initial spelling was later corrected in an *Errata* on the last, unnumbered page of the 1887 *California Academy of Sciences Bulletin,* Volume II, following page 448. However, the *Errata* mistakenly identified a spelling on page 291 of the paper as Guadaloupe and substituted Guadalupe. The actual spelling on the page was Guadeloupe. A second *Errata* was then published, following page 538 in the same volume. This second *Errata* contained the same changes as the first and added a change for the Rock Wren subspecific name from *guadeloupensis* (Ridgeway's spelling) to *guadalupensis*. These *Errata* have not been mentioned in the literature of the island until this paper. In Bryant's *Catalog of the Birds*

of Lower California, Mexico (1889) he cites Ridgway's 1876 paper with the island name as it appeared in print, but all other references refer to the current spelling. The two type specimens of *Oceanodroma macrodactyla* in the CAS collected by Bryant in 1886 are labeled as being from "Guadalupe Is." (Fig. 1).

Next, Townsend (1890) used the spelling Guadaloupe. Then, in a series of papers in 1898, Alfred W. Anthony (1898a, 1898b, 1898c) first used the spelling Guadaloupe, which was followed by Guadalupe (papers in the *Auk* on sequential pages), and again Guadaloupe. In 1900, he used Guadaloupe again, but he finally ended his publication spree with Guadalupe (Anthony 1901).

Rothschild and Hartert (1902) also used both Guadalupe and Guadeloupe, the latter a previously unused spelling. Next were John E. Thayer and Outram Bangs (1908), who published their paper on the status of birds of "Guadaloupe" Island. In reviewing the Thayer and Bangs paper, Joel A. Allen (1909) not only repeated Thayer and Bang's "Guadaloupe" but he also changed the island's name in both Ridgeway's 1876 paper and Bryant's 1887 paper from Guadalupe to Guadaloupe.

von Berlepsch (1906) used the name Guadelupe whereas Townsend (1908) again used Guadaloupe twice. This latter spelling was repeated (in reference to his 1911 visit) in the *Notes and News* section in the *Auk* (Anonymous 1911a). In the *Auk* later that same year, the island was referred to as Guadelupe (Anonymous 1911b). In his 1912 field notes and catalog, Beck used the spelling Guadaloupe. The confusion continued until at least the early 1930s (Wetmore 1933).

This may all seem trivial until one considers the proper spelling of the *Guadeloupe* Island in the Caribbean. In at least one case this has led to confusion that persists to this day. The Academy

FIGURE 1. Labels on the type specimens of *Oceanodroma macrodactyla*, the only bird specimens saved from the fire following the 1906 San Francisco earthquake. Photo courtesy of CAS.

of Natural Sciences (Philadelphia) holds a specimen (#108585) of *Oceanodroma macrodactyla* collected in 1906 by Wilmot W. Brown. The museum lists the specimen as being from the Lesser Antilles. The Chicago Academy of Sciences holds a 1905 specimen of the Caribbean *Elaenia*, *Elaenia martinica* (#1540), which is listed as being from "Mexico, Baja California, Isla de Guadalupe." This specimen was certainly collected in the French possession of Guadeloupe. Some specimens of various species from Guadalupe Island held in museums around the world are still listed as being from Guadeloupe or Guadaloupe (Vertnet).

Species Accounts

Pied-billed Grebe *Podilymbus podiceps*

Jehl and Everett (1985) reported only one specimen taken on 27 October 1957 and stated "location of specimen unknown." That specimen, collected by Carl L. Hubbs, is #246443 in the FMNH. In addition, Hubbs collected another bird of this species three days later (FMNH #246444).

Eared Grebe *Podiceps nigricollis*

Jehl and Everett (1985) reported two collected by Hubbs on 12 February 1957 and another collected on 30 October 1957. The latter was in fact the second specimen of *Podilymbus podiceps* noted in the above account.

Guadalupe Storm-Petrel *Oceanodroma macrodactyla*

Botanist Edward Palmer spent from 1 February to the middle of May 1875 collecting not only plants, but birds and other organisms. For some reason he did not report on or collect any specimens of storm-petrels. He did, however, collect numerous land birds, including specimens of the eight endemic forms that were shortly thereafter described as new to science by Robert Ridgeway (1876).

Walter E. Bryant in 1885–86 was the first ornithologist and first biologist since Edward Palmer to visit the island. In his field notes, Bryant recorded (regarding the storm-petrel) "Its presence on the island was first noticed during a storm, when at midnight I was awakened by a companion who told me that some little owls were flying around the fire near which he was sleeping. Their flight was like that of a bat, so erratic that it was impossible to shoot them. They were never seen in the moonlight but only when the night sky was overcast or after the moon had set." High atop the north end of the island, in soil burrows amongst the roots of the immense Guadalupe Island pines, *Pinus radiata* var. *binata*, Bryant collected at least 32 specimens of what he later believed was a new race (*macrodactyla*) of the very widely distributed Leach's Storm-Petrel, *O. leucorhoa* (Bryant 1887b).

Subsequently, the American Ornithologist's Union decided it was in fact a new *species*, the Guadalupe Storm-Petrel (AOU 1889). The California Academy of Sciences, where many of Bryant's specimens were stored, was destroyed in the 1906 San Francisco earthquake and fire. Of their vast collections of birds, the only two specimens saved were the two type specimens of Bryant's Guadalupe Storm-Petrels. On the other hand, many of the eggs Bryant collected are currently housed in the WFVZ.

A.W. Anthony spent 10 days at Guadalupe in late May 1892. On 26 May he spent one day atop the island in the pines that grow along the northern ridgeline. It was here that Bryant had discovered the *O. macrodactyla* nesting colony. Anthony characterized the species as "abundant" and collected at least four specimens (three of which were nestlings), sex undetermined. Anthony again visited Guadalupe from 18–22 September 1896. On the 18th he went to the top of the island but he reported no evidence of any nesting seabirds. Horace A. Gaylord accompanied Anthony on the visit, and later (Gaylord 1897) related "Regarding the Petrels which breed on the island, the [goat] hunters told us that while doing some stone work in the region of the Petrel colony, they had found

two different species. They described the Guadalupe Petrel and an entirely black one, which together with a wing found on the trail to the cypress forest makes it appear that *O. homochroa* is an inhabitant of this island." Anthony (1898c) subsequently identified the wing as belonging to a race of the Leach's Storm-Petrel, *O. l. kaedingi*.

In March 1897, Anthony again visited Guadalupe and on the 24th and 25th he collected a large series (at least 87) of eggs and skins of *O. macrodactyla*. "That summer he returned and collected young, noting that *macrodactyla* leaves the colony by 10 June" (Jehl and Everett 1985). Although Anthony was becalmed near Guadalupe in July 1897 (Anthony 1898c) there is no published evidence nor any known specimens to suggest he went ashore. He collected at least 10 specimens of *O. leucorhoa* "Off" Guadalupe during that time. The latest he ever actually landed on the island (other than September 1896) was in late May 1892. Jehl and Everett (1985) in their Table 1 did not list Anthony's September visit.

Wilbur W. Thoburn, from Stanford University, was sent by David Starr Jordan of the North Pacific Fur Seal Commission, and who was also President of Stanford, to Isla Guadalupe from 21 June to 2 July 1897, just two months after Anthony's visit earlier the same year (Thoburn 1899). His primary objective was to look for and document Guadalupe Fur Seals, *Arctocephalus townsendi*. Thoburn's minimal accounts of birds the expedition encountered shed little light in part due to some apparent contradictions. He reported the "Bryant's Petrel" (still using *O. leucorhoa macrodactyla*) as being "very common on dark nights. It would fly around the ship uttering a peculiar cry. Occasionally one would strike the rigging and fall to the deck or enter the cabin. Several specimens were secured in this way and kept alive several days." Thoburn's use of the word "specimens*"* clouds things further. For example, in reference to Red-tailed Hawks, *Buteo borealis calurus* [*sic*] he states "Two specimens were seen over the southern part of the island. It was frequently seen in the southern part. No specimens were secured." So 'secured' must have been his indication that specimens were collected, but I have been unable to locate records of any of their avian specimens said to have been *secured*. In the prelude to his short annotated bird list Thoburn notes "The interior of the island was thoroughly explored and nearly every form of bird and insect and plant life was collected." But who did the exploring and collecting is not clear. He states, "To professors Green and Wing fell the very difficult and often dangerous work of exploring the interior of the island, while I gave most of my attention to the coast line." Yet, a map of the island in the same publication (facing page 284) is said to show the "explorations of W.W. Thoburn." The map shows what appears to be a trail leading from what is now called the Northeast Anchorage up to the "Ranch and Spring" and slightly beyond, which would be the location of the large cypress *Cupressus guadalupensis* grove atop the island. If this is indeed the path they followed, they might not have actually carefully examined the nesting grounds in the pines (but the annotated bird list says that three Guadalupe Flickers were collected "among the pines").

William R. Dudley (1899), in reporting on the botany of the island from the same visit stated, "The northwest and much of the central part remained unvisited, chiefly on account of the dryness and heat and the difficulty of transporting water." He did, however, report "not more than 50 [pines] on the northwest ridge." Regardless, based on all the previous information, they may well have been there after Guadalupe Storm-Petrels had completed nesting that year. If they searched the breeding grounds and found them unoccupied, it may have been the source of Anthony's assertion that *O. macrodactyla* left the colony by June 10th. Thoburn was a fervent preacher and Professor of Bionomics (= ecology) at Stanford University. Fur seals were his main focus during the visit. Rufus L. Green was a botanist but was also tasked with creating a topographic map of the island, and Charles B. Wing was a Stanford engineering professor, whose job was also photography during the expedition. Their efforts were spread thin over their brief 10 day visit.

Henry Barroilhet Kaeding accompanied Anthony on his wide-ranging 1897 expedition (visiting many Mexican islands). Several years later he published a summary (Kaeding 1905) of the birds encountered along the way, including those from Guadalupe. Of particular interest are his accounts of the storm-petrels. Regarding *O. kaedingi* he states that "the breeding grounds of this species are as yet unknown, but it is probable that the birds occupy the burrows of the Guadalupe Petrel after the breeding season of the former is closed." Of *O. macrodactyla* he notes "eggs taken on the 25th of March being slightly incubated." He goes on to state "they lay their eggs at least 100 days earlier than the others [storm-petrels]."

W.W. Brown, Henry W. Marsden, and Ignacio Oroso were the next collectors of Guadalupe Storm-Petrels to visit Guadalupe. They visited the island from 1 May to 28 June 1906 (Thayer and Bangs 1908). Up until 17 June they collected a dozen adult *O. macrodactyla*, one downy young, and one egg. They noted "This species is abundant at night about its nesting burrows on the pine ridge at the northern end of the island. Most of the burrows we opened were empty, the breeding season being about over; three, however, contained one young each, and one, one egg." They found no adults in the burrows. They also reported "appalling" predation by cats.

Charles H. Townsend visited Guadalupe in March 1911 aboard the *Albatross*, mostly in search of Guadalupe Fur Seals, *Arctocephalus townsendi*, and Northern Elephant Seals, *Mirounga angustirostris*. Along on the visit were Harold E. Anthony and Pingree I. Osburn. They each collected a storm-petrel that came aboard ship while they were anchored off the island (Townsend 1916). They were initially identified as *O. macrodactyla*, but subsequently determined by Davidson (1928) to be *O. socorroensis* [= *leucorhoa*].

Bent (1922) reports an egg (WFVZ #204444) allegedly of this species collected on 2 July 1910. Data accompanying the egg state that it was collected by W.L. White, a highly suspect egg dealer (Lloyd Kiff in prep, and see Guadalupe Caracara account below). Inasmuch as there were no known scientific visits to Isla Guadalupe in 1910, I believe this record should be disregarded.

As noted above, it was Rollo Beck in the summer of 1912 who is credited with the last record for the Guadalupe Storm-Petrel, although it would be ten years later before anyone looked for the species again (Anthony 1925). Beck collected two downy young (AMNH #749220 & #749217) from burrows among the pines at the north end of the island (Jehl and Everett 1985 erroneously reported that Beck collected three downy young). Davidson (1928) corresponded with Robert Cushman Murphy at the American Museum of Natural History, who informed her that "All our adult examples of *macrodactyla* are labeled Guadalupe Island and were taken during only two different months - namely, March 1897 and May 1906. In addition to these, however, there are a male and female in nestling plumage, collected by R.H. Beck on 3 August 1912 [Fig. 2]. These appear to be true *macrodactyla*…." Davidson (1928) added "The identification of these nestlings is doubtless correct; nevertheless, August seems rather late for young of the species to still be down-clad." She apparently presumed that neither Beck nor Murphy would be wrong, but still felt she needed to add the caveat.

Beck's field notes and catalog from his 1912 visit indicate that in addition to the two nestlings (in burrows among the pines at the north end of the island) a couple of weeks later he collected as many as seven adult storm-petrels atop the island. In his catalog, next to the entries for these adult birds, he placed a question mark (Fig. 3). It is apparent he had doubts that these birds were *O. macrodactyla*. In his notes for 26 August, he also reported that he "Dug into lots of rock piles but petrel burrows all old - spider webs in most. Lots of wings about where cats have caught them."

As it was Beck's first documented visit to the island during the summer, he must have been guided in part by the accounts of the species given by Thayer and Bangs (1908) and Kaeding (1905), enough at least, to plant a seed of doubt in his mind. He was never certain that he had

FIGURE 2. Specimens collected on 3 August 1912 by Rollo H. Beck labeled *Oceanodroma macrodactyla*. Photos courtesy AMNH.

encountered adults of *O. macrodactyla*. The at least seven adult storm-petrels that he collected during that visit all later turned out to be identified as *O. leucorhoa* [= *socorroensis*] (Vertnet).

All this leads to the strong possibility that Kaeding (1905) was correct, and *kaedingi* [= *leucorhoa*] to some extent did occupy the burrows of *O. macrodactyla* after the latter's breeding season. This sequential use of nest sites by storm petrel species or subspecies is known from Isla Guadalupe (Hubbs 1960) and Islas Coronados in Baja California (WTE pers. obs.) and probably occurs elsewhere in Mexico, if not beyond.

In 1972, Jehl examined the two 3 August 1912 specimens and concluded they were *macrodactyla* but did not explain how he reached that determination. However, in March 2019 Peter Pyle (pers. comm.) was able to examine the nestlings and determined that in fact they are *O. macrodactyla* based on "enough of the uppertail covert feathers growing out to confirm that they are white with distinct and broad black tips. This eliminates Leach's." In examining plumages and molt patterns in specimens of adult *O. macrodactlya* at the AMNH, Pyle also suggests a summer breeding season, which is at odds with Kaeding's (1905) assessment (see above).

Blue-winged Teal *Anas discors*

Jehl and Everett (1985) reported that the location of the only specimen, an adult male collected by Hubbs on 30 October 1957, was unknown. It is preserved in the FMNH (#246446).

Osprey *Pandion haliaetus*

In addition to previously reported records, Victor B. Scheffer collected a specimen (MVZ #133098) on 10 June 1955.

Sharp-shinned Hawk *Accipter striatus*

During a three day visit in March 1930 Dudley S. DeGroot (field notes WFVZ) reported a sighting of this species. This is the first and only record for the island. Given the highly migratory nature of this species (Bildstein and Meyer 2000) this bird was most likely transient and not resident.

Guadalupe Caracara *Caracara lutosa*

Although he was the last, Beck was hardly the first collector of the Guadalupe Caracara, as Palmer (1875 – USNM, SDNHM, AMNH, NHMUK), Bryant (1885-86 – CAS and FMNH), and Anthony (1896 – CMNH) had also collected specimens. Palmer was the most prodigious, with at least 24 collected (of at least 38 still in museum collections), including the type specimen now in the USNM. Long before the first specimens were collected, various enterprises worked to make money in one way or another off the large goat populations on the island. The caracaras presented a significant problem to the ranchers as they often attacked their animals, especially the newborn or young. Palmer (in Ridgeway 1876) noted that "Hundreds of the birds have been destroyed by the inhabitants [ranchers], both with poison and fire-arms, without noticeable diminution of their numbers. They are tough, strong birds, requiring a heavy charge of shot to bring them down." Bryant (1887a) reported that the island agent "never missed an opportunity to kill one."

Thus, scientific collecting played only a small role in the demise of the species. Gallo-Reynoso and Figueroa-Carranza (2009) proposed that extinction was precipitated "by the decimation of the fur seals and elephant seals, eliminating the pups, placental tissue, and carcasses that probably sustained these predators/carrion eaters." Long after the pinniped populations were reduced (nearly exterminated) by sealers, goats and a wide variety of other food options clearly sustained a large caracara population. The opportunistic behavior described by Palmer (in Ridgeway 1876) and in Bryant (1887a and 1889) is testimony to the omnivorous nature of the bird, surviving also on caterpillars, other insects, carrion, mice, shell-fish, and small birds. Bryant even collected a caracara that had a storm-petrel foot and feathers in its stomach (species unknown).

After Beck collected nine specimens (MCZ, and shot at two more birds that escaped on 1 December 1900 – Abbott 1933) the next collectors to visit the island (Brown, Marsden, and Oroso, for the Thayer Museum from 1 May – 28 June 1906) especially wanted specimens of the caracara. The island "was ransacked from end to end, but no trace of the caracara could be found." They even killed goats and left them at various locations as bait (Thayer and Bangs 1908). It seems likely that between Beck's 1900 visit and the Thayer expedition, the species had become extinct.

The USNM houses an egg (#B43872) reportedly collected on 28 May 1906 by M.L. White. This was during the time that Brown and Marsden were on the island. It is highly unlikely that this specimen is from Isla Guadalupe. The University of Florida also houses eggs (#s 1136 and 52321) reportedly collected by W.A. Myers (three eggs – 4 March 1880) and H.A. Ward (one egg – 4 March 1880), respectively, both of whom were professional dealers in avian specimens. These records, too, are of dubious origin, as there is no other evidence of a visit to the island during this time. The *Nidologist* (Taylor 1895) contains a heated letter from editor Harry R. Taylor to a dealer in avian specimens (Walter F. Webb) who had advertised Guadalupe Caracara eggs for sale.

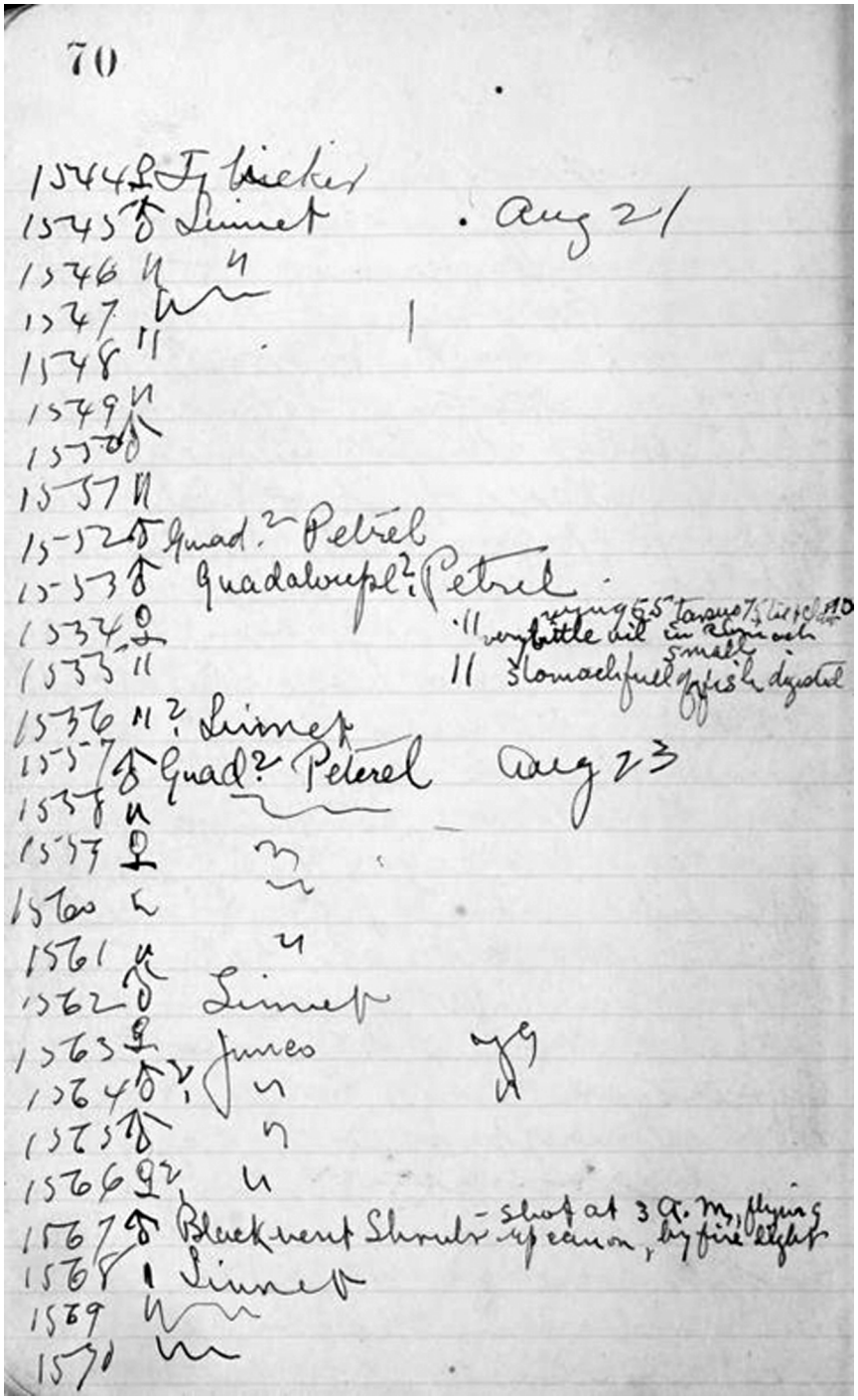
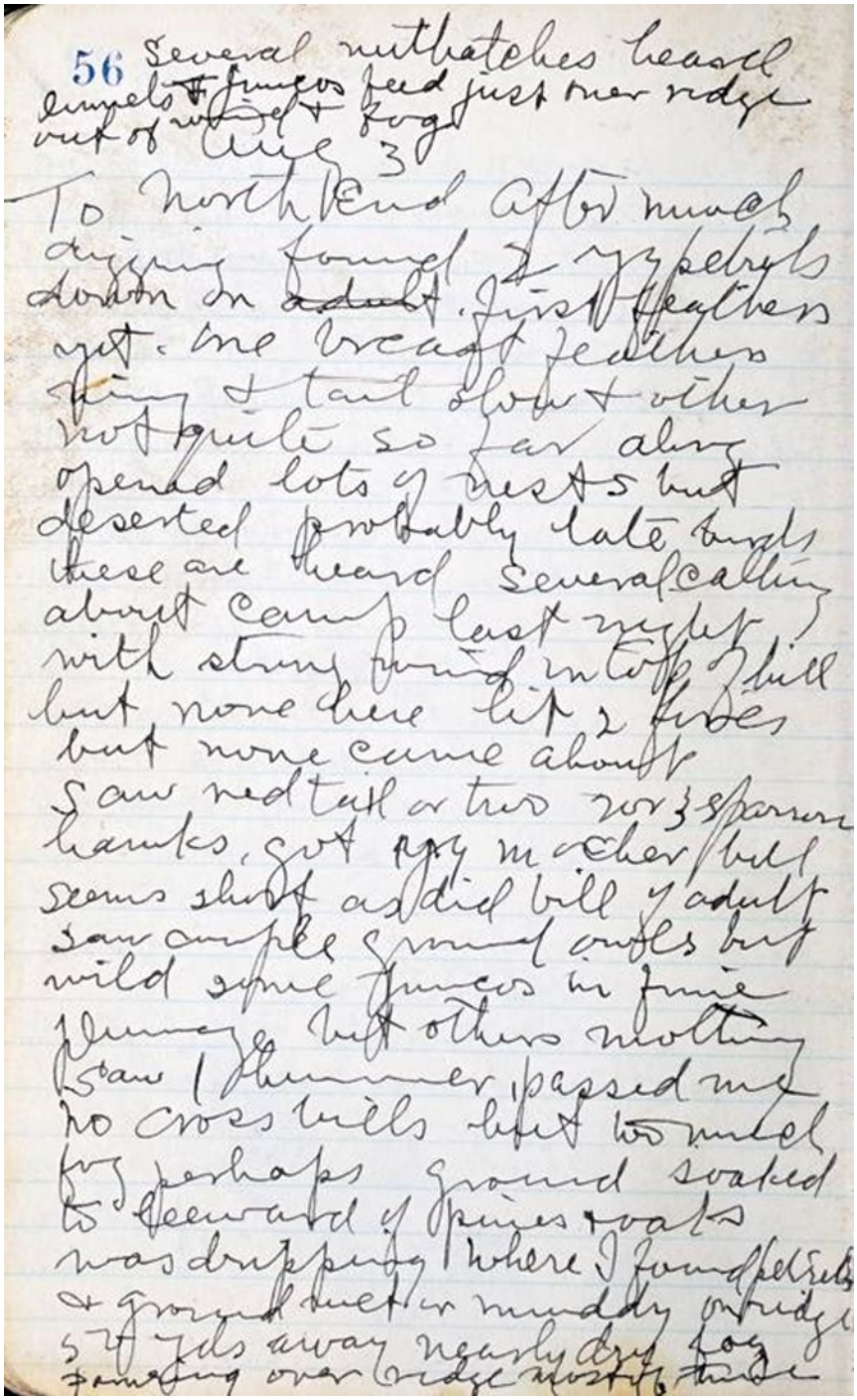


FIGURE 3. A portion of Rollo Beck's collecting catalog from Isla Guadalupe (CAS).



56 Several nuthatches heard
Juncos feed just over ridge
out of camp 3
To North End after much
digging found 2 ♀ pelrls
down in adult. First feathers
yet. One breast feathers
wing & tail down & other
not quite so far along
opened lots of nests but
deserted probably late birds
these are heard several calling
about camp last night
with stray pairs in top of hill
but none here lit 2 fires
but none came about
Saw red tail or two 20 or 3 sparrow
hawks, got ♀ my mocker but
seems short as did bill ♂ adult
saw couple ground owls but
wild some Juncos in juvie
plumage but others moulting
Saw 1 thrasher passed me
no cross bills but wooded
fog perhaps ground soaked
to leeward of pines & oaks
was drizzling where I found pelrls
& ground duet in muddy on ridge
5 or 6 yds away nearly dry fog
forming over ridge most of time

FIGURE 4. Rollo H. Beck's field notes from Isla Guadalupe, 3 August 1912 (CAS). See Appendix A for transcription.

Taylor responded "And I may add, that if successful in purchasing any or all of these eggs, I intend to form a syndicate to place an order with you for a series of eggs of the Dodo…"

Bent (1938) reports that an egg "in the Swann collection is probably authentic." Swann (1925) stated that his egg was collected on 17 April 1897 by W. More. He goes on to state "Only two pairs of birds were seen and the [female] of this pair was shot." There is no record of any Guadalupe Caracara (or any other specimens) collected on this date. This alleged visit took place three weeks after A.W. Anthony, as part of his extensive voyage aboard the *Wahlberg*, had collected numerous specimens of various species on the island in late March. Bent also notes "Charles E. Doe has an egg in his collection which appears to be genuine." Bent does not cite a collection date for either egg, and whether or not they bear any relation to the University of Florida eggs is unknown.

FIGURE 5. The only existing life-mount of a Guadalupe Caracara. Photo courtesy of MCZ

Then there is the curious brief story given by Harry S. Swarth of a hearsay observation by Captain Charles E. Davis, who visited Guadalupe in the summer of 1913 to take "moving pictures of elephant seals found around the island and capture alive some of the younger animals." On a second visit later that summer Davis found the decomposing remains of five or six elephant seals. He reported to Swarth that "several gulls flew up from the carrion, and with them two or three dark-colored birds, which he described as looking like apparent crosses between an eagle and a turkey Buzzard." Swarth apparently thought enough of the information as being "at least suggestive of the possible persistence up to the present time of the supposedly extinct Guadalupe Caracara" to publish the account in the *Condor* (1913). Swarth's note was ignored by Grinnell (1928), Bent (1937), and every other general account of the birds of the island since, including Jehl and Everett (1985). This paper, however, is the first time Davis' visit is somewhat corroborated with an elephant seal filming effort (Gordon 1919), which adds intrigue to the story.

Clinton G. Abbott (1933) summarized the history of the Guadalupe Caracara. He itemizes 37

known specimens, reporting only two taken by W.E. Bryant. Abbott did not include an additional eight birds collected by Bryant. These specimens, and other Guadalupe Island species in the California Academy of Sciences (Anonymous 1894), were lost in the San Francisco earthquake and fire of 1906. This would bring the total number of known caracara specimens collected to 45.

Howell and Cade (1954) reported that the caracara was "last noted in 1903." This statement may somehow be related to the passing comment made by Kaeding (1905) wherein he remarked that an "expedition was sent to Los Revillagigedos by the California Academy of Sciences in 1903. This party spent several months in the region, principally upon Socorro Island, and the report of their work, when published, will undoubtedly add much to the history of the group." Kaeding's paper was principally intended to report on birds observed and collected during the 1897 expedition with Anthony to the majority of islands off the west coast of Baja California, including Guadalupe and all of the Revillagigedos. Howell and Cade also cited Abbott's 1933 paper, but how they concluded 1903 was the last sighting of the caracara is a mystery. Oddly, this report was repeated in the Fifth Edition of the A.O.U. Check-List (1957). As this was not noted in the Fourth Edition of the Check-List (1931), nor in any of the 13 Supplements to the List published between the Fourth and Fifth Editions, the source for the Fifth Edition comment appears likely to come directly from Howell and Cade's 1954 paper. Barton et al. (2004) also cite 1903 as the last report of the species.

Spotted Sandpiper *Actitis macularius*

During the late March 1930 visit to the island Dudley DeGroot (field notes WFVZ) reported "about a dozen on the rocks at the south end." Barton et. al. (2004) reported a single bird observed at the south end of the island on 2 March 2003 as the first record for the island. Based on DeGroot's observations, the first record for the island was in 1930.

Guadalupe Murrelet *Synthliboramphus hypoleucus*

Jehl and Everett (1985) reported that the breeding of this species (formerly Xantus's Murrelet) at Guadalupe was first discovered by Carl L. Hubbs, likely in the 1950s. Hubbs only found this species on two offshore islets, Islote Negro and Islote Afuera. Jehl and Everett also speculated on the existence of nesting on the main island. The USNM contains an egg (#B25236) reportedly of this species collected at "Walrus Bay" [= Whaler's Bay? – now known as Melpomene Cove] at the south end of the island by A.W. Anthony in May 1892. This record was not reported by Grinnell (1928). If valid, it would be the first breeding record of this species on Isla Guadalupe. In March 1930 Dudley DeGroot found eggshells and cat-eaten carcasses of this species near the south end of the island. This evidence would then be the second record of breeding by this species at Isla Guadalupe.

Cassin's Auklet *Ptychoramphus aleuticus*

DeGroot found fresh cat-killed remnants of this species near the south end of the island in 1930. Jehl and Everett credited Hubbs with the first record of breeding in the 1950s, but DeGroot's indirect evidence suggests the species has long nested at Guadalupe.

Guadalupe Flicker *Colaptes auratus rufipileus*

Grinnell (1928) and Greenway (1958) concluded that the last encounter with the Guadalupe Flicker was that of Brown and Marsden, who collected a large series of skins and eggs in June 1906. However, at least 16 specimens were collected by Beck in 1912, which extends the last known occurrence by six years.

Based on known specimens and a short note, professional collector Henry H. Kimball (Kimball 1922) visited Guadalupe from 10-12 October 1913. Because he collected a series of

kinglets, he must have had reached the upper portions of the island. He apparently did not collect any flickers, or any other thought-to-be extinct endemic birds, although there can be little doubt he was aware of their potential existence.

Between Kimball's visit and 1982 there were many expeditions to the island (Jehl and Everett 1985, this paper), but few endured the grueling hike to the top of the island, which required carrying all water necessary for the hike up (1,219 meters +), the length of the stay, and the hike back down to the shoreline. Notable among ornithologists who did make the climb are A.W. Anthony in 1922 (Anthony 1925), Laurence H. Huey in 1923 (Huey 1924), Tom Cade and Thomas R. Howell in 1953 (Howell and Cade 1954), Joseph R. Jehl, Jr. twice in 1970 and once in 1971 (Jehl 1972), and Ken Briggs in 1972 (Jehl and Everett 1985). None of the visits lasted more than one day and night in the cypress or pine groves. None recorded a flicker.

In the late 1970s and mid 1980s access to the top of the island changed dramatically when a rough dirt road was created from near the south end of the island to the cypress grove area, part of an effort to harvest and export goat meat to be sold in Mexico.

In spring, summer, and winter of 1986 and spring 1991, Lorenzo Quintana-Barrios visited Guadalupe and collected an immature female flicker (UABC #359) on 4 December 1986 (Quintana-Barrios et al. 2006). It proved to be a mainland form, *C.a. collaris*.

In January 1988 Steve Howell and Sophie Webb visited the island and apparently took advantage of the new road and spent a day (but not a night) at the cypress grove. They observed no flickers. A couple months later (March 1988) a small party spent a night in the cypress grove and the next day examined the area of the pines (Oberbauer et al. 1989). They found a flicker in the cypress forest but could not tell if the bird was a migrant or not. In 1989 Eric Mellink and Eduardo Palacios took the road and spent a couple hours in the cypress grove (Mellink and Palacios 1989). They observed no flickers.

In early June 1996 Paul R. Sweet (Sweet et al. 2001) spent two days in the cypress forest and discovered that flickers had re-colonized the island, based on observations of nesting birds. They reported that the endemic subspecies had gone extinct in 1906, citing Greenway (1967 [= 1958]). Subsequently they undertook a detailed statistical analysis of the Guadalupe Flicker, making comparisons with 24 specimens in the AMNH, including 10 collected by Beck between 24 July and 19 August 1912.

In 2000 Philip Unitt (SDNHM) observed up to five flickers a day in the cypress forest over a six day period (Quintana-Barrios et al. 2006). In the winter of 2003 Barton et al. (2004) spent two months on Guadalupe and observed two flickers in the cypress grove on 10 March 2003. They also reported that the Guadalupe Flicker was last seen in 1906.

Based on the above, the Guadalupe Flicker was last seen and collected in August 1912 by Beck. The mainland taxon recolonized the island sometime in the 1970s or 1980s.

Ash-throated Flycatcher *Myiarchus cinerascens*

Beck saw one on 23 July 1912 but was unable to collect it and apparently had doubts about the identification (Beck field notes page 46). If correctly identified this would be the first record for the island, and the one collected on 3 September 1986 and reported on by Quintana-Barrios et al. (2006) would then be the second.

Guadalupe Wren *Thyromanes bewickii brevicauda*

As noted in Jehl and Everett (1985), the history of this endemic form was summarized in Grinnell (1928) and Greenway (1958). The last documented occurrence was in 1892 (Anthony 1901). In late October 1898 the Hopkins-Stanford Expedition departed San Francisco for an extended collecting trip to the Galapagos Islands. The primary collectors on the trip were Robert E. Snodgrass

and Edmund Heller (both Stanford graduate students). On 5 November they went ashore at Isla Guadalupe and collected 11 specimens, seven of which were accessioned into the Stanford Museum collection as *Thryothorus brevicaudus,* the then name of the Guadalupe Wren. They apparently spent only a couple hours ashore, certainly not enough time to explore the top of the island, which was the only place the Guadalupe Wren was ever encountered. In the Stanford collection catalog (On-line – in pencil at some unknown later date) the identifications were corrected to *Salpinctes obsoletus guadeloupensis*, the Guadalupe Rock Wren. These specimens are now housed at the California Academy of Sciences.

Howell and Cade (1954) cited 1903 as the last observation of this species, but as with the 1903 sighting of the caracara that they reported, this is unsubstantiated and should be disregarded. The Fifth Edition of the A.O.U. Check-List also report the species as "last seen" in 1903. This date was also repeated uncritically by Barton et al. (2004) and Luna-Mendoza et al. (2005).

Northern Mockingbird *Mimus polyglottos*

The first record for this species was that of Bryant (1887a) who saw two and collected one on 16 March 1886. The second and third records are the heretofore unpublished field notes by Beck who observed three and collected one in the pines at the north end of the island on 23 July 1912 (Beck field notes page #46). This specimen (Field Catalog #1386, AMNH #757984) is shown in the AMNH Vertnet data as being collected on 4 October 1914, which is clearly in error (Beck was not on Guadalupe in 1914) He collected a second specimen (Field Catalog #1438, AMNH #757984) on 3 August 1912. Although the species was subsequently reported as accidental by Howell and Cade (1954), it has been observed many times since their 1953 visit to the island (Jehl and Everett 1985, Quintana-Barrios et al. 2006).

Guadalupe Spotted [Rufous-sided] Towhee *Pipilo maculatus* [*erythrophthalmus*] *consobrinus*

The extinct endemic Guadalupe Spotted Towhee has been widely reported as having been last observed in 1897 (Grinnell 1928; Greenway 1958). What is known for certain is that the last known specimens were collected by Bryant in 1886. Anthony spent a week in late May 1892 collecting on the island. There he collected several Guadalupe Wrens and presumably searched for the towhee. Anthony again visited the island in September 1896. Gaylord (1897) later reported of Anthony that "In the cypress grove he caught a glimpse of a bird which *had the appearance* [emphasis added] of *Pipilo consobrinus*." Anthony himself never claimed to have seen the bird, and in his publication on the Guadalupe Wren (1901) noted that "*Pipilo consobrinus* is now nearly or quite extinct." Lastly, the 1897 record is from Thoburn (1899) who reported in his list of the birds encountered "One specimen" of the Guadalupe Towhee. As discussed in the account above of the Guadalupe Storm-Petrel, the term specimen does not necessarily indicate a bird was collected. Since Thoburn himself apparently did not make the "observation" it should be regarded with suspicion. Also, as noted above, none of the specimens reported as "secured" by Thoburn or his companions have been located.

Red Crossbill *Loxia curvirostra*

Also reported by Howell and Cade (1954) as being last sighted in 1903. The last generally accepted record (Grinnell 1928) was a sighting in March 1897 (Kaeding 1905).

Discussion

The advent of the Internet has enabled significant advances in the science of Ornithology. Chief among the services now available to anyone include online literature searches through sites such as SORA, JSTOR, archive.org, Biodiversity Heritage Library, Hathi Trust, and others. The

Vertnet online database provides access to millions of specimen records, previously essentially impossible for any individual to research without extremely costly and time consuming travel (or burdening collection managers with copious correspondence). Some institutions (e.g., WFVZ) have scanned data cards that accompany specimens, and some have even photographed and posted images of specimens and specimen labels, an effort to be much commended. And more institutions are scanning and making available the field notes of a wide range of researchers, both historical and relatively recent. The value of this cannot be overstated. Often, answers to vexing questions (as demonstrated in this paper) become obvious when put into the context of well-written (or even sloppy – Fig. 4) field notes, and specimen records.

As admirable as all these efforts are, there is still much more to be done. It will likely be decades before errors in the data available on Vertnet are corrected (an effort we all need to assist with) and other institutions around the world add their data. The amount of historic and recent literature remaining to be made available online is staggering, and in many cases complicated by copyright laws and other restrictions.

It would be an extremely serious error for researchers who begin their work in the Internet Age to assume that everything that is pertinent to their studies is available online. If they do, they run the high risk of being exposed at some future time for their disregard of other available resources. Ornithology still requires, and will for some time, work in the musty halls of museums, libraries, and the offices of ossified old researchers.

As can be seen from the information provided above, the early histories of *Oceanodroma macrodactyla* and *O. leucorhoa* on Isla Guadalupe are closely intertwined. For well over 100 years the debate over subspecific variation in the Leach's Storm-Petrel complex in the eastern Pacific has raged on, crying out for new methods to settle the species' long and tortured taxonomic history (See Huntington et al. 1996). This is further complicated by the high likelihood that additional colonies of *O. leucorhoa* on Isla Guadalupe still remain to be documented, especially on the rugged west side of the island near the north end, where birds were heard calling far below in June 2000 from high above in the pine forest (WTE, pers. obs.).

Hope often springs eternal when it comes to presumed extinct species. The north side of Isla Guadalupe is characterized by sheer volcanic cliffs, some towering 1,200+ meters straight up from the sea. There is always the possibility that some *O. macrodactyla* have persisted by nesting in burrows in precipitous slopes that even cats and goats could not reach. If this is the case, someday the species would likely reoccupy its historic nesting grounds. Biologists stationed on the island should be vigilant for this remote possibility.

Perhaps one of the most anomalous aspects of the avifauna of Isla Guadalupe is the absence of records for the Common Raven, *Corvus corax*. This species is abundant on the Baja California peninsula and has been recorded on virtually every island in the Gulf of California and off the Pacific coast of the peninsula, including Clarion Island in the Revillagigedo Islands, from which the type specimen of *C.c. clarionensis* was described.

In summary, careful examination of historic literature, some of which is not scientific in nature, specimen records, and field notes add to and clarify our understanding of the avifauna and history of Isla Guadalupe. There can be no doubt that the historic record still remains incomplete. And given that there has been a nearly continuous presence of biologists on Isla Guadalupe since the early 2000s, there are certainly interesting revelations to be made and species new to the island that have been observed but not yet reported.

Among the resources still unexamined are the field notes of many visitors to the island besides Beck. In time, hopefully, a great deal more information will become more readily available for researchers to examine, assess, and publish.

Acknowledgements

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Literature Cited

Abbott, C.G. 1933. Closing history of the Guadalupe Caracara. *Condor* 35:10–14.

Anonymous. 1894. Three Thousand Bird Skins. *Nidologist* 2(4):55.

Anonymous. 1911a. Notes and News *Auk* 28:292.

Anonymous. 1911b. Notes and News *Auk* 28:389–390.

Anthony, A.W. 1900. Nesting Habits of the Pacific Coast Species of the genus *Ruffinus* [*sic*]. *Auk* 17: 247–252.

Anthony, A.W. 1901. The Guadalupe Wren. *Condor* 3:73.

Anthony, A.W. 1898a. Two new birds from the Pacific coast of America. *Auk* 15:36–38.

Anthony, A.W. 1898b. Four sea birds new to the fauna of North America. *Auk* 15:38–39.

Anthony, A.W. 1898c. Petrels of Southern California. *Auk* 15:140–144.

Anthony, A.W. 1925. Expedition to Guadalupe Island, Mexico, in 1922. The birds and mammals. *Proceedings of the California Academy of Sciences*, ser. 4, 14:277–320.

Allen, J.A. 1909. [Review of] Thayer and Bangs on the birds of Guadaluope [*sic*] Island. *Auk* 26:319–320.

Barton, D.C., K.E. Lindquist, R.W. Henry, and L.M. Luna-Mendoza. 2004. Land bird and waterbird notes from Isla Guadalupe, Mexico. *Western Birds* 35:186–196.

Barton, D.C., K.E. Lindquist, R.W. Henry III, and L.M. Luna-Mendoza. 2005. Notas sobre las aves terrestres y acquáticas de Isla Guadalupe. Pages 103–113 *in* Santos del Prado and E. Peters, eds., *Isla Guadalupe, Restauración y Conservación* (K). Instituto Nacional de Ecologia, México.

Bent, A.C. 1922. Life histories of North American petrels and pelicans and their allies. *United States National Museum Bulletin* 121.

Bent, A.C. 1938. Life histories of North American Birds of Prey (Part 2). *United States National Museum Bulletin* 170. 482 pp.

Bildstein, K.L., and K.D. Meyer. 2000. Sharp-shinned Hawk (*Accipter striatus*), version 2.0. In: A.F. Poole and F.B. Gill, eds., *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, NY, USA. (online: *https://birdsna.org/Species-Account/bna/home*)

Bryant, W.E. 1886. Cerros [*sic*] Island. *Forest and Stream* 27(4):62–64.

Bryant, W.E. 1887a. Additions to the ornithology of Guadalupe Island. *Bulletin of the California Academy of Sciences* 2:269–318.

Bryant, W.E. 1887b. Description of a new subspecies of petrel from Guadalupe Island. *Bulletin of the California Academy of Sciences* 2:450–451.

Bryant, W.E. 1889. A catalogue of the birds of Lower California, Mexico. *Proceedings of the California Academy of Sciences*, ser. 2, 2:237–320.

Davidson, M.E. McClellan. 1928. On the present status of the Guadalupe Petrel. *Condor* 30:355–356.

Dudley, W.R. 1899. Report on the Plants of Guadalupe Island. Pages 280–283 *in* D.S. Jordan, *The Fur Seal and Fur Seal Islands of the North Pacific Ocean*, Part 3. U.S. Government Printing Office, Washington, DC.

Dumbacher, J.P., and B. West. 2010. Collecting Galapagos and the Pacific: How Rollo Howard Beck Shaped Our Understanding of Evolution. *Proceedings of the California Academy of Sciences*, ser. 4, 61, Suppl. II, (13):211–243.

Dunlap, E. 1988. Laysan Albatross nesting on Guadalupe Island, Mexico. *American Birds* 42:180–181.

Gallo-Reynoso, J.P., and A.L. Figueroa-Carranza. 2009. Birds of Prey and the Band-tailed Pigeon on Isla Guadalupe, Mexico. *Western Birds* 40:278–283.

Francheschi, F. 1893. Notes on the flora of Guadalupe Island. *Zoe* 4:130–139.

Gaylord, H.A. 1897. Notes from Guadalupe Island. *Nidologist* 4:41–43.

Gordon, P.R. 1919. Filming the Sea Elephant. *The Wide World Magazine*, October, pp. 485–489.

Green, E.L. 1885. Studies in the botany of California and parts adjacent. *Bulletin of the California Academy of Sciences* 1:179–228.

Green, J.E., and L.W. Arnold. 1939. An unrecognized race of murrelet on the Pacific Coast of North America. *Condor* 41:25–29.

Greenway Jr., J.C. 1958. Extinct and Vanishing Birds of the World. *American Committee for International Wild Life Protection. Special Publication No. 13.* New York, New York. x + 518 pp. (Reprinted by Dover Publications in 1967).

Grinnell, J. 1928. A distributional summation of the ornithology of Lower California. *University of California Publications in Zoology* 32:l–300.

Hanna, G Dallas. 1925. Expedition to Guadalupe Island, Mexico in 1922. General Report. *Proceedings of the California Academy Scienc*es, ser. 4, 14:217–275.

Harris, C.M. 1909. A Cruise After Sea Elephants. *Pacific Monthly* Vol 21:331–339.

Howell, S.N.G., and S. Webb. 1992. Observations of birds from Isla Guadalupe, Mexico. *Euphonia* 1:1–6.

Howell, T.R., and T.J. Cade. 1954. The birds of Guadalupe Island in 1953. *Condor* 56:283–294.

Howell, T.R., and T.J. Cade. 1955. Additional Data on the Birds of Guadalupe Island. *Condor* 58:78.

Hubbs, C.L. 1960. The marine vertebrates of the outer coast. *Systematic Zoology* 9:134–147.

Huey, L.H. 1924. A trip to Guadalupe, the isle of my boyhood dreams. *Natural History* 24:578–588.

Huey, L.H. 1930. Past and present status of the northern elephant seal with a note on the Guadalupe fur seal. *Journal of Mammalogy* 11:188–194.

Huntington, C.E., R.G. Butler, and R. Mauck. 1996. Leach's Storm-Petrel (*Oceanodroma leucorhoa*), version 2.0. In: A.F. Poole and F.B. Gill, eds., *The Birds of North America*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. (online: *https://birdsna.org/Species-Account/bna/home*)

Jehl, Jr., J.R. 1972. On the cold trail of an extinct petrel. *Pacific Discovery* 26(6):24–29.

Jehl, Jr., J., and W.T. Everett. 1985. History and status of the avifauna of Isla Guadalupe, Mexico. *Transactions San Diego Society Natural History* 20:313–336.

Kaeding, H.B. 1905. Birds from the west coast of Lower California and adjacent islands. *Condor* 24:96–97.

Keitt, B., S. Junak, L. Mendoza, and A. Aguirre. 2005.The restoration of Guadalupe Island. *Fremontia* 33:20–25.

Kimball, H.H. 1922. Bird records from California, Arizona, and Guadalupe Island. *Condor* 24:96–97.

Luna-Mendoza, L.M., D.C. Barton, K.E. Lindquist, and R.W. Henry III. 2005. Historia de la avifauna anidante de Isla Guadalupe y las oportunidades actuals de conservación, Pages 115–133 *in* K. Santos del Prado and E. Peters, compliers, *Isla Guadalupe, Restauración y Conservación*. Instituto Nacional de Ecologia, México.

Mellink, E., and E. Palacios. 1990. Observations on Isla Guadalupe in November 1989. *Western Birds* 21:177–180.

Moran, R.V. 1996. The flora of Guadalupe Island, Mexico. *Memoirs California Academy of Sciences* 19([26 July]):1–190 pp.

Murphy, R.C. 1936. *Oceanic Birds of South America*. American Museum of Natural History, New York, New York, USA. 2 vol., xx + 1245pp.

Nelson, E.W. 1921. Lower California and its natural resources. *Memoirs National Academy of Sciences* Vol. 16, First Memoir, pp. 1–194.

Oberbauer T.A., C. Cibit, and E. Lichtwardt. 1989. Notes from Isla Guadalupe. *Western Birds* 20:89–90.

Pitelka, F.A. 1986. Rollo Beck – Old school collector, member of an endangered species. *American Birds* 40(3):385–387.

Pyle, P., K. Hanni, and D. Smith. 1994. Bird notes from Isla Guadalupe, including three new island records. *Euphonia* 3:1–4.

Quintana-Barrios, L., G. Ruiz-Campos, P. Unitt, and R.A. Erickson. 2006. Update on the birds of Isla Guadalupe, Baja California. *Western Birds* 37:23–36.

Richards, A.F., and B.H. Brattstrom. 1959. Bibliography, Cartography, Discovery, and Exploration of the Islas Revillagigedo. *Proceedings of the California Academy of Sciences*, ser. 4, 29(9):315–360.

Ridgeway, R. 1876. Ornithology of Guadeloupe [*sic*] Island, based on notes and collections made by Dr. Edward Palmer, *Bulletin of the United States Geological and Geographical Survey of the Territories* 2:183–195.

Ridgeway, R. 1877. The Birds of Guadalupe Island, Discussed with Reference to the Present Genesis of Species. *Bulletin Nuttall Ornithological Club* 2:58–66.

Rothschild, W., and E. Hartert. 1902. Further notes on the fauna of the Galapagos Islands. Notes on birds. *Novitates Zoologica* 9:381–418.

Swann, H.K. 1925–1936. *A Monograph of the Birds of Prey*. Wheldon and Wesley, London, UK.

Swarth, H.S. 1913. Note on the Guadalupe Caracara. *Condor* 15:228–229.

Sweet, P.R., G.E. Barrowclough, J.T Klicka, L. Montañez-Godoy, and P. Escalante-Pliego. 2001. Recolonization of the flicker and other notes from Isla Guadalupe, Mexico. *Western Birds* 32:71–80.

Taylor, H.R. 1895. Letters to Walter F. Webb. *Nidologist* 2(7):100 and 2(9):130.

Thayer, J.E., and O. Bangs. 1908. The present state of the ornis of Guadaloupe [*sic*] Island. *Condor* 10: 101–106.

Thoburn, W.W. 1899. The Birds of Guadalupe Island. Page 278 *in* D.S. Jordan, *The Fur Seals and Fur-seal Islands of the North Pacific Ocean*, Pt. 3. United States Government Printing Office, Washington, D.C.

Townsend, C.H. 1890. Birds from the coasts of western North American and adjacent islands collected in 1888–89, with descriptions of new species. *Proceedings of the United States National Museum* 13:131–142.

Townsend, C.H. 1908. Fur Seals and the Seal Fisheries. *Bulletin of the Bureau of Fisheries* 28:317–322.

Townsend, C.H. 1916. Voyage of the Albatross to the Gulf of California in 1911. *Bulletin American Museum of Natural History* 35:399–476.

Vasey, G. and J.N. Rose 1890. List of the plants collected by Dr. Edward Palmer in Lower California in 1889. *Contributions United States National Herbarium* 1:21–27.

von Berlepsch. H.G. 1906. On a new form of Oceanodroma inhabiting San Benito Island, off the coast of Lower California. *Auk* 13:185–186.

Wagner, H.R. 1968. *The Cartography of the Northwest Coast of America to the Year 1800* Vol. 1. [reprint of 1937 Berkeley Edition]. N. Israel, Amsterdam. 543pp.

Watson, S. 1876. Botanical contributions. *Proceedings of the American Academy of Arts and Sciences* 11:105–148.

Wetmore, A. 1933. A Skeleton of the Guadeloupe [*sic*] Caracara. *Condor* 35:206.

Appendix A. Transcription of Beck's Isla Guadalupe field notes, page 56 (see Fig. 4, p. 171 herein)

Several nuthatches heard
linnets & juncos feed just over ridge
out of wind & fog
Aug 3
To North End after much
digging found 2 young petrels
down on ~~adult~~ [sic] first feathers
yet one breast feathers
showing & tail show & others
not quite so far along opened lots of nests but
deserted probably late birds
these are heard Several calling
about camp last night
with strong wind on top of hill
but none here lit 2 fires
but none came about
Saw red tail or two 2 or 3 sparrow
hawks, got [illegible = immature?] bill
seems short as did bill of adult
saw couple ground owls [but]?
wild some juncos in fine
plumage but others molting
Saw 1 hummer, passed me
no cross bills but too much
fog perhaps ground soaked
to leeward of pines and oaks
was dripping where I found petrels
& ground wet and muddy on ridge
50 yds away nearly dry fog
pouring over ridge most of time

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The Sea Slug *Phanerophthalmus luteus* (Gastropoda: Opisthobranchia) and its Habitat and Ecology at the Marine Jellyfish Lake (Ongeim'l Tketau), Palau, Western Pacific Ocean

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Sea slugs (Order Cephalaspidea), assigned to *Phanerophthalmus luteus* (Quoy and Gaimard, 1833), occurred abundantly in 1994 in the shallow waters (< 10m) of Jellyfish Lake (Ongeim'l Tketau), Mecherchar Island (Eil Malk Island), Palau, western Pacific Ocean. Jellyfish Lake is in the lower part of a paleo-topographic hole formed in the Miocene reef limestone with steep slopes into the lake from the high part of the vegetated island. In Jellyfish Lake, *P. luteus* live between 3 and 10 m and are most abundant between 4.5 to 7.6 m. They are larger than many found elsewhere and they are more abundant as well, especially on the flatter parts of the lake bottom. The largest specimen was 55 mm long and 33 mm wide. Egg masses occurred attached to algae, logs, and rocks, but had a different distribution than the animals. The sea slugs occurred in lake habitats characterized by much organic debris from plants growing on the slopes above the lake and by benthic algae growing above 10 m in the lake. Egg masses of *P. luteus* also occurred in the lake in abundance. Neither the slugs nor their eggs were observed in surveys of the fringing reefs in the lagoon outside of the island. Although the lake has been characterized as stable, warming induced by El Niño events and previous warming 100 years ago indicate that *P. luteus* has either not been impacted or that it can recover from such events, just as the jellyfish *Mastigias* has done. *Phanerophthalmus luteus* is distributed in the central to western Pacific and Palau lies centrally within its biogeographic range.

Species of the sea slug *Phanerophthalmus* (Cephalaspidea, Haminoeidae) are distributed across the Indo-West Pacific, but little is known about their biology or ecology (Austin, Gosliner, and Malaquias 2018). One of the 17 known species, *P. luteus* occurs abundantly in Jellyfish Lake in the Republic of Palau, Western Caroline Islands in the western Pacific Ocean (see Patris et al. 2012 for an illustrated summary of Ongeim'l Tketau, as Jellyfish Lake is traditionally known, and its biota). During a survey of the opisthobranch gastropod fauna of Palau, we gathered data on sea slugs in the lake that had not been studied before, but which seemed of considerable interest to ecologists working in the lake. We observed the morphology, habitat, ecology and abundance of *P. luteus* in the lake and present those results here.

Palau Archipelago

The Rock Islands

Jellyfish Lake, known locally as Ongeim'l Tketau, is located in an area of raised Miocene reefs on Mecherchar Island (formerly referred to as Eil Malk Island), one of the southern Rock Islands

of the Palau Archipelago (Fig. 1). Mecherchar Island (Fig. 2) lies at 134°21′45″E and 7°9′15″N and is one of 700 islands that constitute the Palau Archipelago (Colin, 2009). Palau, the Rock Islands, Mecherchar Island, and Jellyfish Lake have complex geologic histories involving subduction of the Pacific Tectonic Plate, volcanism, the tectonic rising and sinking of the islands, climate and oceanographic changes, and rising and falling sea levels during the Pleistocene; much of this activity is still underway today (summarized by Dickinson and Athens 2007; Kelletat 1991). The Rock Islands are raised, heavily karstic Miocene limestones containing many marine lakes (Hamner and Hamner 1998). The present islands and lakes formed at least 8,000 years ago as sea level rose from its low, last-glacial extreme of 120 m below current sea level and flooded the karst topography. Because of their unique and unusual dissolved and eroded forms including numerous lakes and islands covered in lush green plants, the Rock Islands were designated a World Heritage Site in 2012. The Rock Islands are managed and maintained by the Koror State Government and the Koror State Department of Conservation and Law Enforcement.

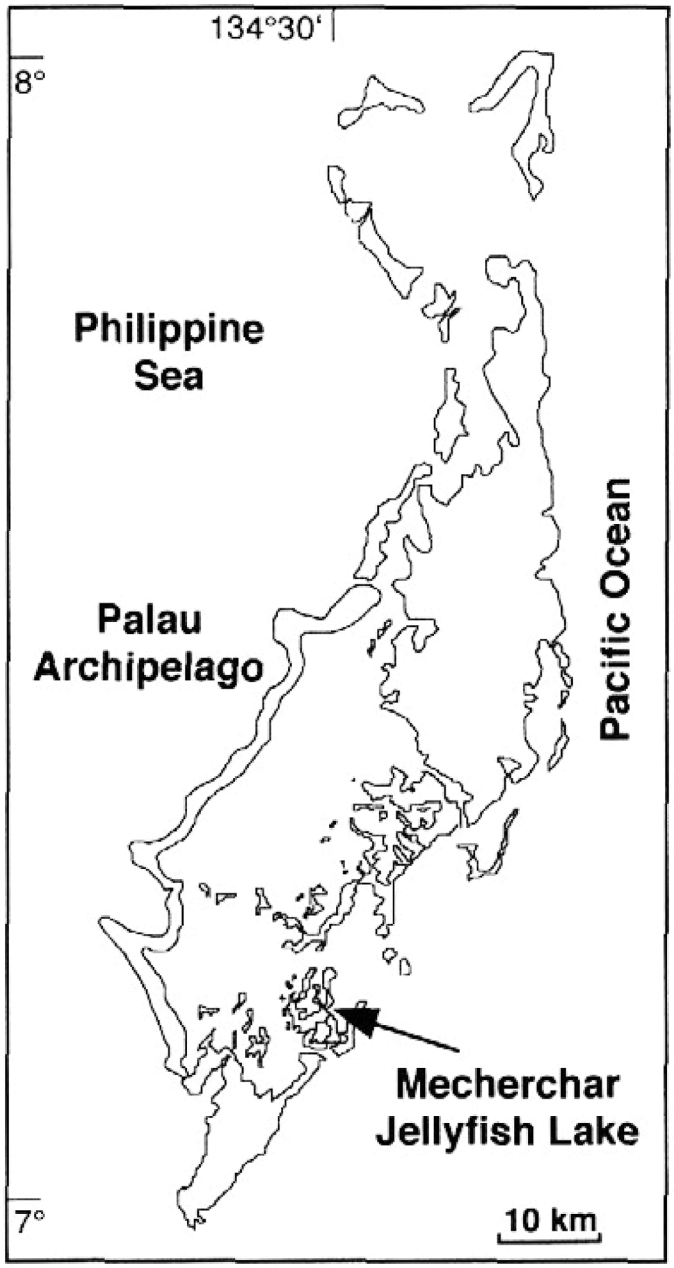

FIGURE 1. The Palau Islands showing the location of Mecherchar Island and Jellyfish Lake.

Among the Rock Islands are a number of remarkable bodies of marine water, like Jellyfish Lake, more or less cut off from the sea. These marine lakes are connected in various degrees and ways to the lagoonal ocean waters with very restricted ocean flows whereas others have large openings to the ocean which control the nature of their biota. Those with more open connections have biotas more like the lagoon whereas the relatively isolated marine lakes are inhabited by lower diversity biotas with high numbers of organisms per

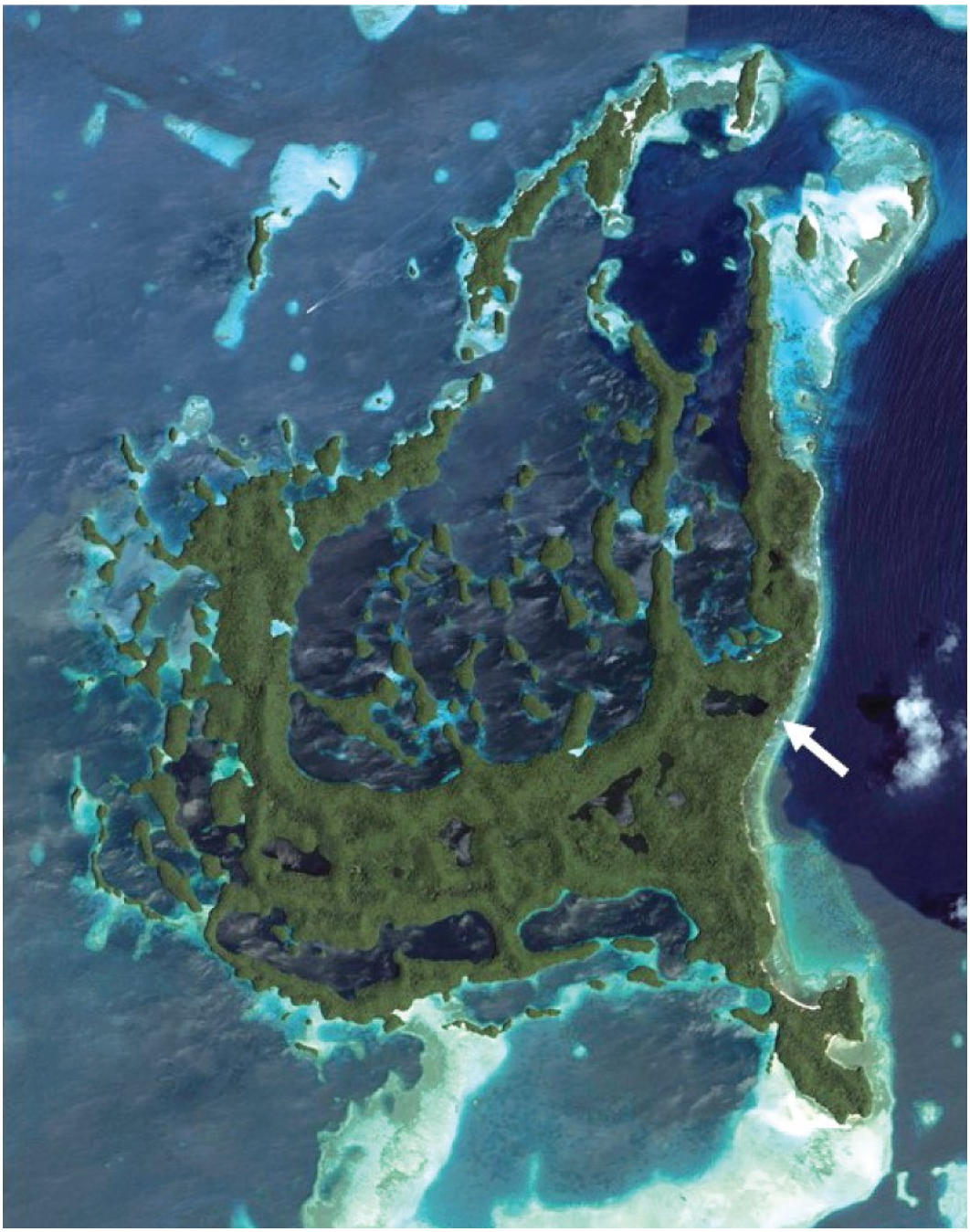

FIGURE 2. Aerial photograph of Mecherchar Island. The island is formed of uplifted Miocene limestone, with multiple lakes, including Jellyfish Lake indicated by the white arrow on the mid-right of the image. The lakes are surrounded by vegetation (green) while fringing reefs in the shallow waters surround the island (white to light blue), representing different marine habitats. *P. luteus* lives abundantly in Jellyfish Lake but was not observed on the reefs outside the island. Aerial photograph courtesy of Dr. Pat Colin.

species, and commonly harsh physical conditions (Hamner and Hamner 1996). These lakes are inhabited by most peculiar but different assemblages of organisms (Hamner and Hauri 1981; Hamner, Gilmer, and Hamner 1982; Fautin and Fitt 1991; Venkateswaran et al. 1993; Lipps and Langer 1999; Dawson, Martin, and Penland 2001; Colin 2009; Patris et al. 2012; Meyerhof et al. 2016) at least some of which are genetically distinct from populations outside the Lake, in other lakes and in the open ocean (Dawson and Hamner 2005a, 2005b). These small ecosystems provide ideal conditions for basic research in ecology and evolution. Each lake has a unique assemblage of organisms derived from the adjacent sea. The ease of study of large numbers of these organisms also presents attractive research opportunities.

Jellyfish Lake

The Lake (Fig. 3A, 4) is set in a paleotopographic hole more than ~ 230 m deep from its rim at the top of Mecherchar Island to its bottom at least 30 m below sea level (Patris et al. 2012). Its steep slopes are heavily-vegetated (Canfield 1981; Cole et al. 1987) with the dead trees and debris (Fig. 3), particularly mangroves, as the major source of organic matter making its way into the lake (Orem et al. 1991; Lyons et al. 1996). The Lake is younger than about 8,000 years as flooding of the Rock Islands by the sea level rise that started about 20,000 years ago following the last Pleistocene glaciation. It is completely closed to the open ocean just outside the island, and is connect-

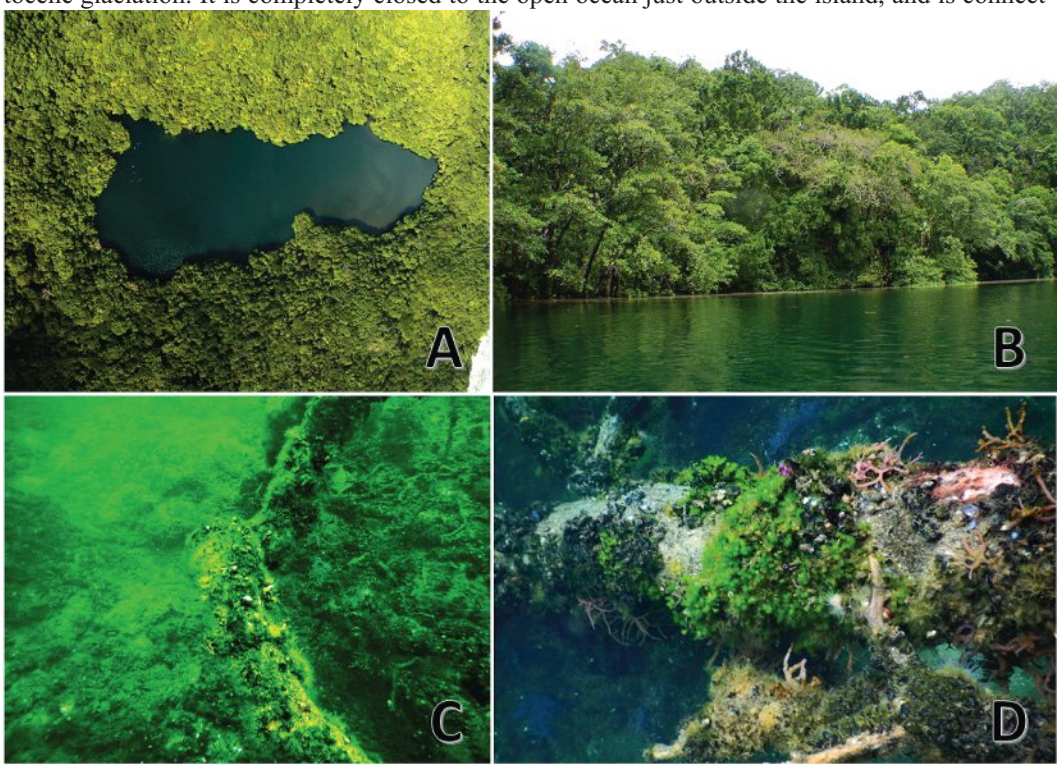

FIGURE 3. Vegetation of Jellyfish Lake, Mecherchar Island. A. The lake, slightly less than 400 m long, is in a hole at least 230 m deep (150 to 200 m from the top of the hole to the Lake's surface and 30 m to the bottom of the lake) in the Miocene limestone. North is at the top of the image. B. Dense terrestrial vegetation, including mangroves at the lake edges, hangs over the lake. The surrounding vegetation contributes organic debris to the lake. C. Bottom of the lake from 0 to 13 m is covered with plant debris and algal growth. Photograph is at 2 m deep looking down slope. D. One of many logs that have fallen into the lake and are now inhabited by a wide variety of algae and animals including *P. luteus*. View is down the log from a depth of about 0.5 m. Credits: A. Aerial photograph courtesy of Dr. Pat Colin. B.-D. Photographs by Jere H. Lipps, 2013.

ed to the sea only by several cracks and fissures through which sea water is tidally exchanged. It contains large numbers of schyphozoans (Golden Jellyfish *Mastigias papua etpisoni* with far fewer *Aurelia* in 1994) estimated at 7.1 ± 1.4 million jellyfish for all size classes and 2.6 ± 0.5 million for those larger than one cm (Cimino et al. 2018), although these were decimated by warming associated with the El Niño event of 1997-1999 (Dawson, Martin, and Penland 2001; Martin et al. 2006; Bruno et al. 2001; Patris et al. 2012). Although by 2012, *Mastigias* recovered in numbers, *Aurelia* did not (Patris et al. 2012).

The lake became famous because of the huge number of jellyfish (Hamner 1982), and it is one of the most popular tourist attractions in the archipelago. From our count of visitors in 1994, we estimated that approximately 30,000 persons snorkeled in the lake that year, but far more (~ 50,000) do so more recently (Colin, 2009). Fortunately, these visits are mostly quite brief, are limited to one corner of the lake from which visitors swim to deeper depths over which they can see the jellyfish (Lipps, personal observation, 2013). Such visitors seem not to have had much impact yet on the biota (Dawson, Martin, and Penland 2001; Patris et al. 2012), and certainly not on *P. luteus*, which lives among the algae and plant debris in the shallow nearshore parts of the lake.

The lake is stratified with the waters above about 13 m well

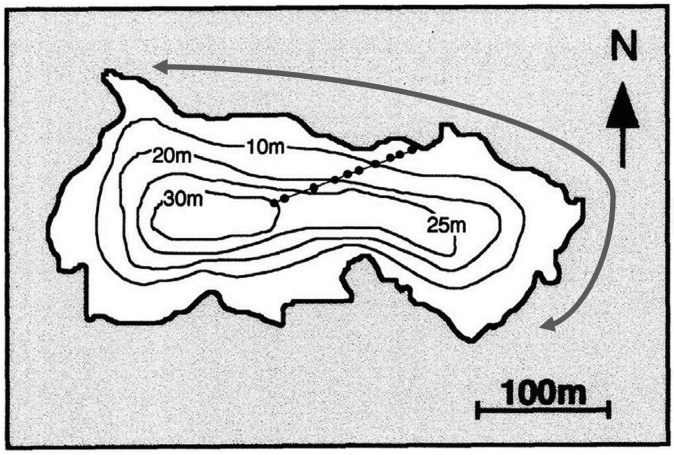

FIGURE 4. Bathymetry of Jellyfish Lake, Mecherchar Island. The gray line with arrows indicates the area in the lake of our marine survey to 10 m deep for sea slugs along the north and east sides of the lake. Black circles indicate the transect and collecting stations for foraminifera used to estimate the depth distribution of *Phanerophthalmus luteus.* Map and transect from Lipps and Langer 1999.

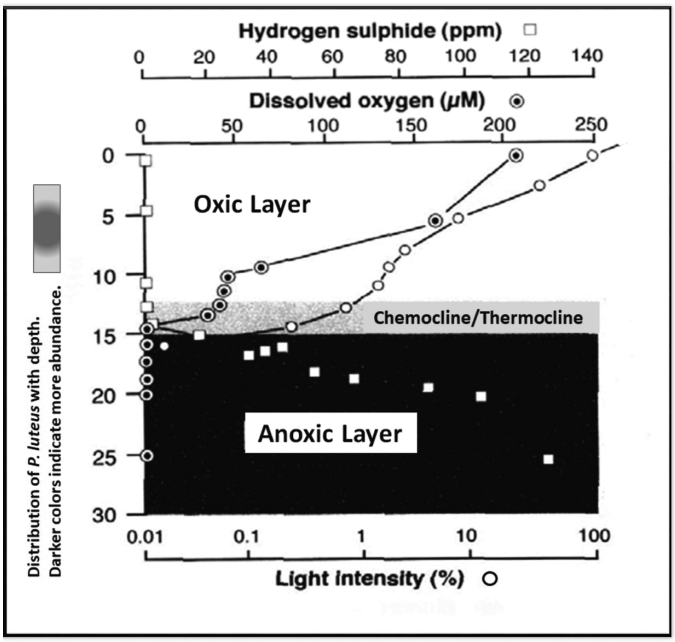

FIGURE 5. Hydrography of Jellyfish Lake. The water column is divided into an oxic and an anoxic zone by a bacterial plate that creates a chemo- and thermocline. The bacteria absorb all the light and digest most of the vegetation (except larger branches). No foraminifera or animals are known to live below the bacterial plate due to the absence of oxygen in the water column. *Phanerophthalmus luteus* is restricted to the upper 3 to 10 m in the oxygenated part of the water column; they are most abundant between 4.5 and 7.6 m. Figure modified from Venkateswaran et al. (1993) by adding the depth distribution of *P. luteus*.

lighted and oxic (Fig. 5), and with normal marine salinity and temperatures (Hamner, Gilmer, and Hamner 1982). Mangroves surrounding the lake shore (Fig. 3B) grow into the water to depths of 2 m (Lipps and Langer 1999). Separating the oxic layer from deeper water is a plate of floating sulfur bacteria about 1 m thick that absorbs all light and digests most organic material falling into it. Below that, the lake is dark and anoxic with high sulfide content in the water and sediment, and uninhabited by metazoans or foraminifera (Hamner, Gilmer, and Hamner 1982; Lipps and Langer 1999).

Methods

On 13 February 1994, we undertook a visual survey of the lake by swimming along the east and north shores in water depths of 0 to 10 m (Fig. 4). In August 2013, Lipps swam along the same track to search for *Phanerophthalmus luteus*. The slugs were quite inconspicuous and hard to find at first. Continued searching under and on logs and algae growing on the bottom revealed both the animals and their egg masses. The distributions of both the animals and the egg masses were recorded in notes. We also swam transects on reefs in the open lagoon adjacent to Mecherchar Island and north and west of Jellyfish Lake.

The size of *P. luteus* is rather difficult to estimate since they are very flexible and flabby (Fig. 6). Therefore, we determined the volume of the animals, and this was done by dropping them into

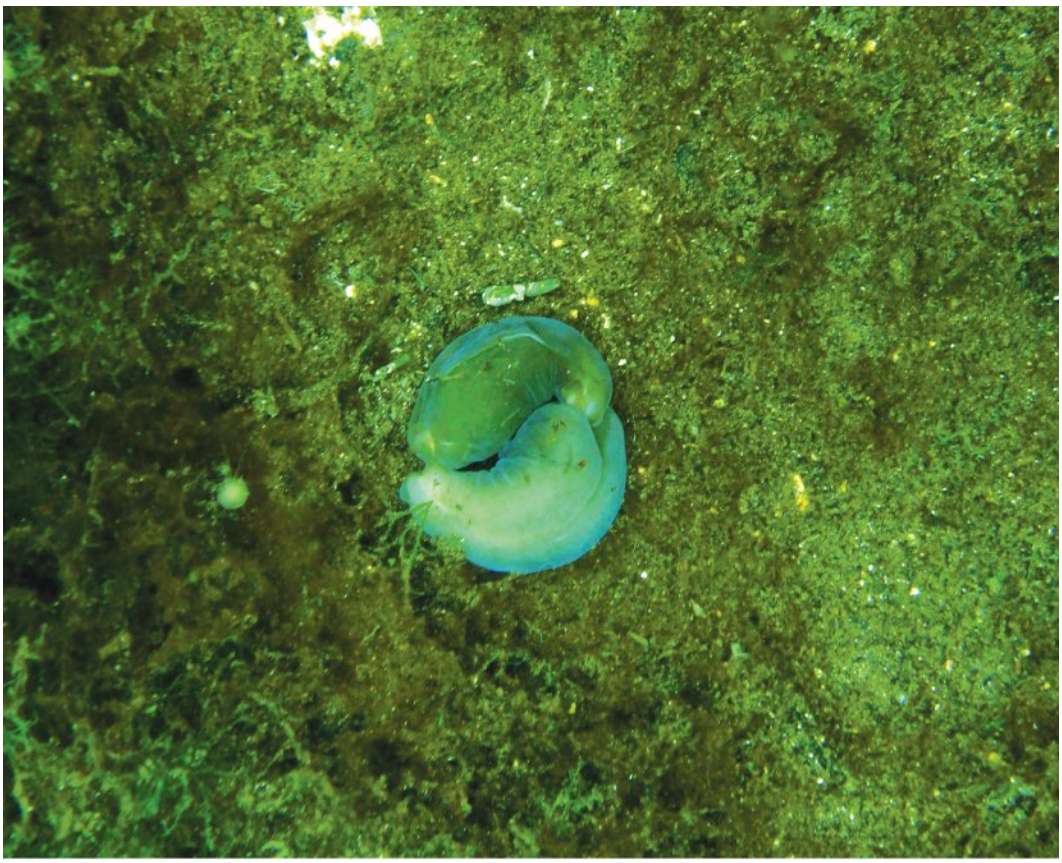

Figure 6. Two *Phanerophthalmus luteus* mating on the bottom of Jellyfish Lake among algae attached to sediment (August 15, 2013). The specimens display the usual whitish to green to greenish blue colors of specimens in Jellyfish Lake. Image by Dr. Michael Dawson.

TABLE 1. Volume (ml) of individuals of *P. luteus* measured in Jellyfish Lake in February 1994.

Specimen Volume (ml)		
2.4	4.8	6.8
3.1	4.9	6.8
3.1	5.0	6.8
3.2	5.1	6.9
3.4	5.2	7.5
3.5	5.4	7.6
3.7	5.6	8.0
3.8	5.8	9.6
4.3	5.9	10.0
4.3	5.9	10.9
4.3	6.0	
4.4	6.1	Average = 5.6
4.4	6.3	Median = 5.3
4.4,	6.7	Mode = 4.3
4.8	6.7	St. Dev. = 1.83

TABLE 2. Longest dimension (mm) of egg masses of *P. luteus* measured in Jellyfish Lake in February 1994.

Greatest Dimension of Egg Masses (mm)		
21	32	41
22	33	42
22	33	42
22	33	
27	37	Average = 32.9
27	37	Median = 33
28	38	Mode = 22
30	38	St. Dev. = 6.30
31	38	
31	41	

a graduated cylinder and measuring the amount of water displaced. Egg masses were measured with a scale while they were in the water so that no deformation of them could happen due to handling.

Results

The sea slug *Phanerophthalmus luteus* was not found above 3 m or below 10 m, and were most abundant at 4.5 to 7.6 m in Jellyfish Lake (Fig. 5). They were considerably more abundant in the eastern part of the lake (Fig. 4) where the bottom is flatter and presumably is a more suitable habitat, but no slugs were found near the entrance to the lake. No slugs were found on steep slopes or on mangrove roots in the water. They commonly occurred as single individuals, pairs, or aggregations of up to dozen animals under the edges of logs or masses of green algae (Fig. 6). In August 2013, fewer slugs were present in the algae. The slugs we found were whitish to green or greenish blue. The volumes of 38 animals ranged from 2.4 to 10.9 ml (Table 1). The largest of these had a length of 55 mm and a width of 33 mm. The sample may not be representative of the population as a whole because the animals were examined in the field where smaller ones were more difficult to find.

Egg masses of *P. luteus* occurred among the animals themselves and on algae along the sides of the lake in February 1994 but no egg clumps were observed in August 2013. In some places, the egg masses and slugs did not co-occur. The masses were rather oblong and attached to solid surfaces, including rocks, logs, green algae and other plants (Fig. 7). Twenty-three egg masses found in a group measured in the longest direction ranged in size from 21 to 42 mm, with an average of 32.9 mm and median of 33 mm (Table 2). Densities of egg masses on three 50 cm sections of an

Figure 7. Egg masses (more or less spherical to oblong white objects) of *Phanerophthalmus luteus* attached to filamentous and other algae on a slope in Jellyfish Lake. Photograph taken November 16, 2009, courtesy of Lori J. Bell.

approximately 10 cm diameter log were 7, 16 and 17; on green algae three 50 by 50 cm quadrats contained 62, 44, and 37 masses. The shallowest egg mass was found at 0.6 m, the deepest at 6 m. Egg masses were not abundant above 3 m. Below 6 m the bottom was soft and provided little material that might be a place for the slugs to attach their egg masses. Very few egg masses were found near the entrance to the lake on the northeast part of the lake. Like the slugs, no egg masses were seen on steep cliffs or on mangrove roots. They occur only on level to gently sloping bottoms where they can be attached to algae and other solid substrates. The egg masses in February 1994 contained developing embryos.

We found no slugs or egg masses in the open ocean surrounding Mecherchar Island. There, fringing and patch reefs are abundant (Fig. 2). We surveyed a number of those in the lagoon for slugs and egg masses and found none.

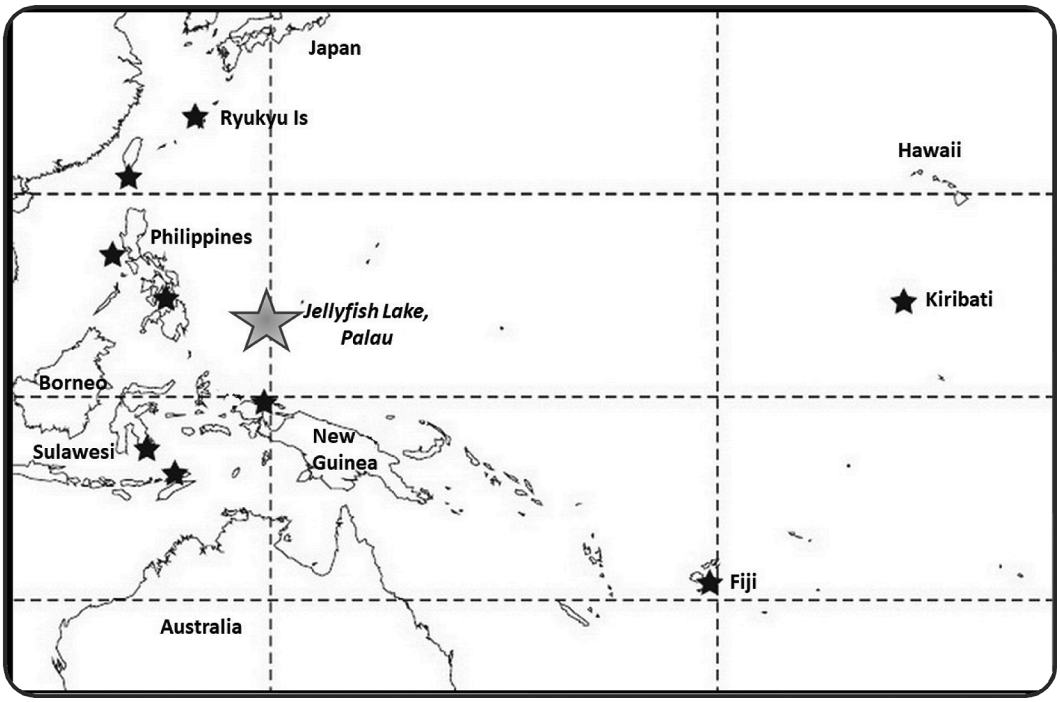

FIGURE 8. Central and Western Pacific showing the distribution of *Phanerophthalmus luteus* (black stars) and the location of Jellyfish Lake, Palau (large gray star). Modified from distribution map for *P. luteus* in Austin, Gosliner, and Malaquias (2018, fig. 23).

DISCUSSION

Morphology and Systematics of *P. luteus*

The animals of interest are sea slugs of the order Cephalaspidea, assigned by us to *Phanerophthalmus luteus* (Quoy and Gaimard, 1833). Originally, we assigned our specimens to *P. smaragdinus* (Ruppell and Leuckart 1831), as did others (Patris et al. 2012), but in a recent revision of species of *Phanerophthalmus*, Austin, Gosliner, and Malaquias (2018) did not recognize *P. smaragdinus*, putting it in synonymy with several other species. Using their criteria, our specimens are most similar to *P. luteus*. We base this determination on the facts that the animals are generally green, greenish white or greenish blue, the shell is partly exposed by the mantle cavity, and *P. luteus*'s known distribution embraces Palau. The other species that biogeographically overlap in

the western Pacific are distinctly different and not similar to *P. luteus.* Other morphologic and genetic details of this species are given in Rudman (1972) and Austin, Gosliner, and Malaquias (2018).

In Jellyfish Lake, the slugs were of unusually large size. The largest specimen in Jellyfish Lake was 55 mm long and 33 mm wide which is among the largest individual of any species in the genus. The slugs at Jellyfish Lake were clearly larger and more abundant than in open ocean situations elsewhere in the Indo-Pacific. This is a common feature of organisms found in these restrictive and isolated marine lakes. We also know of one well-documented case of opisthobranchs sometimes attaining unusually large size when they occur outside of their ordinary habitat, the anaspidean *Phyllaplysia taylori* Dall, 1900 (Beeman 1970). In northern California and elsewhere in the Oregonian province, these *P. taylori* are common and well camouflaged on the sea-grass *Zostera marina*. They feed upon diatoms and other organisms that live on the plants. Animals kept in outdoor tanks at the Hopkins Marine Station flourished off of the sea-grass. They attained a much larger size than those from nearby Elkhorn slough (respectively a maximum weight of 15.03 g and 1.6 g). Why *P. luteus* should attain larger size in unusual habitats is unknown but may be related to food supply, as implicated by the Hopkins study, or by a reduction of predation on mid- or larger sized animals. Certainly, the habitats of *P. luteus* in Jellyfish Lake are richer in organic materials, algae, phytodetritus, and periphyton growing on the substrates along with the slugs. Like *Mastigias papua etpisoni, P. luteus* could also show genetic differences once they are analyzed from other occurrences of this species in the central and western Pacific Ocean.

Egg Masses

In Jellyfish Lake, *P. luteus* lays very abundant egg masses attached to algae (Fig. 7) or other substrates at particular times during the year. The difference in daylight distribution of the egg masses and the animals themselves could mean that the animals move toward shallower water or stay hidden during the day. Our study, done in the middle of the day when the animals were found under algae, logs or the edges of rocks, indicates that the animals likely emerge from hiding at night when they then deposit the egg masses. The egg masses of *P. luteus* differed from those of *P. perpallidus* from Bali and *P. purpura* from Maui which were much smaller, 12 mm and 22 mm, had a somewhat different shape and color (Austin, Gosliner, and Malaquias 2018, fig. 29). The egg masses of opisthobranchs, however, quite generally take up water with time, hence their size is not very informative. Further study of *Phanerophthalmus* eggs is warranted.

Biogeography

The genus *Phanerophthalmus* is distributed from the east coast of South Africa, Kenya, Reunion Island, and Madagascar, across the Indian Ocean to the Seychelles and Lakshadweep, Nicobar and Andaman Islands and through Papua New Guinea, New Caledonia, the Philippines, to Palau, Guam, Hawaii, and Japan (Kay 1979; Colin and Arneson 1995; Gosliner, Behrens, and Valdés 2008; Apte 2009; Sreeraj, Sivaperuman, and Raghunathan 2012a, 2012b; Narayana and Mohanraju 2013; Kiruba-Sankar et al. 2016; Yonow and Jensen 2018; Austin, Gosliner, and Malaquias 2018). It likely occurs more widely in the Indo-Pacific but its species are rarely reported animals. The various species have different biogeographic ranges (Austin, Gosliner, and Malaquias 2018).

The occurrence of *P. luteus* at Jellyfish Lake is well within the known biogeographic range of the species (Fig. 8) in the central and western Pacific Ocean (Austin, Gosliner, and Malaquias 2018, fig 23). The *P. luteus* in Jellyfish Lake are generally larger and more abundant than those found elsewhere in its biogeographic range. This is likely due to more abundant food, fewer pred-

ators, less seasonal change and quieter waters inside the lake. The reefs in the lagoon have, however, quite different habitats than those found within Jellyfish Lake. The reefs are in open ocean settings without large organic inputs, less benthic algae, variable temperatures, and generally rougher water while the mangrove-associated habitats in the lake had much organic matter and debris and lower oxygen content not found outside the enclosed lakes.

Habitat and Ecology

In general, *P. luteus* seems to occur in water shallower than 10 m across its biogeographic area including in rocky intertidal, coral rubble, back reef, organic-rich mangrove and algal habitats. That description fits well with the Jellyfish Lake occurrence where mangroves hang over the water and the sediments are rich in organic matter that falls into the lake (Fig. 3). The foraminifera from the lake are a fauna that that is typically associated with mangroves elsewhere in the Pacific (Langer and Lipps 2003, 2006; Lipps and Langer 1999). Indeed, these mangrove faunas are consistent across most ocean basins and hence provide excellent markers for sea level and tidal changes (Horton et. al 2005).

Species of *Phanerophthalmus* were assumed to be herbivorous (Rudman 1972) on algae, although only one species *P. luteus* of several examined had food in their guts (Austin, Gosliner, and Malaquias 2018, fig. 28). That specimen had several species of centric and pennate diatoms in its gut. Diatoms, both benthic and the planktonic *Chaetoceros affinis*, occur in abundance in Jellyfish Lake (Hamner, Gilmer, and Hamner 1982; Hara et al. 2002; Konno et al. 2010). *P. luteus* likely consumes both types of diatoms, the benthic ones as part of the periphyton on substrates where it lives and the planktonic kinds after they settled to the algae or sediment on the bottom. Periphyton is abundant on logs, smaller plant debris, on algae but less so on muddy substrata.

Jellyfish Lake, usually considered ecologically stable, has experienced changes in temperature, salinity and other factors due to El Niño events (Dawson, Martin, and Penland 2001; Martin et al. 2006; Patris et al. 2012), and longer-term sea level and climate changes (Dickinson and Athens 2007). During the 1997–1999 El Niño, the Golden Jellyfish *Mastigias papua etpisoni* containing symbionts in their tissues declined to low numbers from a population in the millions and the Moon Jelly *Aurelia* was completely extirpated from the lake and did not recover (Patris et al. 2012). On a longer time of ~ 100 years ago, a core taken at 10 m depth in Jellyfish Lake showed a change from older carbonate to the present siliceous sediment and also in the benthic foraminiferal biota during the "Little Ice Age" time (Kawagata 2005). Over 1000s of years, sea level has risen first at 4000 years ago higher than present sea level but then retreating to the present level at least by 2000 years ago. These events indicate that the lake is a dynamic place over times longer than what ecologists have been able to study that likely impacted populations of animals, including *P. luteus,* plants and microbes.

Conclusions

The marine slug *Phanerophthalmus luteus* occurs in the restricted marine Jellyfish Lake (Ongeim'l Tketau), Mecherchar Island, Palau, well within the known biogeographic range of the species in the central and western Pacific Ocean. However, the population in the lake is denser and the animals are larger than open ocean occurrences, probably because of a limited lake biota that may lack predators, of the organic-rich habitat that provides more food, and of the quieter conditions in the lake. The animals were most abundant between 4.5–7.6 m depths although they were seen as isolated specimens as shallow as 3.0 m. The slugs lay egg masses that are attached to firm substrata or algae on the shallow lake floor. The eggs are found most abundantly in the same depth

range with the exception of several found at 0.3 m. These distributions indicate that *P. luteus* may occasionally move to shallower water to lay their eggs, although most are laid where the slugs are most abundant too. The slugs prefer to live near or under the abundant sunken logs and plant debris or filamentous algal mats on nearly level bottoms. Neither animals nor eggs occur on steep slopes or on mangrove roots. Individuals and egg masses of *P. luteus* were not found in the fringing and patch reefs in the open lagoon bordering Mecherchar Island.

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References

Apte, D. 2009. Opisthobranch fauna of Lakshadweep Islands, India, with 52 new records to Lakshadweep and 40 new records to India: Part 1. *Journal of the Bombay Natural History Society* 106(2):162–175.

Austin, J., T. Gosliner, and M.A.E. Malaquias. 2018. Systematic revision, diversity patterns and trophic ecology of the tropical Indo-West Pacific sea slug genus *Phanerophthalmus* A. Adams, 1850 (Cephalaspidea, Haminoeidae). *Invertebrate Systematics* 32(6):1336–1387.

Beeman, R.D. 1970. An ecological study of *Phyllaplysia taylori* Dall, 1900 Gastropoda: Opisthobranchia with an emphasis on its reproduction. *Vie et Milieu Série A*: *Biologie Marine* 21(1-A):189–212.

Bruno, J.F., C.E. Siddon, J.D. Witman, P.L. Colin, and M.A. Toscano. 2001. El Niño related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* 20:127–136. doi:10.1007/s003380100151.

Canfield, J.E. 1981. Palau: diversity and status of the native vegetation of a unique Pacific island ecosystem. *Newsletter of the Hawaiian Botanical Society* 1981:41–49.

Cimino, M.A., S. Patris, G. Ucharm, L.J. Bell, and E. Terrill. 2018. Jellyfish distribution and abundance in relation to the physical habitat of Jellyfish Lake, Palau. *Journal of Tropical Ecology* 34(1):17–31. doi**:** 10.1017/S0266467418000044.

Cole, T.G., M.C. Falanruw, C.D. MacLean, C.D. Whitesell, and A.H. Ambacher. 1987. *Vegetation survey of the Republic of Palau*. Resource Bulletin PSW-22. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. Berkeley, CA: University of California Press, Berkeley, California, USA. 13 pp.

Colin, P. L. 2009. *Marine Environments of Palau*. Indo-Pacific Press, San Diego, California, USA. 414 pp.

Colin, P. L., and C. Arneson. 1995. *Tropical Pacific Invertebrates*. Coral Reef Press, Beverly Hills, California, USA. 296 pp.

Dawson, M.N., and W.M. Hamner. 2005a. Rapid evolutionary radiation of marine zooplankton in peripheral environments. *Proceedings of the National Academy of Sciences of the USA* 102:9235–9240.

Dawson, M.N., and W.M. Hamner. 2005b. A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. *Journal of the Royal Society Interface* 5:35–150.

Dawson, M.N., L.E. Martin, and L.K. Penland. 2001. Jellyfish swarms, tourists, and the Christ-child. *Hydrobiologia* 451:131–144.

Dickinson, W.R., and J.S. Athens. 2007. Holocene paleoshoreline and paleoenvironmental history of Palau: Implications for human settlement, *The Journal of Island and Coastal Archaeology* 2(2):175–196. doi: 10.1080/15564890701623639.

Fautin, D.G., and W.K. Fitt. 1991. A jellyfish-eating sea-anemone (Cnidaria, Actiniaria) from Palau – *Entacmaea medusivora* sp. nov. *Hydrobiologia* 216:453–461. doi:10.1007/BF00026499.

Gosliner, T.M., D.W. Behrens, and A. Valdés. 2008. *Indo-Pacific Nudibranchs and Sea Slugs: A Field Guide to the World's Most Diverse Fauna*. California Academy of Sciences, San Francisco, California, USA. 426 pp.

Hamner, W.M. 1982. Strange world of Palau's salt lakes. *National Geographic* 161:264–282.

Hamner, W.M., R.W. Gilmer, and P.P. Hamner. 1982. The physical, chemical and biological characteristics of a stratified, saline, sulfide lake in Palau. *Limnology and Oceanography* 27:896–909.

Hamner, W.M., and P.P. Hamner. 1998. Stratified marine lakes of Palau (Western Caroline Islands). *Physical Geography* 19(3):175–220. doi:10.1080/02723646.1998.10642647.

Hamner, W.M., and I.R. Hauri. 1981. Long-distance horizontal migrations of zooplankton (Scyphomedusae: *Mastigias*). *Limnology and Oceanography* 26:414–423.

Hara, Y., T. Horiguchi, N. Hanzawa, K. Ishida, A. Yokoyama, R. Hoshina, H. Kudoh, A. Ochi, and M. Konno. 2002. The phylogeny of marine microalgae from Palau's marine lakes. *Kaiyo Monthly* 29:19–26 [in Japanese].

Horton, B.P., J.E. Whittaker, K.H. Thomson, M.I.J. Hardbattle, A. Kemp, S.A. Woodroffe, and M.R. Wright. 2005. The development of a modern foraminiferal data set for sea-level reconstructions, Wakatobi Marine National Park, southeast Sulawesi, Indonesia. *Journal of Foraminiferal Research* 35:1–14.

Kawagata, S., M. Yamasaki, R. Genka,and R.W. Jordan. 2005. Shallow-water benthic foraminifers from Mecherchar Jellyfish Lake (Ongerul Tketau Uet), Palau. *Micronesica* 37(2):215–233.

Kay, E.A. [1979]. *Hawaiian Marine Shells*. Bishop Museum Press, Honolulu, Hawaii. xvii+652 pp.

Kelletat, D. 1991. Main trends of Palau Islands' coastal evolution, identified by air and ground truthing. *GeoJournal* 24:77–85.

Kiruba-Sankar, R., T. Immanuel, M.P. Goutham-Bharathi, and S. Dam Roy. 2016. Additions to the opisthobranch fauna of Nicobar group of islands, India. *Indian Journal of Geo-Marine Sciences* 45(2):319–322.

Konno, S., N. Inoue, D.U. Hernández-Becerril, and R.W. Jordan. 2010. *Chaetoceros affinis* blooms in a Palauan meromictic marine lake. *Vie et Milieu* 60(3):257–264.

Langer, M.R., and J.H. Lipps. 2003. Foraminiferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. *Coral Reefs* 22:143–154.

Langer, M.R., and J.H. Lipps. 2006. Assembly and persistence of foraminifera in introduced mangroves on Moorea, French Polynesia. *Micropaleontology* 52:343–355.

Lipps, J.H., and M.R. Langer. 1999. Benthic foraminifera from the meromictic Mecherchar Jellyfish Lake, Palau (western Pacific). *Micropaleontology* 45:278–284.

Lyons, W.B., R.M. Lent, W.C. Burnett, P. Chin, W.M. Landing, W.H. Orem, and J.M. McArthur. 1996. Jellyfish Lake, Palau: Regeneration of C, N, Si, and P in anoxic marine lake sediments. *Limnology and Oceanography* 41:1394–1403.

Malaquias, M.A.E., J. Mackenzie-Dodds, P. Bouchet, T. Gosliner, and D.G. Reid. 2009. A molecular phylogeny of the Cephalaspidea *sensu lato* (Gastropoda: Euthyneura): Architectibranchia redefined and Runcinacea reinstated. *Zoologica Scripta* 38:23–41.

Martin, L.E., M.N. Dawson, L.J. Bell, and P.L. Colin. 2006. Marine lake ecosystem dynamics illustrate ENSO variation in the tropical western Pacific. *Biology Letters* 2:144–147.

Meyerhof, M.S., J.M. Wilson, M.N. Dawson, and J.M. Beman. 2016. Microbial community diversity, struc-

ture and assembly across oxygen gradients in meromictic marine lakes, Palau. *Environmental Microbiology* 18(12):4907–4919. doi:10.1111/1462–2920.13416.

Narayana, S., and R. Mohanraju. 2013. New record of a headshield slug *Phanerophthalmus smaragdinus* (Gastropoda: Opisthobranchia) from Andaman Islands, India. *Journal of Threatened Taxa* 5(7): 4113–4114.

Orem, W.H., W.C. Burnett, W.M. Landing, W.B. Lyons, and W. Showers. 1991. Jellyfish Lake, Palau: Early diagenesis of organic matter in sediments of an anoxic marine lake. *Limnology and Oceanography* 36:526–543.

Patris, S.W., M.N. Dawson, L.J. Bell, L.E. Martin, P.L. Colin, and G. Ucharm. 2012. *Ongeim'l Tketau: Jellyfish Lake*. Coral Reef Research Foundation and Etpison Museum, Palau. 44 pp.

Rudman, W.B. 1972. The herbivorous opisthobranch genera *Phanerophthalmus* A. Adams and *Smaragdinella* A. Adams. *Proceedings of the Malacological Society of London* 40:189–210.

Sreeraj, C.R., C. Sivaperuman, and C. Raghunathan. 2012a. An annotated checklist of opisthobranch fauna (Gastropoda: Opisthobranchia) of the Nicobar Islands, India. *Journal of Threatened Taxa* 4(4): 2499–2509. doi.org/10.11609/JoTT.o2783.2499-509.

Sreeraj, C.R., C. Sivaperuman, and C. Raghunathan. 2012b. Report on ten newly recorded opisthobranchs (Opisthobranchia, Gastropoda) from Andaman and Nicobar Islands, India. *International Journal of Oceanography and Marine Ecological System* 1(2):50–59. ISSN 2224–249x / doi: 10.3923/.ijomes.2012.50.59.

Venkateswaran, K., A. Shimada, A. Maruyama, T. Hjgashlhara, H. Sakou, and T. Maruyama. 1993. Microbial characteristics of Palau Jellyfish Lake. *Canadian Journal of Microbiology* 39:506–512.

Yonow, N., and K.R. Jensen. 2018. Results of the Rumphius Biohistorical Expedition to Ambon (1990). Part 17. The Cephalaspidea, Anaspidea, Pleurobranchida, and Sacoglossa (Mollusca: Gastropoda: Heterobranchia). *Archiv für Molluskenkunde* 147(1):1–48.

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