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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 152 : ARTICLE 6 NEW YORK : 1973

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 152, article 6, pages 365–440, figures 1–12, tables 1–25, maps 1–8

Issued December 31, 1973

Price: $3.50 a copy

This article completes Volume 152

Printed in Great Britain by Lund Humphries

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ABSTRACT

SMITTINIDAE (BRYOZOA, ECTOPROCTA) from Hawaiian waters are compared with related species from the Galapagos Islands, Gulf of California, central and southern California in the eastern Pacific. Twenty-eight taxa are recognized, as follows: *Hemismittoidea corallinea*, new genus, new species; *H. osburni*, new species; *Pleurocodonellina lahainae*, new genus, new species; *Smittoidea pacifica*, new species; *Smittina kukuiula*, new species; one species of *Codonellina* and 22 species of *Parasmittina*, 15 of which are new. Scanning electron microscopy revealed many morphological and developmental details distinguishing the species and higher taxa. Distribution records in Hawaiian waters show isolation not only at the specific level from the Indo-Pacific and coastal eastern Pacific but also inter-island isolation due to unknown environmental factors.

INTRODUCTION

THE BRYOZOAN FAMILY SMITTINIDAE is well represented in the Hawaiian Islands, primarily by a complex of species of the genus *Parasmittina*. It appears to be one of the most successful groups of bryozoans found there in shallower waters, both in numbers of individuals and in numbers of species. The genus *Smittina* is represented only by a single specimen. The *Smittoidea* are represented by a single new species, but a new genus allied to it is described as *Hemismittoidea*. Another new genus, similar to *Codonellina*, is described as *Pleurocodonellina*.

Collections were made from 92 stations at various locations on the five major Hawaiian Islands, between 1966 and 1970. Methods included skin and Scuba diving, settling plate exposure, and boat or dock scrapings; samples from coral reefs were taken with hammer and chisel by divers. Specimens were air dried, and some fragments were Cloroxed for cleaning; membranes were not dissolved completely thus retaining opercula and avicularian mandibles where possible. Most photography is by scanning electron microscopy (SEM), using a JELCO instrument, at 25 kilovolts accelerating voltage. Gold-coating of 300 Å thickness was done with a vacuum evaporator, model JEE–4B.

ACKNOWLEDGMENTS

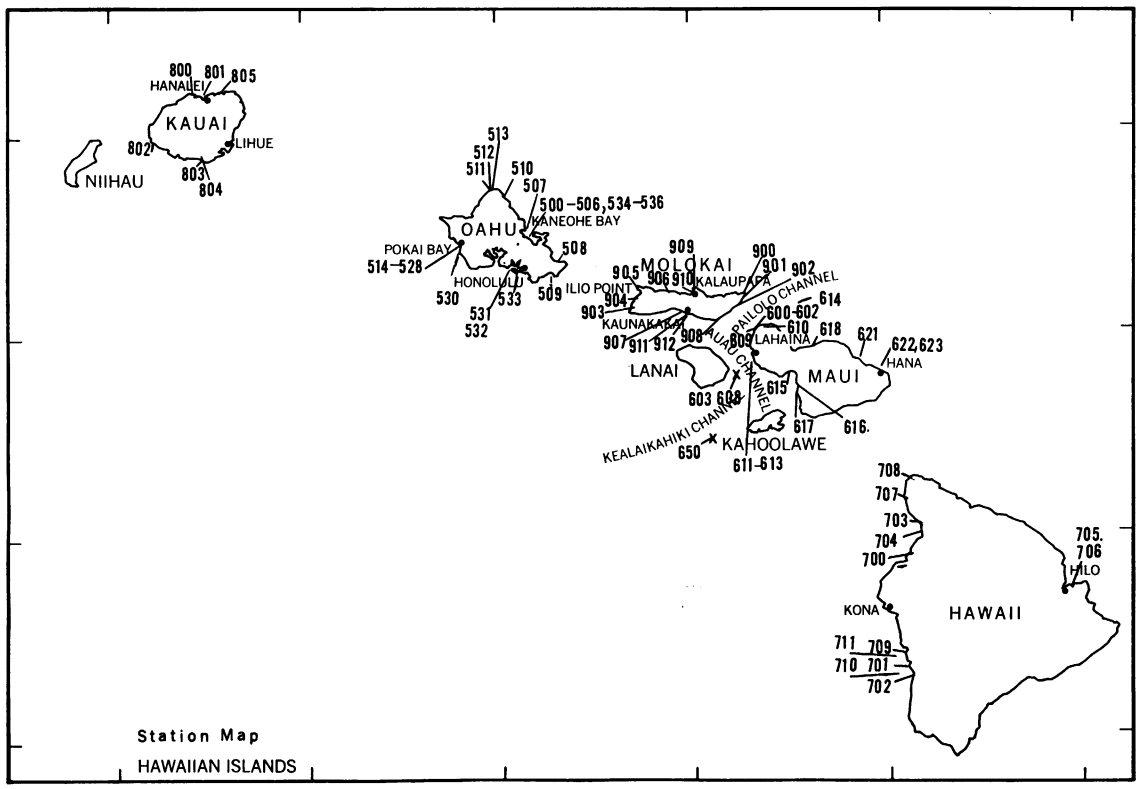
Field collecting in Hawaii was supported in part by National Science Foundation grants GB5208 and GB7723, as were studies at the National Museum of Natural History, Smithsonian Institution, the British Museum (Natural History), the Zoologisch Museum, Amsterdam, and the Allan Hancock Foundation.

Appreciation is expressed in particular to Miss Patricia L. Cook of the British Museum (Natural History) for her assistance during our studies there of the *Siboga*, *Challenger*, and other tropical collections, and for other helpful discussions with her and with Dr. Anna B. Hastings. In Amsterdam, Dr. S. vanderSpoel gave valuable assistance. At the National Museum of Natural History Drs. Alan Cheetham and Richard Boardman were most cooperative in making the *Albatross* and other collections available for examination. Dr. William K. Emerson, of the American Museum of Natural History, lent a previously unidentified collection made in Hawaii by the late A. E. Verrill. Collections from the Bernice P. Bishop Museum, Honolulu, were lent by Drs. Lucius Eldredge and Dennis Devaney. The late Vernon Brock donated some specimens.

Cooperation during field work from Drs. Sidney Townsley, Phillip Helfrich, and John Maciolek of the University of Hawaii is greatly appreciated. Extensive diving was done by Drs. James McVey, Stanley Swerdloff, and Richard Wass, and by Messrs. Bob Nishimoto, Greg Stanton, and Maurice Renaud, then students at the University of Hawaii.

Scanning electron microscopy was done through the courtesy of Dr. Henry Lee, of the Lee Pharmaceuticals, South El Monte, California, with Mr. Malcolm Kateley serving as technician.

Mr. Alan Banner, who collected at Mokumanu Island, was lost while diving off Western Samoa in April, 1972; a special word of appreciation is extended herewith to his parents, Dr. and Mrs. A. H. Banner of the University of Hawaii.



MAP 1. Collecting stations.

ABBREVIATIONS

AHF, Allan Hancock Foundation
AMNH, the American Museum of Natural History
BMNH, British Museum (Natural History)
BPBM, Bernice P. Bishop Museum, Collection Numbers, 100–400 series
JELCO, Japan Electronics Company (scanning instrument)
P–000, Puritan-American Museum Expedition station numbers, Baja California; J. Soule, collector
SEM, Scanning electron Microscopy
S-000-67, Soule station number, 500–900, followed by last digits of year collected
UH, University of Hawaii
USNM, National Museum of Natural History, Smithsonian Institution

SOULE HAWAIIAN EXPEDITION STATION LIST

OAHU

Coconut Island, Kaneohe Bay, lee side raft, steel plates suspended on rope

S-500a-66. July 27, 1966, 4.6 m., 82°F. water temperature.

S-500b-66. July 27, 1966, 7.6 m., 79°F.

Coconut Island, University of Hawaii Marine Station docks

S-501-66. July 27, 1966.

S-502-66. Aug. 1, 1966.

Coconut Island, University of Hawaii floating docks 0–1.0 m.

S-503-67. Aug. 2, 1967.

S-504-67. Aug. 10, 1967.

Coconut Island, glass slide rack suspended from raft

S-505a-66. July 27–Aug. 30, 1966, exposure, 3 m.

S-505b-66. July 27–Aug. 30, 1966, exposure, 6 m.

Sampan Channel, buoy no. 25, reef NE of Coconut Island, James McVey, diver.

S-506-66. July 27, 1966, 3–8 m.

Mokumanu Island, Alan Banner, collector.

S-507-66. Aug. 21, 1966, 25 m.

SW of Black Rock Island, Mason Lee and Rick Scholenberger, divers.

S-508-66. July 31, 1966.

Kahana, Bay, SE side, J. McVey and Dick Wass, divers.

S-509-66. July 30, 1966.

Hauula Beach, McVey and Wass, divers.

S-510-66. July 30, 1966.

Pupukea Beach, off lava shelf, McVey and Wass, divers.

S-511-66. July 30, 1966, 5–8 m., rock bottom.

Pupukea Beach, McVey, Wass, and Bob Nishimoto, divers.

S-512-67. Aug. 28, 1967, 5 m., coral off lava shelf.

S-513-67. Aug. 28, 1967, 14 m., coral bottom.

Pokai Bay, Waianae, artificial reef

S-514-67. July 9, 1967, 21 m., McVey, diver.

S-515-67. July 11, 1967, 21 m., McVey and Stan Swerdloff, divers.

S-516-67. July 13, 1967, 15–16 m., McVey and Swerdloff, divers.

N of Pokai Bay, 1/2-mile offshore of pillbox

S-517-67. July 26, 1967, 8 m., McVey, diver.

Pokai Bay artificial reef, McVey and group

S-518-67. Aug. 1, 1967, 8 m.

S-519-67. Aug. 7, 1967, 26 m.

S-520-67. Aug. 8, 1967, 8 m.

S-521-67. Aug. 4, 1967, 8 m.

S-522-67. July 6, 1967, 21 m.

S-523-68. Rack down Mar. 7, 1968, taken up Apr. 10, 1968. On pipe; coral and lava beach, loose rubble bottom.

S-524-67. July 8, 1967, 8 m.

S-525-68. Aug. 3, 1968, 23 m.

S-526-68. Sept. 3, 1968, 14 m., McVey and G. Stanton, divers.

S-527-68. Sept. 6, 1968, 26 m.

S-528-68. Dec. 3, 1967–Jan. 20, 1968, settling rack 14–15 m.

Maili Point

S-530-66. Aug. 28, 1966, 9–12 m., coral and sand, McVey and Wass, divers.

AlaWai Yacht Harbor, AlaWai Marine, Ltd. boat works, scrapings from local houseboats

S-531-67. June 27, 1967.

S-532-67. June 7, 1967.

Off Waikiki, Kapiolani Park, 0.5 mile, McVey, Stanton, and John Maciolek assisting

S-533-67. Aug. 6, 1967, 15 m., sand and rock bottom.

Coconut Island, Kaneohe Bay

S-534-67. Aug. 7, 1967, floating docks.

S-535-68. Sept. 4, 1968, floating docks.

S-536-68. Sept. 10, 1968, plankton sample.

MAUI

Napili Bay, McVey and Wass, divers.

S-600-66. Aug. 5, 1966, 3 m., 78°F., rock and coral bottom.

S-601-66. Aug. 6, 1966, 3 m., 78°F.

S-602-66. Aug. 7, 1966, 6–8 m., coral reef.

AuAu Channel black coral beds between Lahaina, Maui, and Lanai Island; Bryozoans collected from harvested coral

S-603-66. Aug. 7, 1966, 46 m., Mike King and John Lawson, divers, of Skindiving-Hawaii, Inc.

S-604-65. Aug. 26, 1965, 52 m., Bob Agee, diver, of Maui Divers, Inc.

S-605-67. Aug. 11, 1967, 53 m., King and Lawson, divers.

S-606-67. Aug. 17, 1967, 48–52 m., King and Lawson, divers.

S-607-66. Aug. 6, 1966, 46 m., King and Lawson, divers.

S-608-66. Aug. 10, 1966, 46 m., King and

Lawson, divers.

Pohakupule Beach

S-609-66. Aug. 6, 1966, 6 m., rock and sand, McVey and Wass, divers.

Honolua Beach

S-610-66. Aug. 6, 1966, 12–15 m., 79°F., McVey and Wass, divers.

Mala Wharf

S-611-66. Aug. 7, 1966, 3 m., rock bottom, McVey and Wass, divers.

S-612-66. Aug. 7, 1966, 11 m., at end of pier, McVey and Wass, divers.

Off Lahaina Pier 0.5 mile

S-613-66. Aug. 7, 1966, 12–15 m., coral patches, rubble and sand. Glassbottom boat courtesy of Chris Rose; McVey, Wass, Ray Croteau, divers.

Oneloa Beach near Honokahua

S-614-66. Aug. 7, 1966, 8 m., 79°F., McVey and Wass, divers.

NW Maalaea Bay

S-615a-67. Aug. 12, 1967, 5 m., near Kapoli Park on SW coast between Papawai Pt. and Maalaea. Lava rock and good coral ledge, rubble bottom. *Porites compressa*, *Pocillopora meandrina*, and *Montipora verrucosa*; McVey and Stanton, divers.

S-615b-67. Aug. 12, 1967, 9 m., same location.

SE of Maalaea Bay, N of Makena

S-616-67. Aug. 12, 1967, 5–6 m., 79°F., *Montipora* present. McVey and Stanton, divers.

Keawakapu Village, SE shore

S-617-67. Aug. 12, 1967, 5 m., 79°F., McVey and Stanton, divers.

E of Paia, N coast

S-618-67. Aug. 12, 1967, 5 m., 80°F., loose rock, flat rock; purple *Montipora*; water cloudy. McVey and Stanton, divers.

Okumehame Gulch, 2 miles E of Olowalu

S-619-67. Aug. 12, 1967, 11 m., sand patches, coral fingers, *Porites*. McVey and Stanton, divers.

Keanae Peninsula, N coast

S-621-67. Aug. 13, 1967, 5–6 m., 79°F., on lava flow, heavy surge. *Porites compressa*, *P. lobata*, *Montipora*. McVey and Stanton, divers.

Hana Bay

S-622-67. Aug. 13, 1967, 6–8 m., 79°F. *Montipora* on concrete pier pilings. McVey and Stanton, divers.

S-623-67. Aug. 13, 1967, 3–5 m., on pier pilings.

Kealaikahiki Channel

S-650-67. Nov. 11, 1967, 110 m., between Maui and Kahoolawe Islands. Stan Swerdloff, collector. Trawl hit coral on uncharted seamount.

HAWAII

Puako, S Kohala District

S-700-66. Aug. 15, 1966, 5 m., 81°F., Bob Nishimoto, diver.

Honaunau, Kona coast, N side of bay

S-701-66. Aug. 14, 1966, 3 m., 80°F., rock, dead and live coral. Nishimoto, diver.

Hookena, Kona coast

S-702-66. Aug. 14, 1966, 3–5 m., 80°F., rock, dead and live coral. Nishimoto, diver.

Kawaihae Bay, N of bridge, Mahukona Rd.

S-703-66. Aug. 15, 1966, 4–5 m., 80°F., *Porites*. Nishimoto, diver.

Kawaihae, Spencer Beach Park

S-704-66. Aug. 15, 1966, 6 m., Nishimoto, diver.

Hilo-Keaukaha

S-705-67. July 15, 1967, 8 m., McVey and Swerdloff, divers.

S-706-67. July 15, 1967, 14 m., raining, freshwater surface lens, 76°F.; 8 m., 81°F., *Montipora*. McVey and Swerdloff, divers.

Mahukona Beach Park

S-707-67. July 16, 1967, 12–14 m., 82°F., rich live coral, bryozoans sparse. McVey and Swerdloff, divers.

Honoipu-LORAN Station, 2.5 miles W of Hawi turnoff

S-708-67. July 16, 1967, 7–9 m., strong current. McVey and Swerdloff, divers.

Off Cook's Monument, Kona coast

S-709-68. Aug. 6, 1968, 12–26 m., McVey, collector.

Off City of Refuge, Honaunau

S-710-68. Aug. 6, 1968, 15–18 m., McVey, collector.

Off Cook's Monument, Kealakekua Bay

S-711-68. Aug. 6, 1968, 34 m., McVey, collector.

KAUAI

Haena Bay, Haena Pt.

S-800-67. July 1, 1967, 6 m., 76°F. at surface, colder at edge of coral reef circling bay entrance. McVey and Swerdloff, divers.

Naue, Lumahai Bay, between Lumahai River and Waipa River, W of YMCA camp

S-801-67. July 1, 1967, 6–9 m., 80°F., strong surge zone, growth sparse. McVey and Swerdloff, divers.

Barking Sands Beach, W coast

S-802-67. July 2, 1967, 6–9 m., 79°F., sand aggregate and lava bench, coral offshore; water clear, calm. McVey and Swerdloff, divers.

Off Kukuiula Harbor breakwater, S coast
S-803-67. July 3, 1967, 13–16 m., 77°F., surf heavy, raining, water clear; harbor very muddy. McVey and Swerdloff, divers.
S-804-67. July 3, 1967, 5 m., 81°F., clear. McVey and Swerdloff, divers.

Kalihiwai, N coast
S-805-67. July 3, 1967, 12–15 m., *Lithothamnion*, *Montipora*, discoid bryozoans only. McVey and Swerdloff, divers.

MOLOKAI

Halawa Bay, SE coast
S-900-66. Aug. 19, 1966, 3–5 m., rock boulders. McVey and Wass, divers.

Pukuoluu below Puuohoku (Murphy's Ranch)
S-901-66. Aug. 19, 1966, 5 m., rock and *Porites*. McVey and Wass, divers.

N of Waialua
S-902a-66. Aug. 19, 1966, 5 m., coral. McVey and Wass, divers.
S-902b-66. Aug. 19, 1966, 2 m., rock and coral.

Kakaako Gulch, S of Kepuhi
S-903-66. Aug. 20, 1966, 4–6 m., 79°F., McVey and Wass, divers.

Papohaku Beach (sand dunes)
S-904-66. Aug. 21, 1966.

Ilio Pt., W side, abandoned LORAN station
S-905-66. Aug. 21, 1966, 9–12 m., McVey and Wass, divers.

Moomomi, N coast
S-906-66. Aug. 21, 1966, 8 m., rubble bottom, visibility poor. McVey and Wass, divers.

Kaunakakai, offshore reef, 1 mile W of Harbor Wharf, 0.5 mile offshore
S-907-67. Aug. 19, 1967, 14 m. Bill Van Heukelin of Oceanic Institute, McVey, and Maurice Renaud, divers.

NE of Pukuoluu (Pukoo?)
S-908-67. Aug. 19, 1967, 6–12 m., McVey, Renaud, Van Heukelin, divers.

W side Makanalua peninsula (Kalaupapa)
S-909-67. Aug. 20, 1967, McVey and Renaud, divers.

N edge Kalaupapa Harbor, N coast
S-910-67. Aug. 20, 1967, 6 m., McVey and Renaud, divers.

Kaunakakai offshore reef, 1 mile E of wharf, 0.5 mile offshore
S-911-67. Aug. 19, 1967, 14 m., Van Heukelin, McVey, and Renaud, divers.
S-912-67. Aug. 19, 1967, 2 m., Van Heukelin, McVey, and Renaud, divers.

SYSTEMATIC ACCOUNTS

ORDER CHEILOSTOMATA

SUBORDER ASCOPHORA

FAMILY SMITTINIDAE LEVINSEN, 1909

THE GENERA of the Smittinidae, as revised by Osburn (1952), constitute a varied assemblage of species which usually, but not always, have a median denticle (lyrula). The various combinations of perforate and imperforate frontals and ovicells, and the positions of the suboral and frontal avicularia, serve to separate the genera. It seems possible that not all the genera included by Osburn belong in the same family, but his separations have improved the characterizations of the species involved.

Osburn limited the *Smittina* and *Codonellina* to species having a porous frontal ("tremocyst"); *Parasmittina*, *Smittoidea*, *Rhamphostomella*, *Cystisella*, *Hemicyclopora*, *Alismittina*, and *Porella* are now characterized by having an imperforate frontal ("pleurocyst"), usually with marginal pores ("areolae"). Although this separation is distinctive, there is a considerable parallelism in form between perforate and imperforate species.

The genus *Smittina* Norman, 1903 (*Smittia* Hincks, 1879 preoccupied) is now limited to species with a perforate frontal, perforate ovicells, and a median suboral avicularium. The genus *Smittoidea* Osburn also has median suboral avicularia and perforate ovicells, but the frontal is imperforate. *Parasmittina* was described by Osburn as having a pleurocyst frontal, with a row of marginal areolar pores and in some cases with additional pores, with a lyrula (denticle) and cardelles (hinge teeth) usually well developed, and with ovicells perforated with one to many pores. Avicularia are usually present, distributed variously, but never median, suboral; they originate from areolar pores on one side or the other.

Previously published records on smittinids from Hawaii include only *Parasmittina marsupialis*

(Busk), 1884; *P. delicatula* (Busk), 1884; *P. areolata* (Canu and Bassler), 1927; and *Codonellina anatina* (Canu and Bassler), 1927. Osburn also listed *Smittoidea reticulata* (MacGillivray), 1842 as occurring in Hawaii.

The species previously described from Hawaii were again found by the present investigators, as were a number of new or previously unrecognized species. The *Challenger* and *Albatross* collections from Hawaii were very limited in scope and mostly taken from deeper water.

We saw evidence suggesting both island isolation and ecological separation, which apparently accounts for the degree of speciation. Although it has not been our wish to perform extensive splitting, examination of the numerous undamaged specimens collected by hand has given a much greater appreciation of the less obvious differences that are pointed out herein. More than 1000 specimens of smittinids have been mounted and sorted during this work, and the new species described are generally well represented in numbers of specimens. Comparisons were also made with specimens from the eastern Pacific and the Galapagos Islands, resulting in some taxonomic revisions of species previously reported from those regions.

Of particular importance has been our observations of the association between bryozoans and the coral reef ecology, which has in the past received little notice. Bryozoans are among the first macrofauna to colonize on pocilloporid and montiporid corals, settling on the surfaces between polyp cups. Discoid colonies are often observed in such locations.

In the colony areas where the older, dying, or dead polyps are found, incrusting bryozoans compete with filamentous green algae, colonial tunicates, and sponges for available substrate. As these colonies develop, the corals are in turn colonized on the surfaces by hydroids, polychaetes, crustaceans, and small mollusks and sponges until the bases are riddled with the channels of larger invertebrates. However, the multilaminar incrustations of the bryozoans seem to aid in retaining the surface integrity of the corals, in competition with the eroding biota. Thus they may contribute to reef stabilization to a greater degree than might be expected in proportion to their biomass. The bryozoans are often among the most prominent biota in terms of available surface occupied.

HEMISMITTOIDEA, NEW GENUS

DIAGNOSIS: Zooecia with imperforate frontal and distinct areolar pores; apertures rounded with 2–6 spines, peristome low, median denticle and distinct sinus present. One avicularium present in median position and confluent or adjacent to sinus arising from one distal pore and median peristomal pore. Ovicells with a row of larger pores distally and scattered smaller pores centrally, or scattered large pores.

TYPE SPECIES: *Hemismittoidea corallinea*, new species.

Hemismittoidea corallinea, new species

Figure 1A–D

DIAGNOSIS: Colonies forming multilaminar crust on corals and on treelike bases of black coral. Zooecia elongate, rounded distally, with raised granular frontal. Single or double row of small areolar pores present, plus one or more small pores at base of avicularian chamber. Aperture rounded, with six spines in young zooecia; peristome low with distinct, U-shaped sinus. Peristome rim becoming thickened, beaded, little raised. Single median, or almost median avicularium present, with triangular mandible. Denticle quite wide, anvil-shaped, and deep set. Cardelles strong, hooked proximally; operculum inserting below denticle, rising above cardelles and slanting upward to distal rim. Distal walls slanting forward also. Ovicells small, immersed, with few small pores centrally and large overgrown pores around distal rim.

ETYMOLOGY: Named on the basis of the common association of the species with corals.

HOLOTYPE: AHF Bryozoan no. 159.

PARATYPE: BPBM K442.

TYPE LOCALITY: S-513-67, Pupukea, Oahu, at 11–12 m., coral bottom.

DISTRIBUTION: Kaneohe Bay, Oahu: S-500a-66, S-500b-66, S-506-66, S-507-66; western Oahu: S-513-67; S-515-67, S-516-67, S-517-67, S-520-67, S-522-67, S-527-68, S-530-66. On Maui, S-601-66, S-607-66, S-608-66, S-610-66, S-611-66, S-612-66, S-613-66, S-618-67, S-619-67, S-621-67, S-622-67. On Molokai, S-907-67, S-911-67 (rare); Hawaii, S-703-66, S-705-67, S-706-67, S-708-67 (rare). BM401, Hauula, Oahu. Total, 134 specimens.

DESCRIPTION: Colonies are white, yellowish, or greenish forming unilaminar or rarely multilaminar crusts on true corals or on the bases of

black coral trees. Some colonies are discoid, with raised edges, usually forming thin crusts. Zooecia are small, elongate, quadrate, or pentagonal, and fairly regular in arrangement. The distal wall is curved and slants forward from the basal wall. The frontal is somewhat raised and granular; increasing calcification makes it shiny and rugose. The aperture is rounded and bears six spines. The peristome is at first a thin collar, little raised, but becomes thickened and beaded. The sinus is distinct, a large U-shape, with a single avicularium situated at the proximal edge (fig. 1A, B). The avicularium appears to be median in position, directed proximally or skewed slightly, as in the genus *Smittoidea*. However, the avicularium arises as a chamber at the base of the peristome on one side, connected to a distal areolar pore next to the peristome. It extends around the base of the peristome to the sinus, and the rostrum and the mandible arise at the edge of the sinus, directed almost at right angles to the orientation of the developing chamber (fig. 1D). In the *Smittoidea* the suboral avicularium arises from a chamber connected on both sides to distal pores, extending around the entire proximal portion of the peristome. Examination of the type species of *Smittoidea prolifica*, as well as part of *S. reticulata* (MacGillivray) of Osburn (1952) and his *S. transversa* (Busk) shows that the bilateral chamber is typical of *Smittoidea*, in the Hancock collections, and hence the unilateral chamber of *H. corallinea* differs from that genus.

The avicularium rostral chamber opens into the sinus through a pore above the denticle. The rostral sides are elevated, with fine serrations, and the hinge bar is strong, with a short, stout center ligula. The mandible is a wide triangle, with heavy marginal sclerites and two internal sclerites near the tip. Avicularia are never paired, as they are in parasmittinids.

The operculum is arched distally, and nearly straight proximally, with a reinforcing marginal sclerite rim around the distal and lateral portions. In older zooecia the sclerites are quite heavy and the operculum is dark orange. The denticle is very wide, with flaring tips (anvil shaped), and deeply set, sloping downward. The paired cardelles (hinge teeth that articulate with the operculum) are strong, and hooked proximally. The operculum is inserted above the cardelle tips and under the denticle, but it slopes upward to the distal margin of the primary aperture, paralleling the slope of the distal wall.

The ancestrula is ovoid-hexagonal, and budding distally produces two zooecia that are oriented almost at right angles to each other. Subsequent buds originate from the lateral walls as well as two distal walls. The origin of the body walls does not follow the rectangular pattern commonly seen in parasmittinids, in which longitudinal folds rise in the basal wall several zooecial lengths in advance, and transverse walls arise one or two lengths distally. In *H. corallinea*, such a pattern is rarely seen. More usual is the extension of folds at an angle from the sides of the zooecia at the level of the first spines, and also in some cases, from the center of the distal wall curve (from the three distal corners of the hexagon, or pentagon).

Lateral walls bear a row of small pores lying between buttresses arched above the basal wall. The lower lateral wall is thinner than the upper part, which has a palisade appearance from the calcification of the frontal around the areolae, and it bears a few additional lateral pores. Distal walls of the alternating zooecia are similar to the lateral walls, but there are also large basal pores or channels at the lower corners. In the few zooecia that are rectangular, distal walls have three or four pores across the lower portion, plus larger basal corner pores, and a few tiny pores scattered in the rest of the wall.

In developing zooecia, the primary calcified frontal grows in an arc from the proximal margins, while the peristome begins to form at the distal edge. Lateral growth of the lower portions of the rims of the peristome form the paired cardelles, and the upper portions grow toward the median proximal edge of the aperture where they turn in to form the lateral portions of the wide denticle. The growing frontal fills in between the two tips to form the central part of the denticle. The secondary layer of frontal calcification is laid down before the avicularium rostrum is formed, so that the rostral cavity is easily seen (fig. 1D).

Ovicells are formed at the growing edge of the colony as soon as the primary calcified frontal layer is completed on the proximal end of the next distal zooecia. The ovicell hood has six to eight large pores around the distal portion, plus scattered tiny pores centrally, but all seem to be covered over rapidly. Secondary calcification proceeds on both the distal zooecium and the ovicell hood at about the same time (fig. 1B).

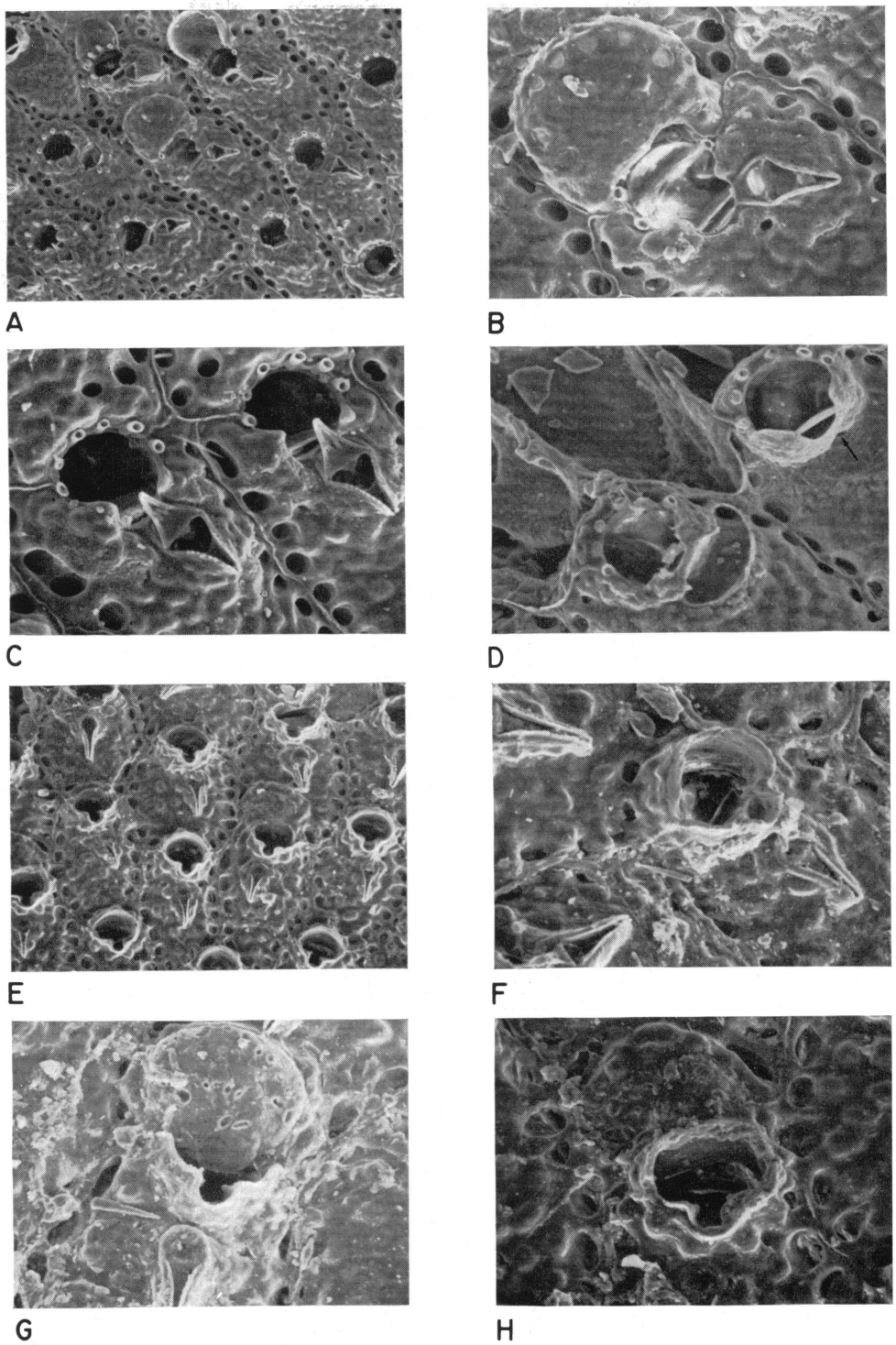


FIG. 1. A–D. *Hemismittoidea corallinea*, new species. See description for measurements of actual size. A. Growing edge of colony with developing ovicells. B. Mature ovicell with closed pores, avicularium skewed to side. C. Apertures with spine scars, open avicularia. Note that a portion of the aperture is distal to the transverse wall line. D. Developing avicularian chamber connected to sinus pore (arrow) opening above denticle and areolar pore. Note extending lateral wall folds in colony growth. Spicules from *Thalamoporella* lie across areolar pores. E–H. *Smittoidea pacifica*, new species. E. Colony, with median avicularia. F. Tubular peristome with channeled sinus groove, wide denticle. G. Young ovicell with distal peristome open. H. Older ovicell with peristome tubular and encroaching frontal ring distally.

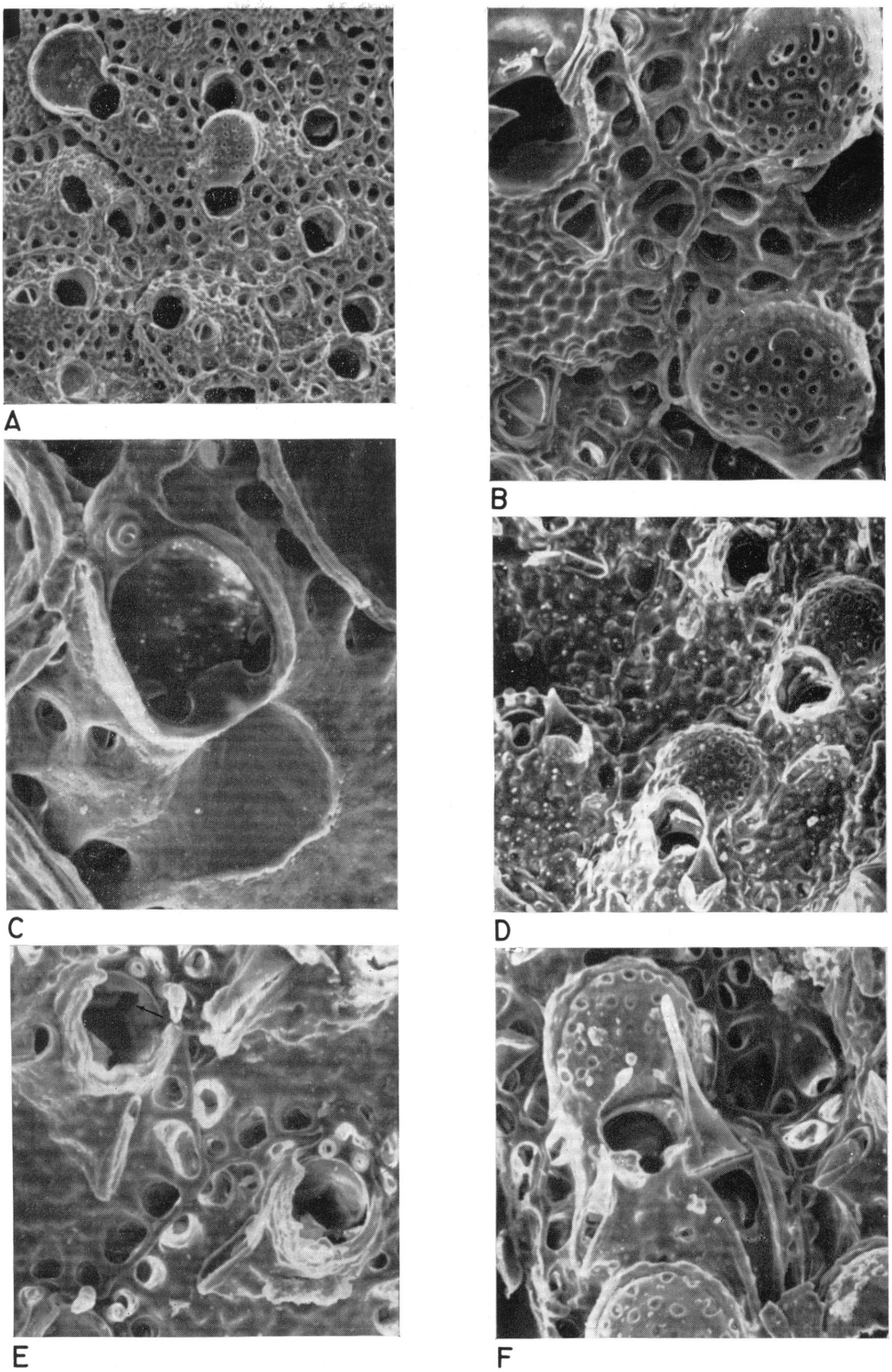


FIG. 2. A–C. *Hemismittoidea osburni*, new species. A. Colony with developing ovicell, median avicularia. B. Ovicells; lower ovicell with curved *Thalamoporella* spicule on top. C. Developing avicularium chamber connected to pore beneath denticle and lateral areolar pore. D. *Parasmittina triangularis*, new species. Colony with rimmed ovicells, short triangular avicularium. E, F. *Parasmittina crosslandi* (Hastings). E. Apertures showing paired frontal avicularia, slit in distal peristomal wall (arrow), two spines. F. Ovicell with long acute and short acute frontal avicularia.

The spines or their bases can be seen in fertile peristomes, and remain visible when the ovicells are complete; rarely in older zooecia the peristome fills in around the spines, making the peristome tubular.

The development of the avicularium and the nature of the ovicells distinguish *Hemismittoidea corallinea* from the *Smittoidea*. This species resembles the *S. levis-S. reticulata* complex, discussed under *S. pacifica*, new species. The ligulate avicularium hinge bar is similar to that figured by Harmer (1957, pl. 64, fig. 26) for the type of *Smittia trispinosa* var. *munita* (Hincks), but the avicularium in that species is much larger and is laterally placed. *Smittina acaroensis* Levinsen (1909, p. 342, pl. 18, fig. 12) has a ligulate avicularium bar, but the median avicularium has a rounded mandible. *Smittia calceolus* of P. H. MacGillivray (1887a, p. 69, pl. 2, fig. 3) appears to be similar to the new species, especially in the appearance of the ovicells. Powell (1967b, p. 380, pl. 17, fig. D) described *Smittoidea calceolus* as being foliaceous rather than incrusting and with a ligulate, triangular, median avicularium.

TABLE 1
MEASUREMENTS (IN MICRONS) OF *Hemismittoidea corallinea*

	Minimum	Maximum	Average	Number
Denticle width	60	60	60	2
Zooecium length	380	440	407.5	8
Zooecium width	270	380	315	8
Aperture length	100	120	108	5
Aperture width	120	120	120	5
Ovicell length	160	180	175	4
Ovicell width	200	240	210	4
Avicularium length	120	130	122.5	4
Avicularium width	50	60	52.5	4

Hemismittoidea osburni, new species

Figure 2A–C

Smittoidea reticulata (MacGillivray): OSBURN, 1952, p. 409 (part; from the Gulf of California). SOULE, 1961, p. 34.

DIAGNOSIS: Colonies unilaminar or multilaminar, incrusting on shell and other bryozoans. Frontals level and finely beaded; white or covered with a yellow ectocyst. Primary aperture oval, wider than high; secondary aperture pyriform, higher than wide. Peristomal collar low, without sinus notch or fold and wide denticle near surface, sloping downward slightly from frontal ledge, lying inside proximal peristome. Cardelles moderate in size, not deeply set. Two to four spines visible on growing edges of colonies. Small frontal avicularium median, but originating from a median pore at base of peristome and single distolateral pore, which is characteristic of new genus *Hemismittoidea*. Avicularium separated from peristome, its rostrum ovoid and little raised, not arched, and with complete hinge bar. Mandible is short, wide triangle, directed proximally. Avicularia occasionally missing.

ETYMOLOGY: Named for the late Raymond C. Osburn, author, friend, and teacher of the present authors.

HOLOTYPE: AHF Bryozoan no. 161.

TYPE LOCALITY: AHF station 2186, Cabeza Ballena, southern tip of Baja California.

DISTRIBUTION: Osburn (1952) listed Isla Partida and Raza Island; Soule (1961) listed Puritan Stations 089, Los Frailes Bay; 131 off Salinas Bay, Carmen Island; 173 Puerto Refugio, Angel de la Guarda Island, all from the Gulf of California. Depths from 40 to 70 m. (rare).

DESCRIPTION: Specimens in the Allan Hancock Foundation collections identified as *Smittoidea reticulata* by Osburn consist of two distinct forms. The Galapagos specimens are placed under *Smittoidea pacifica*, new species, in the present paper, and represent those stated by Osburn to have the bilateral avicularian chamber connections. The Gulf of California material is herein redescribed and placed in the genus *Hemismittoidea*, because examination with scanning electron microscopy has shown a unilateral connection for the avicularium.

A small species, *H. osburni* forms a unilaminar, occasionally multilaminar, colony on shell and other bryozoans. It is rare, and has not been found in shallower waters in the Scuba zone. The frontals are finely granular and level, with small areolar pores in young colonies; in older colonies frontals are beaded, with large areolae. Apertures are wider than high, and the peristome is raised in oral lappets that may give a pyriform appearance to the secondary aperture. The peristome is thin and lacks a sinus notch or groove; it forms a low rim around a proximal oral shelf that bears the medium-wide denticle. The denticle is not so wide as that of *S. pacifica*

and is set nearer to the surface. The cardelles are moderate in size, and shallow set. Two to four spines occur in the distal gap of fertile zooecia; other zooecia have a peak in that region of the peristome.

The small triangular frontal avicularium originates with a chamber, formed around the base of the peristome, which extends between a median pore and a distolateral areolar pore. The median pore opens through the low peristome directly below the denticle, but unlike *H. coral-linea*, the main sinus area does not remain confluent with the rostrum. The rostrum appears to be median or slightly skewed, and is ovoid in shape, except for the acute tip. The mandible is very small, a short, wide triangle, and the entire rostrum does not exceed 100 microns in length. In contrast to most parasmittinids, neither *Smittoidea* nor *Hemismittoidea* seems to bear other frontal or marginal avicularia.

Ovicells are recumbent, and the front of the hood is perforated by a number of small pores. The distal portion of the hood is partly covered by encroaching frontal, which does not seem to overgrow the hood further. Specimens from the northern Gulf of California seem to have slightly larger ovicell pores than those from the southern Gulf of California. Apertures of ooecia are oval, wider than high, with the inner oral shelf near the surface.

The *Smittoidea reticulata* of Lagaaij (1963, p. 196, pl. 6, fig. 11) from the Gulf of Mexico appears to be quite similar to the above specimens from the Gulf of California. Examination of Lagaaij's slide USNM 648041 confirms the superficial resemblance. However, his colony appears to have the typical bilateral *Smittoidea* connections for the median avicularium. The denticle is moderately wide, and the ovicells are immersed.

Lagaaij compared his specimens with those of *Smittina reticulata* in the British Museum, and he stated that the similarity was perfect, except for the presence of two spines in the British material. He did not give the number of spines on his material, nor show any in his figure.

According to Harmer (1957, p. 915) the type of *Smittia reticulata*, described by J. MacGillivray (1842, p. 467) from Aberdeen, Scotland, does not exist. Specimens identified as *Smittia reticulata* in the Hincks collection of the British Museum which were examined by us, showed a considerable range of variation. BMNH slide 1963.3.30.196 from Hardinger Fjord, Norway; Slide 97.5.1.877 from Guernsey; and slide 11.10.1.1453 from Berterbury Bay (illustrated by Hincks [1880a, pl. 48, fig. 2] as a "variety"), all show a pyriform aperture with a very small avicularium at the base of the proximal peristome. Ovicells are not immersed, and not hooded by the peristomal brim. The denticle is moderate in size, shallow set, and truncated.

Hincks's specimen BMNH 99.5.1.915 from the Adriatic, shows a somewhat longer avicularium, ovicells hooded and not immersed, and the denticle deep set. Hincks's specimen BMNH 99.5.1.916 from Britain, also shows a somewhat longer avicularium, small and acute mandible, a distinct sinus, the peristome raised laterally, and a narrow denticle. Two to four spine scars were seen, and ovicells were raised, as in Hincks's illustration (1880a, pl. 48, fig. 1). It is this last specimen that Lagaaij (1963) cited as an example of the similarity to his Gulf of Mexico material.

Harmer (1957, p. 915) in briefly discussing *Smittina reticulata* (now placed in *Smittoidea*) pointed out some of the above differences. According to him, *Smittina marmorea* (Hincks, 1880a, pl. 36) is similar, but the avicularium, which is often not quite median, is separated from the peristomal sinus. On BMNH slide 99.5.1.916 labeled *Smittina reticulata*, the same colony shows some with individuals with avicularia included in the peristome and some lying outside but contiguous to it. Our examination of this slide revealed that the avicularium chamber appears to be connected bilaterally and is small and ovoid with an acute mandible. Ovicells are

TABLE 2

MEASUREMENTS (IN MICRONS) OF *Hemismittoidea osburni*

	Minimum	Maximum	Average	Number
Denticle width	40	50	42	5
Zooecium length	380	560	438	10
Zooecium width	250	340	299	10
Aperture length	100	100	100	5
Aperture width	110	120	118	5
Ovicell length	200	220	205	6
Ovicell width	180	240	220	6
Avicularium length	180	110	101.7	6
Avicularium width	60	60	60	6

not immersed. The denticle is fairly narrow and near the surface.

It appears that a neotype should be designated for *Smittoidea reticulata*, in the interests of stabilizing identifications and distribution records. As BMNH slide 99.5.1.916 resembles the illustration of Hincks (1880a, pl. 48, fig. 1), it is suggested that the slide might be designated the neotype.

SMITTOIDEA OSBURN, 1952

Smittoidea pacifica, new species

Figure 1F–H

Smittoidea reticulata (MacGillivray): OSBURN, 1952, p. 409 (part; from the Galapagos Islands and Halape, Hawaii).

DIAGNOSIS: White, incrusting, unilaminar form found on coral, shell, rock, and other bryozoans. Zooecia elongate, subhexagonal. Primary aperture oval, wider than high, having tall, thin peristomal collar surrounding entire aperture. Distinct proximal sinus present, either as vertical folding in collar or as notch. Denticle extremely wide and anvil-shaped. Cardelles very small, in some cases almost touching tips of denticle. Avicularium median, suboral, sometimes skewed, but with chamber invariably connected to distal pore on each side of peristome, as in typical *Smittoidea*. Rostrum rounded distally, rostral sides raised, finely serrate, much narrowed at tip. Ovicells small, recumbent, with few scattered small pores. Ooecial peristome incomplete at first, filling in on older individuals. Areolar pores small, frontal glassy, beaded, very occasionally reticulate. No spines seen on Hawaiian specimens.

ETYMOLOGY: Named for the Pacific locality of the species.

HOLOTYPE: AHF Bryozoan no. 160.

PARATYPE: BPBM K 443.

TYPE LOCALITY: S-513-67. Pupukea Oahu, at 11–12 m.

DISTRIBUTION: S-522-67, S-530-66; S-613-66, S-614-66; S-703-66, S-705-67, S-709-68; S-905-66, S-910-67; BPBM 401; UH910; 3–24 m. A fairly rare species, 28 specimens in all, from Hawaii. From the Galapagos Islands, AHF station 155–34, Tagus Cove, Albemarle Island; 40 meters.

DESCRIPTION: This species was identified by Osburn (1952, p. 410) as *Smittoidea reticulata*, from Halape, Hawaii. Colonies are small, incrusting, unilaminar, and found on a variety of substrata including the bryozoan *Steginoporella magnilabris*. Zooecia are white, shiny and translucent or glassy, with beaded frontals. Areolar pores are small and rarely show any other ridges, which are typical of *Smittoidea reticulata (sensu-lato)*, extending inward to the avicularium. One colony from S-709-68 showed reticulate zooecia on the margin; it was from deeper waters than the others. Zooecia are elongate, ovoid to hexagonal, rounded distally, and usually in alternate rows. The aperture is oval, wider than high, and has a tall, thin peristomal collar. The collar usually encircles the aperture and has a vertical fold that forms a distinct sinus groove down to the denticle, but in some individuals the sinus is a notch instead. The denticle is very wide, deep set, and widened into lateral tips to give an anvil shape (fig. 1F). The cardelles are small, formed at the tips of the lower peristomal rim, and almost touching the denticle tips at times.

The median avicularium forms as a bulge at the base outside the peristomal collar, retaining a connection on both sides of the peristome with the first distal areolar pore. The avicularium base is rounded distally and the mandible is directed proximally, but may be skewed to one side where the frontal is short or crowded, or on ovicelled zooecia. The rostral sides are raised, arched upward and narrowed, with finely serrate edges. The mandible is very narrow and acute. The hinge bar is complete, angled slightly forward, and may be thickened at the ends so that the opesial premandibular area of the rostrum is reduced to a circle. Six spines were seen on one zooecium from the Galapagos, but none was found on Hawaiian specimens.

The growing edge of the colony rarely shows straight lateral wall extensions. As in the *Hemismittoidea*, the lateral wall folds, which appear to be double, form at either side of the peristome and grow outward at an angle. As zooecia are alternate and subhexagonal, these folds contribute the proximal walls of adjacent zooecia. The walls then form a Y, to round off the distal end of the distal zooecium. Occasionally there is a distinct basal fold contribution to the distal wall, but it is more commonly primarily a lateral wall extension. Such wall formation is found in *Smittoidea prolifica* and the "*S. reticulata*" from the Gulf of California (*Hemismittoidea osburni*).

Lateral walls have a row of small pores on the lower wall between buttresses, and the upper

part of the wall has palisades from the ridges of the areolar pores. A few pores may occur in the upper portion of the wall. Distal walls may show a few small pores, but more commonly there are three larger pores between buttresses. Corner pores are larger and seem to have prominent tissue cords passing through them.

The ovicell is formed at the growing edge of the colony at the same time that the ooecial peristome is forming. There is no evidence of spines on fertile peristomes. The ovicell hood is small and is laid down on the forming primary frontal of the next distal zooecium. The hood may be complete and secondarily calcified before the peristome and secondary frontal of the distal zooecium is complete. The peristome of the ooecium is incomplete at first (fig. 1G) but closes across on older ooecia, making the peristome tubular and the aperture deep set (fig. 1H). The ovicell hood bears irregularly distributed small pores which remain exposed when the adjacent frontal encroaches and forms a beaded ring around the mature ovicell. No ovicell opercula were seen. As the openings of older ovicells were narrow and deep set, it seems possible that the ova escape before the peristome is completed distally across the front of the ovicell. One ancestrula, presumed to be of *S. pacifica* and found in Hawaiian material was oval, partly ringed with spines, and without a calcareous frontal area.

Hincks (1880a, p. 346) gave the distribution of *Smittia reticulata* as Norway, France, the Aegean, the Adriatic, the Falkland Islands, and New Zealand. Hincks (1881b, p. 123) described a variety from Bass Straits with a single lateral avicularium, and remarked that the normal *S. reticulata* of J. MacGillivray occurred there also.

Paul H. MacGillivray (1883, p. 135) described *S. reticulata* var. *spathulata*, the name he gave to Hincks's variety, and remarked that occasionally there was a small avicularium on the side opposite the large spatulate one. Hincks (1884d, p. 283) again illustrated his variety from Victoria with a single spatulate avicularium, and Harmer (1957, p. 934) included this citation in his *S. tropica*. Powell (1967b, p. 381) placed P. H. MacGillivray's variety in a new species, *Parasmittina macphersonae*, and tentatively included Hincks's 1881 variety as well as a number of other citations of the variety *spathulata*. It is clear that these are not the *S. reticulata* of J. MacGillivray.

Paul H. MacGillivray (1895, p. 93) referred to his *Smittia calceolus* (1887) as a variety of *S. reticulata*. His illustration (1887a, p. 69, pl. 2, fig. 3) shows a moderately wide, anvil-shaped denticle, and a pyriform aperture with the peristome raised on either side. It has an ovoid-triangular avicularium of the *reticulata* type and location. Harmer (1957, p. 920) separated *S. calceolus* from his *S. levis*, based on the pyriform aperture of *S. calceolus*. Powell (1967b, p. 380, pl. 17, fig. b) showed the characters of *S. calceolus* well as described by MacGillivray, and added that the colony is foliaceous.

Osburn (1952, p. 409) confused the type locality of *S. reticulata*, attributing J. MacGillivray's 1842 species to Australia instead of Aberdeen. It seems probable that *S. reticulata* does not occur in the Pacific.

Examination of Canu and Bassler's National Museum of Natural History collections shows that specimen 8496, labeled *Smittina reticulata* MacGillivray, Albatross Station D2815, between Santa Cruz and San Salvador Islands in the Galapagos Islands, is like our *Smittoidea pacifica*, new species, from Hawaii. (See Canu and Bassler, 1930, p. 27). Specimens in the Hancock collections from the Galapagos Islands are also identical with *Smittoidea pacifica* from Hawaii. It seems clear that the Galapagos should be deleted from the geographical distribution records of *Smittoidea reticulata*.

Canu and Bassler's specimen of *S. reticulata*, USNM 8112, from Station 5151 southwest of the Philippine Islands, is quite similar to *Smittoidea pacifica*, except that the frontal is more reticulate than that of the Hawaiian specimens and the avicularium is longer. Specimen USNM 8113, from Station 5179, shows some zooecia with reticulate frontals and some with beaded frontals. Specimens labeled *Smittina ophidiana* Waters, 1879, var. *marginata*, new variety (Canu and Bassler, 1929, p. 339), USNM 8114, Station 5147, and USNM 8115, Station 5151, show a greater degree of reticulation than the Hawaiian material, and seem to belong to Canu and Bassler's "*S. reticulata*." Waters's *S. ophidiana* (1879, p. 40) was originally characterized as having a long center avicularium with bifurcate mandible tip, and is thus an inappropriate identification for Canu and Bassler's specimens.

Harmer (1957, p. 919) placed Canu and Bassler's "*S. reticulata*," their "*S. ophidiana* var. *marginata*," and their "*S. trispinosa* var. *munita*"

from the Philippines (1929, pp. 337–341) in synonymy with *Smittia levis* Kirkpatrick (1890), which is, in our opinion, also an error.

Harmer (1957, p. 919) widened the description of *Smittia levis* Kirkpatrick (1890b, p. 620, pl. 16, fig. 8) to include a number of specimens with a considerable range of variation. Kirkpatrick described and figured his type specimen as having a "well-marked pectinate ridge" and the avicularium as being in the "centre of the front wall." Examination of his type specimen in the British Museum shows a strongly serrate (pectinate) rim running horizontally along the distal edge of the primary aperture. This can be seen very clearly in developing zooecia and ovicells, but is less easily seen in older zooecia with tubular peristomes. The secondary aperture has a strong sinus notch with a wide denticle. The medium-sized triangular avicularium is set well below the sinus, and the rostral chamber is connected on both sides of the peristome, as in typical *Smittoidea*. The areolae are quite large.

In Harmer's material of "*Smittina levis*" examined by us at the British Museum (Natural History) his specimen 348K (1957, pl. 63, fig. 1) has avicularia resembling more those of *Hemismittoidea corallinea*, although the development is not clear. The ovicells, however, differ in size, number of pores, and degree of immersion. His specimen 412F is similar, but the avicularium is separated from the sinus. Harmer's specimens 20L (BMNH slide 1430), 348K (slide 1431), 412F (slide 1432), and 541.13 (slide 1433) all lack the distinctive pectinate ridge associated with *S. levis* Kirkpatrick. Harmer's specimen 20L has a raised, inward-curved peristome with a sinus notch, a very long frontal avicularium, and very large areolae. It is like his figure 3, plate 63, and virtually identical to Canu and Bassler's USNM specimen 8113 from the Philippines examined by us. Harmer's 541.13 (BMNH slide 1433) has three specimens, one of which is like 20L. This particular form might perhaps either be considered as a separate Indo-Pacific species, or included in *Smittoidea pacifica*, new species. There is some indication that the greater degree of reticulation is an environmentally induced feature of deep-water colonies, or of older colonies. In the more reticulate specimens, the avicularia are the same shape, but appear to be larger, and more elongate. The Hawaiian material is from shallower waters than the material collected by the *Albatross* and *Siboga*

TABLE 3
MEASUREMENTS (IN MICRONS) OF *Smittoidea pacifica*

	Minimum	Maximum	Average	Number
Denticle width	100	120	110	4
Zooecium length	470	520	499	10
Zooecium width	300	350	315	10
Aperture length	130	150	142.5	10
Aperture width	120	140	131	10
Ovicell length	160	160	160	3
Ovicell width	210	220	216.7	3
Avicularium length	180	180	180	5
Avicularium width	60	65	61	5

Also included in *Smittina levis* by Harmer is Cambridge specimen 51, from the Owston collection from Japan (Harmer, 1957, pl. 62, fig. 5). It has the distinctive pectinate ridge, but bears either a long, pointed avicularium or a semicircular one in adjacent zooecia on the same colony. Harmer discussed the occurrence of the various avicularian forms, but it seems to us that the differences are too marked to include so many under a single species. Certainly the constancy of the avicularium shape in our *Smittoidea pacifica* material would tend to indicate that it is a genetic factor.

PARASMITTINA OSBURN, 1952

Parasmittina crosslandi (Hastings), 1930

Figure 2E, F

Described by Hastings from Taboga Island, Panama, and listed by her from Gorgona, Colombia, and the Galapagos Islands, *Parasmittina crosslandi* was subsequently reported by Osburn (1952, p. 418) from the Galapagos Islands and from Colombia northward in the Gulf of California to Tiburon Island. Soule (1961) recorded the species from the Gulf of California, and Soule and Soule (1964) extended the range to Scammon's Lagoon, Baja California.

Hastings (1930, p. 726, pl. 13, figs. 75–79) characterized the species as having two or three spines, a narrow denticle, tubular peristome with sinus groove, and small, ligulate, paired frontal avicularia, one of which may be replaced by an enlarged acute form. The large avicularian rostrum may be low or it may be much inflated, with the edges either smooth or with small serrations. The mandible has a triangular basal

sclerite and acute blade which curves down over the frontal for most of the length of the zooecium. Ovicells are raised, with many large pores. Frontals form a ring around the ovicell hoods but do not encroach on the hoods themselves. Peristomes, which become complete distally, may form proximal spouts and lateral oral projections.

The forms like that described by Hastings in the Hancock eastern Pacific collections seem to be restricted to the coastal waters off Mexico and Central America, and to the Gulf of California. New material from Taboguilla, Panama, sent for identification by Amada Reimer and collected by Charles Birkeland, agree with the described characters well. A Hancock Foundation specimen from the Galtsoff collection from Panama (fig. 2E, F) shows that the rostra of the small subspatulate (ligulate of Hastings) paired avicularia are canted toward the zooecial margins. The peristome is low distally, usually with two stubby spines, in fertile zooecia. A vertical gap occurs in the figured specimen in the interior distal wall below the spines. This suggests that distal walls in this species are formed by extension of lateral walls of adjacent zooecia rather than by transverse folding, at least in part, although the gap has not previously been recorded.

Osburn (1952, p. 418) expanded the description to include forms with three to five spines and some with large oval avicularia. He incorporated the *Smittina trispinosa* var. of Canu and Bassler (1930, p. 27) from the Galapagos Islands with large, blunt avicularia in *Parasmittina crosslandi*. Examination of Canu and Bassler's specimens USNM 8498 and 8499 indicate that, in our opinion, neither the Canu and Bassler specimens nor the Osburn specimens labeled *P. crosslandi* from the Galapagos Islands belong to that species. They are placed in the present paper in *P. dolabrata*, new species.

A portion of the *Parasmittina crosslandi* of Soule and Soule (1964, p. 27) from Station P-5, Scammon's Lagoon, Baja California, and from Soule (1961) in the Gulf of California, are recognized herein as belonging to another new species, *Parasmittina triangularis*. Those from P-3, Scammon's Lagoon are of *P. crosslandi*.

The typical *Parasmittina crosslandi* in the Gulf of California occurred at *Puritan*-American Museum stations P-087, Pulmo Reef; P-093, San Lorenzo Reef; P-102, off Isla Ballena; P-108, off Isla Partida; P-111, off Isla San Francisco; P-119, off Isla San Diego; P-120, off Isla San Diego; P-124, off San Marcial Rock; P-127, off Isla Monserrate; and P-160, off Isla Tiburon. All others listed from the Gulf of California by Soule (1961) are now recognized as belonging to *P. triangularis*. Distributions of the two species overlap only at P-108 (Isla Partida), and P-160 (Isla Tiburon). Specimens from P-144, off Isla Coronados, differ slightly from both species. The peristomes are tubular, without a sinus groove or notch, and the large avicularia are slightly spatulate rather than acute. Depths of *P. crosslandi* in the Gulf of California were mostly quite shallow, ranging from about 1 to 40 m.

The *Lepralia trispinosa* Johnston of Busk from Carpenter's Mazatlan collection (Busk, 1855, p. 3) is most probably *P. crosslandi*. Slide 92.9.6.6 (BMNH) consists of two tiny fragments of about eight zooecia each. There are several of the tiny recumbent ligulate avicularia, but no large avicularia of any sort. Peristomes are spout-shaped proximally and the denticle is narrow.

Several other specimens showed only small avicularia; one from P-089, Bahia Los Frailes; two from P-108, Isla Partida; one from P-133, Isla Carmen; and one from P-144, Isla Coronados.

Reports of *P. crosslandi* from southern California in industrial ecological surveys have been erroneous; the specimens were of the *Hippomonavella longirostrata* (Hincks) of Osburn, which has a very similar superficial resemblance, but

TABLE 4

MEASUREMENTS (IN MICRONS) OF *Parasmittina crosslandi*

	Minimum	Maximum	Average	Number
Denticle width	40	40	40	5
Zooecium length	460	520	484	7
Zooecium width	300	320	304	7
Aperture length	100	120	104	7
Aperture width	170	180	112.9	7
Ovicell length	170	200	176.7	6
Ovicell width	180	220	193	6
Giant Avicularium				
length	180	220	200	3
width	80	90	83	3
Small Avicularium				
length	100	120	113	3
width	40	40	40	3

lacks the median denticle and has a broad overhung sinus.

Hastings (1930) mentioned that *Parasmittina crosslandi* was similar to O'Donoghue's *Smittina hexagonalis* (1924, p. 46, pl. 3, fig. 15) from South Africa but it has a wide denticle. Cook (1968, p. 214) cited *P. crosslandi* as present in tropical west Africa.

The *Smittina trispinosa* var. *munita* of Marcus (1937, p. 102, pl. 21) appears to be similar to *Parasmittina crosslandi*, but his 1938 citation (p. 44, pl. 10) of *S. trispinosa* var. *munita* indicated the presence of large interzooecial avicularia.

Parasmittina triangularis, new species

Figure 2D

DIAGNOSIS: An incrusting species, with small, paired, proximally directed frontal avicularia, beaded frontals, and small areolar pores. Peristome tubular, with sinus groove or notch, and medium to wide, anvil-shaped denticle. Two short spines set in distal gap of fertile peristomes. Frontal avicularia small, subspatulate, not common; one possibly replaced with larger, short triangular avicularium with raised, spoutlike rostrum. Ovicells recumbent, with many pores. Encroaching frontal forming ring around ovicell hood but not covering it.

ETYMOLOGY: Named for the equilaterally triangular shape of the large avicularium mandible.

HOLOTYPE: AHF Bryozoan no. 171.

TYPE LOCALITY: P-151, off Isla San Marcos, about 20 m., on shell. Gulf of California.

DISTRIBUTION: Gulf of California: P-108, off Isla Partida; P-150, off Isla San Marcos; P-151; P-159, off Isla Tiburon, 20 m.; P-160, 40 m. off Isla Tiburon; P-161, 60 m., off Isla Tiburon; P-162, about 80 m., off Isla Tiburon. P-3, Scammon's Lagoon, Baja California. Also in California Academy of Sciences collection, Station D-24B from Las Animas Rocks, NE of Isla San Jose, at about 45 m.; collected by D. Adcock and B. Marcum from a black coral colony. Depths ranged from about 1 to 80 m.; commonly in depths over 10 m.

DESCRIPTION: The species has a close resemblance to *Parasmittina crosslandi*, and was formerly included in that species. Examination by SEM shows clearly that both small and large avicularia differ. In *P. crosslandi* the paired small avicularia may be very slim with a rounded tip, or oval, or rarely slim and acute. The submandibular opesia has a bar across it (fig. 2E, F). The large avicularia replacing one of the pair are little raised, with occasional serrations near the tip and a long, acute mandible in *P. crosslandi*. In *P. triangularis*, the small avicularia may be single or paired and are common. When present they are slim with a rounded tip and the submandibular area has a bar distal to the opesial opening. The larger avicularia are elevated, with an acute spoutlike tip, and an equilaterally triangular mandible (fig. 2D). The large triangular rostra are much smaller than those in *P. crosslandi*, being limited to connections with only two adjacent areolae. Those of *P. crosslandi* extend most of the length of the frontal, and no gradation in condition between the short triangles and the long avicularia were found on individual colonies.

The apertures of both species are tubular, with a sinus groove or notch that may become extended into spouts and projections. Two or three spines or spine scars occur in the distal gap of fertile peristomes. The denticle is variable, usually wide and anvil-shaped or truncated. Ovicells are also similar in both species, having about 24 pores. The adjacent frontals form a beaded ring around the ovicell margins but do not encroach on the central porous area. Ovicells are raised but recumbent in *P. crosslandi*, and more immersed in *P. triangularis*. The peristome closes distally on the ovicell, leaving a triangular labellar area below the brim and above the aperture in both species. Both species incrust

TABLE 5
MEASUREMENTS (IN MICRONS) OF *Parasmittina triangularis*

	Minimum	Maximum	Average	Number
Denticle width	60	70	63.7	3
Zooecium length	400	420	408	5
Zooecium width	280	380	324	5
Aperture length	120	180	148	5
Aperture width	120	160	132	5
Ovicell length	180	200	195	4
Ovicell width	220	220	220	4
Avicularia (giant)				
Length	130	160	142.5	4
Width	60	80	65	4
Avicularia (small)				
Length	50	60	56.7	3
Width	30	30	30	3

stems of algae and worm tubes, giving rise to erect colonies in some cases; *P. triangularis* was more frequently found on shell.

Parasmittina alanbanneri, new species

Figure 3A–C

DIAGNOSIS: Small incrusting, unilaminar colonies formed on coral and shell. Zooecia quite small, with glistening beaded frontals and small areolar pores. Peristome tubular, with sinus channel, or notch. Three to six spines present in young zooecia, becoming incorporated into peristomal collar. Denticle very wide, anvil-shaped, slanting downward; cardelles opposite denticle tips small and hooked proximally. Small, paired or single, lateral avicularia short or long, mostly acute with few having narrowly spatulate tips. Rostral edges little raised and smooth, directed laterally or proximolaterally. One of paired avicularia possibly replaced by larger, long, acute avicularium having low smooth rostral edges; occasionally there is a tiny serrate rounded tip on each side of the rostrum. Ovicells exposed, recumbent, with many pores. Frontal ringing ovicell distally, also encroaching on brim of ovicell formed by completion of tubular peristome.

HOLOTYPE: AHF Bryozoan no. 162.

TYPE LOCALITY: Mokumanu, Oahu, S-507-66; collected by the late Alan Banner, for whom the species is named. Banner was lost when attacked by a shark off Western Samoa, in April, 1972.

DISTRIBUTION: The species is not common and seems to be mostly restricted to bays. On Oahu, Pokai Bay and Maili: S-517-67, S-520-67, S-521-67; at Kaneohe Bay: S-500b-66, S-506-66, S-507-66. On Molokai: Halawa Bay, S-900-66; Maui, S-613-66, S-615-67; on Hawaii, S-701-66, S-702-66, S-703-66, S-705-67, S-709-68; 23 specimens in all.

DESCRIPTION: *Parasmittina alanbanneri* is one of several species which have slim, lateral avicularia directed proximally or proximolaterally; they may be single on some zooecia, but are more commonly paired. In this new species, avicularia are mostly acute, and are directed more laterally than in similar species such as *P. areolata*, *P. uncinata*, *P. tropica*, and *P. serrula*. On some of the small avicularia, a tiny additional pore is seen in the rostral submandibular area, such as was illustrated by Waters (1909, pl. 17) in *P. tropica*. Large areas of some colonies have no avicularia, and in other zooecia, one of the small avicularia may be replaced by a long, triangular avicularium. Its mandible has a short, triangular sclerite at the base, and in some cases there is an additional transverse bar through the center of the triangle. The rostral chamber may be elevated or not, but the edges are rarely raised; sometimes a small, serrate, rounded, erect tip occurs at the ends of the rostral edges.

Zooecia are small, shiny, and with a glassy, beaded, or rugose frontal; areolar pores are small. In young zooecia, the three to six spines are quite visible; some are very long, whereas others are short and stout, with a telescoping structure based in sockets (fig. 3C). The sinus is at first only a notch, but the peristome grows upward, filling in around the spines to form a tubular structure. Tall, irregular projections may form atop the peristome, and the sinus becomes a deep vertical groove or fold. Ridges may extend down the fold to the sides of the wide denticle. The denticle is so wide that it appears to fill almost the entire aperture; as the distal wall slants forward and upward beneath the aperture, the clearance between the denticle and the wall is smaller than is usual (fig. 3B). The cardelles are small, set opposite the tips of the anvil-shaped denticle, and hooked in a proximal direction. The operculum is thin, horseshoe-shaped, and often sits atop the denticle in dried specimens so that the denticle is hidden.

Ovicells are numerous, often in rows; they form around the bases of the spines, occasionally leaving some spines visible at the aperture. Ovicells are raised, but recumbent on the next distal zooecium (fig. 3A, B shows several stages in developing ovicells). They bear numerous pores, which remain uncovered when the adjacent frontal fills in around the hood distally. The peristome fills in behind the aperture to form a brim on the ovicell hood; where the peristome is not quite complete, it produces a labellar appearance similar to that noted by Hastings (1930, p. 726, pl. 13, fig. 76) in *Parasmittina crosslandi*. Some ovicells have a small operculum.

The new species resembles *P. crosslandi* (fig. 2E, F), in the shape of the peristome, ovicells, and large avicularia. However, *P. crosslandi* has a much narrower denticle, and only two to three spines, as compared with the wide anvil-shaped denticle and three to six spines seen in *P. alanbanneri*.

The tubular peristome with a sinus groove, and the exposed ovicells, are similar to those of *Parasmittina tropica* (*Smittia tropica*, Waters, 1909, pl. 17, figs. 10–14). The paired lateral avicularia are thin spatulas in *P. tropica*, rather than the triangular ones in *P. alanbanneri*. Waters mentioned only two spines in his species. Both are small species.

Harmer's *Smittina nasuta* (1957, p. 927, pl. 64, figs. 1–5) resembles the new species in having a tubular peristome and four to six spines, some of which are jointed and some are flattened. The avicularia differ, however, as *S. nasuta* has long or short spatulas, ovals, or larger spoon-shaped avicularia. The denticle is narrow.

The *Smittia tubula* of Kirkpatrick (1888, p. 79, pl. 10, fig. 6) is also similar, in the tubular peristome and the number of spines. Kirkpatrick described the avicularia as being small and rounded, on one side of the orifice, whereas Harmer (1957, p. 941) stated that specimens of *S. tubula* collected by Thornely have acute avicularia, usually unilateral, which ascend the peristome almost to the top of the collar. Kirkpatrick figured some lines on the frontal which are unexplained. He described the denticle as wide. These characters suggest the *Smittina projecta* of Okada and Mawatari (1936, p. 66, fig. 5). *Parasmittina tubulata* Osburn (1952, p. 420, pl. 49, figs. 1–4) is a much larger species, with an unusually large peristome, and a narrow denticle. The very wide denticle of *P. alanbanneri*, new species, separates it from many parasmittinids, as mentioned; the non-serrate avicularium rostra also distinguish it from *P. serrula*, another new species. *Parasmittina alanbanneri* is not a common species; its distribution overlaps that of *P. serrula* at only five of 13 stations where *P. alanbanneri* occurs, or five of 30 stations where *P. serrula* is found.

TABLE 6
MEASUREMENTS (IN MICRONS) OF *Parasmittina alanbanneri*

	Minimum	Maximum	Average	Number
Denticle width	50	60	56	5
Zooecium length	380	480	405	10
Zooecium width	280	360	313	10
Aperture length	100	120	110	10
Aperture width	100	120	108	10
Ovicell length	180	200	193	3
Ovicell width	200	220	210	3
Avicularia (giant)				
Length	180	200	184	7
Width	40	50	45	7
Avicularia (short)				
Length	100	110	105	4
Width	20	25	22.5	4

Parasmittina serrula, new species

Figure 3D–F

DIAGNOSIS: *Parasmittina serrula*, small, glistening species with tubular peristome and vertical sinus groove, with three to six heavy spines, and with small, single or paired lateral avicularia, directed proximally. One lateral avicularium possibly replaced by large, curving avicularium with strongly serrate rostral edges. Primary aperture wider than high, with slightly serrate border, strong cardelles, and narrow to medium denticle. Frontal beaded, shiny, and areolar pores small. Ovicell with 12 or more large, irregular pores. Ooecial peristome closing distally at same time ovicell completed, growing across from sides to form tubular peristome. Ovicell remaining raised, recumbent, but not sunken; a fold of adjacent frontal ringing but not covering ovicell.

ETYMOLOGY: The name *serrula* means "little saw," from the Latin diminutive of *serra*, referring to the serrate edges of the giant avicularium rostrum.

HOLOTYPE: AHF Bryozoan no. 163.

TYPE LOCALITY: S-601-66, Napili Bay, Maui, at 3 m.

DISTRIBUTION: One of the most widely distributed and most common smittinids on the Islands; its distribution is centered on Maui and Molokai, with less frequent occurrences on Kauai, Oahu, and Hawaii. On Oahu: S-500b-66, S-511-66, S-512-67, S-513-67, S-530-66; Kauai: S-802-67, S-803-67, S-805-67; Molokai: S-900-66, S-901-66, S-905-66, S-907-67, S-908-67, S-910-67, S-911-67; Maui: S-600-66, S-601-66, S-606-67, S-609-66, S-610-66, S-612-66, S-613-66, S-614-66, S-615-67, S-616-67, S-619-67, S-650-67; Hawaii: S-701-66, S-706-67, S-707-67, S-708-67, S-710-68. Total of 153 specimens. Depth range 3–130 m.

DESCRIPTION: Colonies are unilaminar, incrusting, primarily occurring on coral, and occasionally on shell. Zooecia are quite small, shiny, and have a beaded frontal. Areolar pores are small, a single row, with a few additional

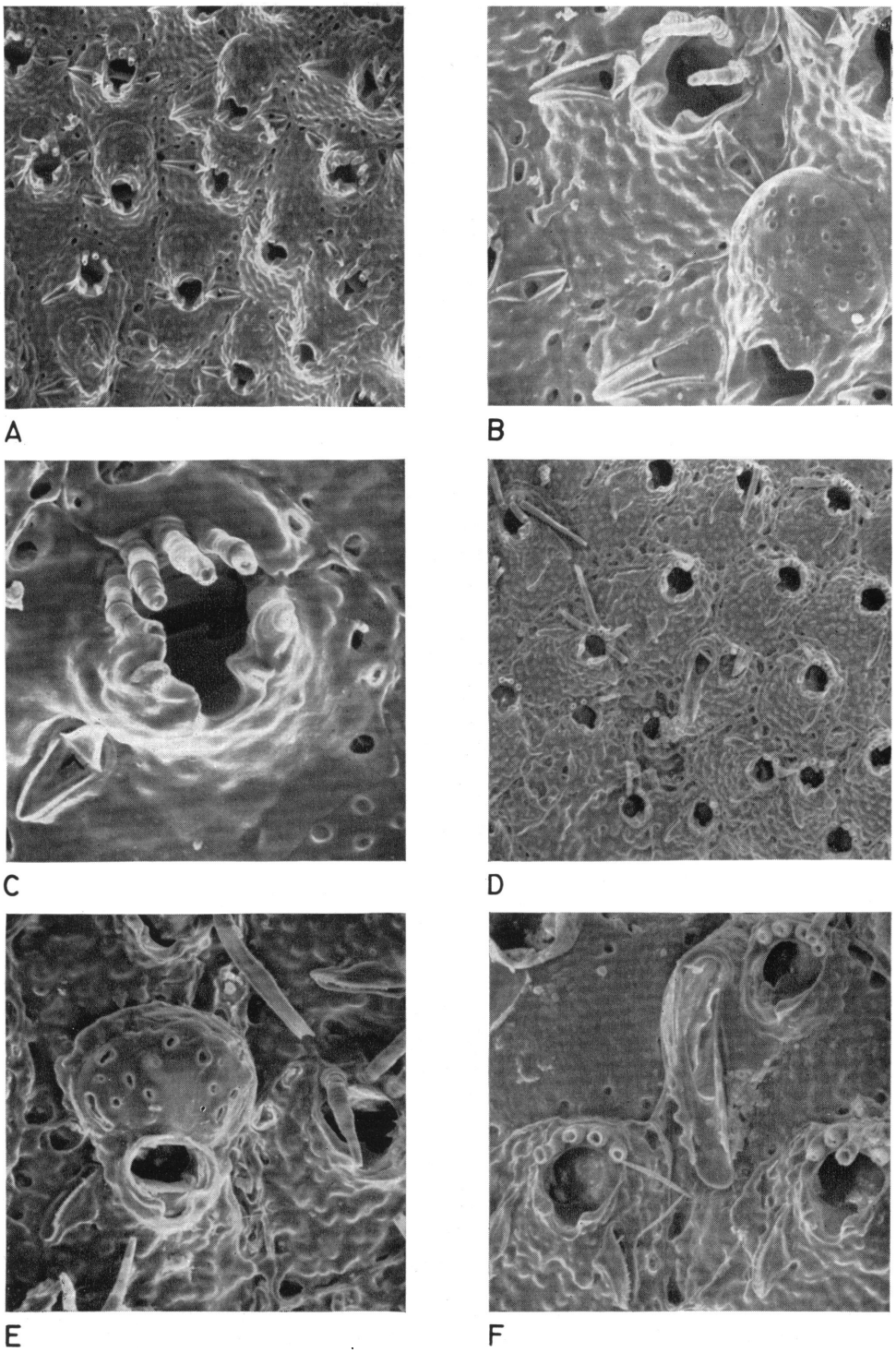


FIG. 3. A–C. *Parasmittina alanbanneri*, new species. A. Colony with tubular peristomes, 3–6 spines, acute avicularia. B. Immersed ovicell, part of developing ovicell. C. Aperture with spines, wide deep denticle, sinus groove. D–F. *Parasmittina serrula*, new species. D. Colony with 4–6 spines on zooecia. E. Ovicell with few pores. F. Giant lateral avicularium with serrate rostral edges, internal communication pores. Note narrow denticle.

frontal pores (fig. 3D). There are usually four large spines which commonly remain attached and are quite noticeable. Spines are formed by infolding of the distal flap (fig. 3F). The spine bases appear to function like a ball and socket joint. The spines may or may not show a telescoping structure typical of other smittinids; some are flattened or squared rather than round, and they tend to droop forward over the aperture like fingers.

The ancestrula has a small cryptocyst with eight spines around the opesia. Zooecia in the next two rows (zone of astogenic change) often bear six spines. Young colonies frequently are found in the cups of older stony corals where the polyps are dead.

The primary aperture is wider than high, with an inner rim ending in strong cardelles. The outer rim almost meets proximally in the center, separated by a small tongue of frontal; these parts fuse to form the narrow to medium-sized denticle. The distal rim may show a slight serration when young. The peristome becomes deepened, with a pronounced vertical sinus groove rather than a notch. On some colonies, the peristome region adjacent to the sinus groove may form tall projections, or the entire peristome may deepen and the sinus groove become spoutlike.

The small, paired lateral avicularia lie below the peristomal area. The rostrum appears to lie on its side, and is spout-shaped, with a finely serrate beak. During development, the small avicularia seem to arise in conjunction with the first lateral pore to appear on the primary frontal, and to connect with the base of the peristome on one side of the sinus. Occasionally only one small avicularium is present, and it may be more centrally placed, but the rostrum retains the appearance of lying on its side. The mandibles are quite narrow, fragile, with acute or rounded tips; in mature zooecia, the small avicularia seem to be almost calcified over and the mandibles gone.

The large avicularia form in contact with at least four lateral areolae and one distal pore. The rostrum rises along the lateral wall and extends across the frontal to the base of the sinus. Occasionally, at the growing edges of the colony, the rostral chamber can be seen to be open to the basal wall, and the areolar pores of the zooecial frontal can be seen inside the rostral chamber (fig. 3F). The rostral submandibular opening is bluntly triangular, with the premandibular area a small semicircular form. The beak curves over the frontal, and the rostral edges are curved up, with very large serrations along the sides. The large avicularia are more common on colony areas with many ovicells. Mandibles vary in width, some being very slim, tapered, and acute; others are slightly widened in the mid-blade area. Both sorts are curled along the sides in dried specimens.

Ovicells are raised, with some 12 to 20 large pores (fig. 3E). During the formation of the ovicells, the gap in the peristome where the spines are situated begins to close at the same time that the ovicell globe is developing. The advancing edge of the ovicell globe has finger-like projections which finally fuse at the tips, leaving the pores open between them. The globe is double-layered. The closed peristome is tubular, and may form a brim on the ovicell, or irregular projections. Ovicells are raised, recumbent, and do not commonly become immersed, but may have a ring of encroaching frontal built up against them. No avicularia were seen on the ovicells.

Both lateral and distal walls appear to be formed from folds of the basal wall. The orientation of zooecia is such that the distal wall area of one individual abuts a portion of the lateral wall of another. The lateral wall folds at the growing edge of the colony usually extend outward in a curve, rather than forming in boxlike fashion, so that there is often no distinction between lateral and distal walls. As soon as the lateral and distal walls are established, a distal flap, which will form the spines, begins to extend upward. The frontal membrane appears to grow distally all the way to the distal flap. The primary calcified frontal appears to grow inward from both the proximal and distal corners, forming an oval opening in conjunction with the portion of the peristomal arch ending at the cardelles. The upper rim of the peristome ultimately comes together in the median proximal position to become the denticle.

The lateral walls bear a row of many small pores along the basal portion while the distal wall area bears about four small pores in the basal area, plus a larger opening at each basal corner. The lateral walls become invested with secondary frontal calcification, and extend upward above the frontal area to give the appearance of a multilayered wall lying between zooecia.

Parasmittina serrula resembles closely one specimen illustrated by Harmer (1957, pl. 64, fig. 23) as *Smittina tropica* 113B, from India. That particular specimen has four spine scars, a tubular peristome, long serrate rostra, and uncovered ovicells with numerous pores. It has a notched peristome rather than a sinus fold or groove, however. Waters, in his illustration of *Smittia tropica* (1909, p. 174, pl. 17, figs. 10–13) showed a similar peristome and ovicells, but his small avicularia are narrowly spatulate, with parallel sides, and the larger avicularia are triangular, with the rostral tips raised on each side. Waters showed only two spines, as did Harmer in plate 64, figures 25 and 27.

Harmer has placed a number of specimens having slim, paired lateral avicularia in his *Smittina tropica*, and perhaps extended its characters too widely. Osburn (1952, p. 411) based his genus *Parasmittina* on the presence of paired lateral avicularia. It now seems likely that there are a number of species sharing that characteristic, which also have one of those avicularia replaced occasionally with a larger avicularium, either triangular, subspatulate or spoon-shaped.

Powell (1967a, pl. 3, fig. 14) showed a mature colony, from the Red Sea, of *Parasmittina tropica*, in which the avicularia have the typical peaks at the rostral tips, as shown by Waters. His material seems to agree with the Waters's material from the Red Sea, the type locality, more accurately than Harmer's does. Cook (1968, p. 215) reported *P. tropica* from West Africa, noting the small zooecia, tubular peristomes, and the lightly calcified ovicells.

Parasmittina serrula has the small size, tubular peristome, and uncovered ovicells of *P. tropica*, but the edges of the rostra in the new species are strongly serrate instead of having peaked tips. Hooked tips do occur in *P. uncinata*, new species, which has much larger zooecia and submerged ovicells.

Peristomal extensions in the form of proximal spouts, lateral peaks, or a brim on the ovicell are frequently found on *P. serrula*. The new species does not seem to form multiple layers, although some frontal budding is found. New ancestrulae sometimes settle on the old colonies, forming entirely new colonies.

Smittia rostriformis Kirkpatrick (1888, p. 80, pl. 8) from Mauritius is similar to the new species, as Kirkpatrick showed it in figure 7, but figures 7a and 7b show frontal and ovicell avicularia, such as are found in *Parasmittina areolata*. Thornely (1905, p. 123) cited specimens from Ceylon, but stated that the avicularia of *Smittia rostriformis* might be directed either up or downward; this is unlike Kirkpatrick's description, and unlike the present material.

TABLE 7
MEASUREMENTS (IN MICRONS) OF *Parasmittina serrula*

	Minimum	Maximum	Average	Number
Denticle width	20	30	26	10
Zooecium length	320	400	368	10
Zooecium width	260	310	284	10
Aperture length	80	90	84	10
Aperture width	60	75	66	10
Ovicell length	220	—	—	1
Ovicell width	240	—	—	1
Avicularia (giant)				
Length	240	260	252	5
Width	60	65	63	5
Avicularia (short)				
Length	75	80	79	6
Width	30	35	31.5	6

Parasmittina serrula is similar to *P. alanbanneri*, new species, in having small, single, or paired, lateral avicularia directed proximally, a tubular aperture, uncovered ovicells, and small zooecial size. The most notable difference is in the serration of the avicularian rostra of both small and large avicularia in *P. serrula*. The denticle of *P. serrula* is narrow to medium in width and usually truncate, whereas it is quite wide, and anvil-shaped in *P. alanbanneri*.

Parasmittina circularis, new species

Figure 4A–D

DIAGNOSIS: White, incrusting species, with yellowish mandibles and opercula, and with glistening, iridescent epitheca, with round aperture, tapered, acuminate denticle, and hooked cardelles. Peristome thickened ring or roll, occasionally slightly raised into lappets. Apertures possibly becoming tubular and sunken with age. Sinus fold and notch absent. Avicularia commonly small, lateral, paired or single, acute or oval, directed proximally. One of pair frequently replaced by short, wide, triangular avicularium raised into spoutlike tip. Rarely, one is replaced by greatly elongated, spoon-shaped avicularium. Rostral chamber originating from

frontal pores on one side at the base of peristome and lateral areolar pores; much inflated, and zooecium becoming much elongated to accommodate large avicularium. Ovicells at first globose, with many pores in the central area; becoming sunken, covered both proximally and distally with encroaching frontal, leaving small crescent of pores exposed. Peristome possibly forming hood or brim on ovicell.

ETYMOLOGY: From the Latin *circular, -atus*, to form a circle; refers to the shape of the aperture.

HOLOTYPE: AHF Bryozoan no. 164.

TYPE LOCALITY: S-612-66, Lahaina, Maui; 11 m.

DISTRIBUTION: Oahu: S-527-68, Pokai Bay, 21 m. Two specimens found here had no large spatulas, but were alike in other respects. As the species is rare, insufficient grounds were seen to justify separation. On Maui: S-608-66, S-609-66, S-611-66, S-612-66, S-613-66, S-650-67; about 30 specimens in all; depth range 3–120 m.

DESCRIPTION: *Parasmittina circularis* has small, paired or single, slender lateral avicularia, directed proximolaterally, as in a number of parasmittinid species. The avicularia are short, slim, with acute or rounded tips. One of the pair is often replaced by a wider, triangular avicularium with a raised rostrum and a spoutlike tip. More rarely, one avicularium is replaced by a very long, spoon-shaped avicularium which arises from frontal pores on one side and four or five areolar pores. The zooecium is much elongated beneath to accommodate the long mandible (fig. 4A). Other small, oval or acute avicularia are scattered along the frontal margins, oriented variously. None of the rostra appear to bear serrations. In the triangular avicularia, the hinge bar is complete, sometimes with a small spur (ligula) which projects into the premandibular space. The submandibular opesial space is bluntly triangular in shape.

The aperture is round, with widened, flat peristomal ring (fig. 4C); hence the name *circularis*. The peristome may become tubular, and sunken. The denticle is at first very near the surface, but is deep set in the older, sunken colonies. There is no sinus fold or notch. The denticle is acuminate, or truncate, and narrow. The cardelles are pointed, directed toward the tip of the denticle but not hooked downward. Two spine scars are occasionally found. The yellowish operculum is horseshoe-shaped, with a marginal sclerite which terminates at the cardelle articulations. The colonies are incrusting, usually white, and with a heavy, glistening, sometimes iridescent, epitheca covering them. The frontal is coarsely granular, with large areolar pores and some additional frontal pores. Zooecia are small.

The basal wall appears to be composed of two layers, and lateral walls are formed by upward folding. The folds of the wall are not completely fused vertically, so that a few tiny openings show on the basal surface. Lateral walls have a row of six to eight large pores; the upper layer is contributed in part by the frontal and has a palisaded appearance between the areolae, some of which seem to open through the lateral walls also. Distal wall formation appears to be complex, with contributions in some zooecia from distal folds and in others from lateral wall extension. The distal walls show scattered pores, distributed irregularly.

Ovicells are at first globose, but become covered both proximally and distally by encroaching frontal, until only a crescent of pores remains exposed (fig. 4B, D). The ovicell brim is formed by the distal growth of the peristome, which has a distinct, thick, white rim. Where colonies have formed a thick crust, spaces for future ovicell development are marked as depressions, still containing the distal spines or spine bases. Ovicell opercula can sometimes be dissected from mature ovicells. As in other Hawaiian species in which opercula are found in the ovicells, the operculum is placed almost vertical to the zooecial operculum, sometimes separated by a peristomal ledge and sometimes not. It is necessary to break open the ovicells from the distal side to see the opercula in place. It seems possible that the opercula are in place only while the ova develop, and perhaps the zooecial peristome does not close over distally until the larva has escaped.

While *Parasmittina circularis* has slim, paired avicularia, as are seen in a number of parasmittinids, the replacement of these with either a short triangular avicularium, or a very long, spoon-shaped avicularium seems to be unique. The parasmittinid species *Escharella spathulata* (Smitt, 1873, p. 60, pl. 10, fig. 200), *Parasmittina macphersonae* (Powell, 1967b, p. 381), and *Smittina areolata* (Canu and Bassler, 1927, p. 23) have long, labellate or spatulate avicularia, but all of these have a channeled or notched aperture. The peristomal ring of *P. circularis* is distinctive, as is the glistening epitheca.

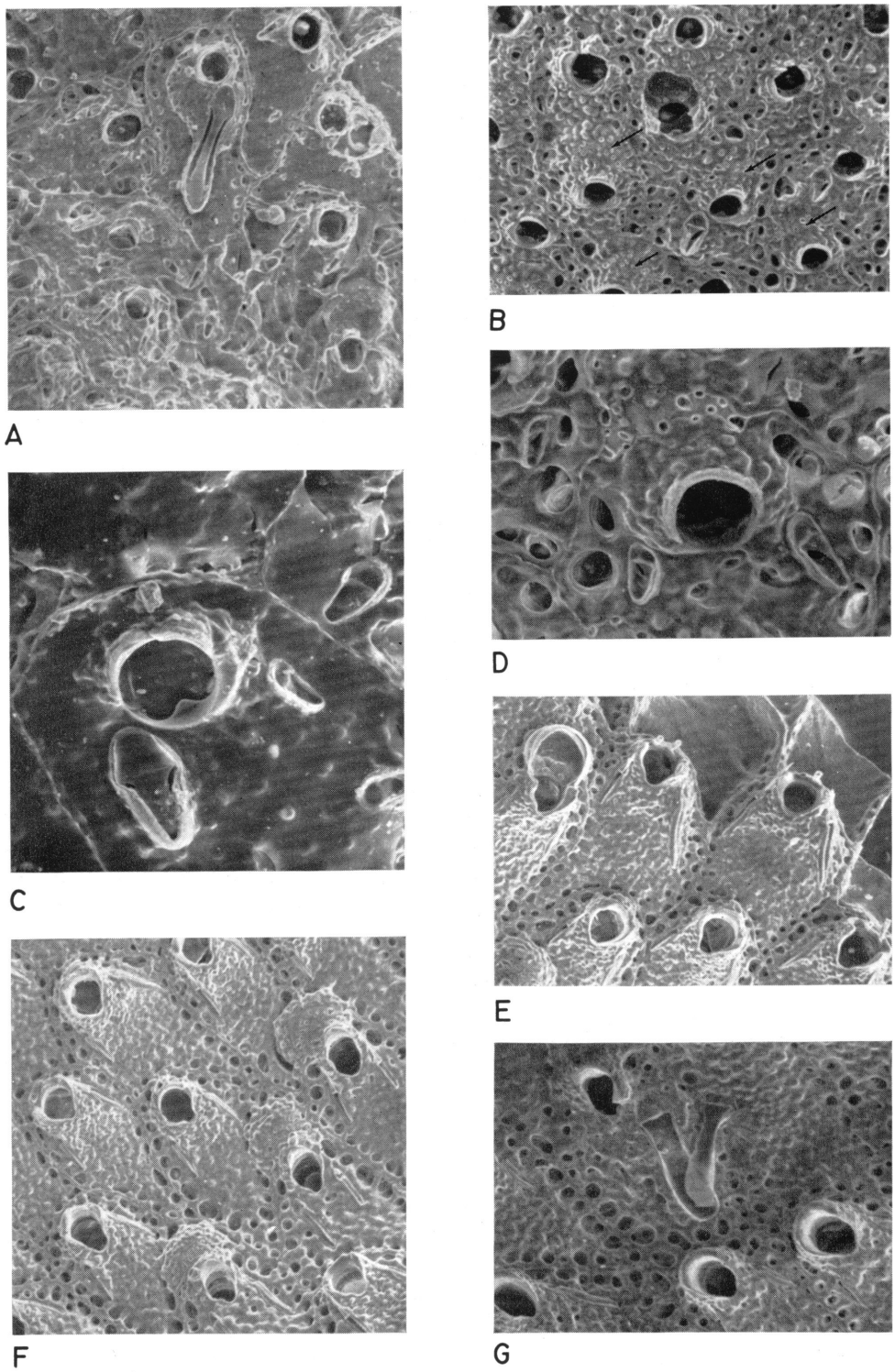


FIG. 4. A–D. *Parasmittina circularis*, new species. A. Colony with huge spoon-shaped avicularium. B. Older, heavily calcified colony with rimmed, immersed ovicells (arrows). C. Heavy ectocyst, circular aperture, acuminate denticle. D. Ovicell immersed except for a small strip of pores, white brim. E–G. *Parasmittina areolata* (Canu and Bassler). E. Developing edge of colony with lateral wall folds. F. Colony with pyriform apertures, paired long, slim avicularia. Tiny avicularium on distal rim of middle left zooecium; note suboral pore in some zooecia which may also bear tiny avicularium. G. Loose mandible lying on rostrum of giant avicularium.

TABLE 8
MEASUREMENTS (IN MICRONS) OF *Parasmittina circularis*

	Minimum	Maximum	Average	Number
Denticle width	15	20	16	10
Zooecium length	540	680	598	10
Zooecium width	300	490	397	10
Aperture length	120	140	124	10
Aperture width	90	120	109	10
Ovicell length	180	200	190	4
Ovicell width	220	190	237.5	4
Avicularia (giant)				
Length	420	430	425	2
Width	100	120	110	2
Avicularia (short-narrow)				
Length	120	130	122.5	4
Width	30	30	30	4
Avicularia (triangle)				
Length	120	120	120	4
Width	60	80	72.5	4

Parasmittina areolata (Canu and Bassler), 1927
Figure 4E–G

DISCUSSION: Described by Canu and Bassler (1927, p. 23) from the *Albatross* collections off Hawaii, *Smittina areolata* was distinguished by them as having a pleurocyst frontal with separations distinct, large areolar pores, and an irregular, elliptical peristome. The avicularia were lateral, directed proximally, very long and thin, transformed sporadically into large avicularia with tongue-shaped mandibles.

Examination of the type specimen, USNM 8443, shows the characters described, but also shows that there is occasionally a small, almost median, frontal avicularium directed toward the sinus, apparently originating from one of several scattered frontal pores which remain uncalcified. Although Canu and Bassler described the zooecia as elongate, irregular, and badly oriented, the young colonies are actually more regularly arranged than in many smittinids, tending to form flat incrustations, with the zooecia arranged more or less in alternate rows. The older colonies show a somewhat heaped, multilaminar colony.

The slim, paired lateral avicularia of *Parasmittina areolata* are mostly longer than those of the previously described species in this paper. The small and large avicularia have very finely serrated rostral edges, but the rostra are not much elevated.

As seen in the type material, *P. areolata* tends to produce a pyriform aperture, with the peristome raised distally, and descending gradually almost to the level of the frontal at the proximal rim; occasionally a wide, U-shaped sinus is formed. This gives the aperture a hooded appearance, especially in the large, regularly arranged zooecia of the primary layer of the colony. The small distal avicularia, usually placed at the top of the distal rim, add to the hooded appearance (fig. 4F, G). The primary aperture is deep set, and has a narrow denticle, with strongly hooked cardelles directed proximally. The operculum is horseshoe-shaped, with a thin, chitinous, distolateral marginal sclerite. The ectocyst of the colony is white or yellowish, and the frontal is finely granular.

The ovicells originally described as large, are actually smaller than many parasmittinid ovicells, and they become immersed and obscured, except for a crescent of small pores. A proximal lip or brim on the ovicell hood, bearing a tiny, pointed or rounded avicularium, is sometimes present. Ovicells form on zooecia which lack the distal peristome wall, in the gap occupied by two spines. An ovicell base forms from the distal wall, lying on top of the frontal of the next distal zooecium. A double-layered hood appears, which grows upward to form a translucent globe with irregular pores. The peristome may or may not fill in to form the ovicell brim, and the encroaching frontal causes the pores to become obscured and the ovicells immersed. Ovicell opercula may be found.

Prior to the growth of the secondary layers of the colony, numerous tiny, pointed or blunt avicularia may appear on the frontal. Usually the lateral walls begin to extend above the frontal at the same time. Budding sometimes occurs, in which a single zooecium forms exactly on top of another without at first occluding the parent aperture.

Canu and Bassler (1928b, p. 30) reported *Smittina areolata* from Brazil, but remarked that these specimens had no "distal pore" and no small avicularia on the frontal, which differentiated it from *S. trispinosa spathulata* (Smitt), also from Brazil. Yet their type of *S. areolata* from Hawaii shows both distal avicularian scars and small frontal avicularia. The Floridian *Escherella spathulata* (Smitt, 1873) seems to be very close to

S. areolata and the latter might be a synonym. The giant avicularia of Smitt's illustration seem to be slightly longer and more spoon-shaped (*op. cit.*, pl. 10, fig. 200) than in *Parasmittina areolata*, but variations alone might account for this.

We have examined USNM 7594 of *Smittina trispinosa spathulata* from Florida, Canu and Bassler's plesiotype figured (1928a, p. 114, pl. 15, figs. 9–13). Contrary to Canu and Bassler's retouched illustration (*op. cit.*, fig. 9) we find that the denticle and cardelles are in the usual positions, with the cardelles opposite the tips of the denticle and hooked somewhat downward, rather than lying beside the denticle. It is very similar to *Parasmittina areolata*, although *S. trispinosa* var. *spathulata* (=*P. spathulata*, Osburn, 1952, p. 415) generally shows the apertures to be more sunken in a common crust, rather than distinct and separate as in *P. areolata*.

Examination of USNM 8558 of *S. trispinosa* var. *spathulata* from the *Norseman* expedition, east of Bahia, Brazil, shows that hooked avicularian rostra are present, with subacute triangular mandibles, in addition to the slim lateral, and long spatulate, avicularia. It is close to *Parasmittina uncinata*, new species, from Hawaii.

Osburn's *Parasmittina spathulata* citations from the Galapagos Islands of Hancock material are included in a new species, *P. dolabrata*, in the present paper. It is like Canu and Bassler's *Smittina trispinosa* var., from the Galapagos Islands (1930, p. 27, pl. 4, figs. 1–5), and in the Hancock collections, a number of specimens of this form were included in material labeled *Parasmittina crosslandi*, by Osburn. The characters ally *P. dolabrata* with *P. californica*, *P. parsevali* and *P. raigiformis*, in preference to *P. areolata* or *P. spathulata*.

Powell (1967b, p. 382) remarked that his species *Parasmittina macphersonae* resembled *P. spathulata* except for the fact that Canu and Bassler had illustrated the cardelles of that species as being situated at the proximal border of the orifice. This difference does not exist in any of the material of that species examined by us, including their plesiotype. It is possible that Powell's species is synonymous with *P. areolata* as the large avicularia are tongue-shaped. Both might be synonyms of *P. spathulata*, but that species has been much confused by various authors.

Canu and Bassler's *Smittina trispinosa granosa* from the Philippines (1929, p. 345, pl. 42, figs. 1, 2), USNM 8126, has cardelles placed low, beside a moderate denticle and has very long spatulate or spoon-shaped giant avicularia, much like that in *P. circularis*, new species. The frontal of Canu and Bassler's *granosa* is very shiny, with large glassy granules.

TABLE 9
MEASUREMENTS (IN MICRONS) OF *Parasmittina areolata*

	Minimum	Maximum	Average	Number
Denticle width	15	30	20	10
Zooecium length	800	840	806	10
Zooecium width	340	420	386	10
Aperture length	130	170	153	10
Aperture width	120	140	134	10
Ovicell length	180	200	197	7
Ovicell width	240	260	247	7
Avicularia (giant)				
Length	500	—	—	1
Width	120	—	—	1
Avicularia (short–narrow)				
Length	120	160	138	5
Width	25	30	29	5
Avicularia (long–narrow)				
Length	220	300	236.7	6
Width	40	40	40	6

It should be noted that MacGillivray (1895, p. 96, pl. 12, fig. 30) described a new species as *Smittia areolata*. His species, however, had an oval median avicularium and no others. This would presumably place the species in the genus *Smittoidea*. It seems to resemble Kirkpatrick's *Smittia levis* somewhat, or the *Smittina levis* of Harmer (1957, pl. 63, fig. 2). As Canu and Bassler's *S. areolata* must be placed in the genus *Parasmittina*, it seems permissable to allow Canu and Bassler's name to stand, although it was occupied at the time they used it.

Kirkpatrick (1888, p. 80, pl. 8, fig. 7) described *Smittia rostriformis* as having small avicularia on the frontal and ovicell brim, as well as paired lateral avicularia. The shape of the enlarged avicularia, however, he described as hastate (spear-shaped), while those of *P. areolata* are more tongue-shaped. The rostral margins of both species are finely serrate. Kirkpatrick's *S. rostriformis* var. (1890) differs only in having the tiny avicularium along the border instead of on the ovicell brim. Harmer included *S. rostriformis* var. (1890) in *Smittina tropica* (1957, p. 936)

but expressed doubt that the original 1888 form is synonymous.

DISTRIBUTION: *Albatross* Station 4072, holotype USNM 8443, from the northeast coast of Maui, 102–108 m. depth; *Albatross* Station 3823, south coast of Molokai, 142–406 m.; S-650-67, collected by Stan Swerdloff, in Kealaikahiki Channel between Maui and Kahoolawe Islands, 120 m.; S-516-67, S-519-67, S-520-67, Pokai Bay, Oahu, 8–28 m. Not a common species.

Parasmittina uncinata, new species

Figure 5A–C

DIAGNOSIS: Yellowish, incrusting species with large, heaped zooecia. Avicularia paired or single, short or long, thin, and directed proximally. One sometimes replaced by wider and longer subspatulate lateral avicularium with rostral edges slightly raised and finely serrate. Also, some zooecia with single, large avicularium originating on peristome and extending proximally; rostrum not much elevated but margins rising to two tips, as in claw hammer, on which name *uncinata* is based. Large mandible having triangular base with narrow blade having parallel sides and rounded tip. Also many tiny rounded or pointed avicularia originating at or near areolar pores.

Frontal coarsely granular, with large or small areolar pores, plus additional pores associated with bases of avicularia. Primary aperture round, with narrow median denticle. Peristome possibly raised into tube with proximal slit, or possibly peaked distally or laterally with wider sinus notch. Two or three spines in low distal rim of fertile zooecia. Ovicells at first raised, with many pores, becoming immersed. Maui population lacking denticle entirely.

ETYMOLOGY: From the Latin *uncinatus*, hooked; refers to the tips of the avicularium rostrum.

HOLOTYPE: AHF Bryozoan no. 165.

TYPE LOCALITY: S-516-67, Pokai Bay, Oahu; 15–16 m.

DISTRIBUTION: On Oahu, S-500a-66, S-500b-66, S-506-66, S-508-66, S-515-67, S-516-67, S-517-67, S-518-67, S-519-67, S-520-67, S-521-67, S-522-67, S-526-68, S-530-66; 68 specimens from Pokai Bay, 75 in all. On Maui (toothless form), S-606-66, S-611-66, S-613-66, S-615-67; 70 specimens. Hawaii, S-707-67, 6 specimens; Kauai, S-803-67, 1 specimen.

DESCRIPTION: *Parasmittina uncinata* is another of the species with slim, paired or single, lateral avicularia directed proximally on the frontal. These originate from two or three frontal pores beside the peristome plus a lateral peristomal pore, to form a chamber that extends along the base of the peristome to the median proximal notch (fig. 5A). The inflated frontal places the slim avicularia in a position of reclining somewhat on their sides. As in *P. tropica* (Waters, 1909, p. 174), one of the frontal avicularia may be replaced by a larger avicularium. In *P. tropica*, the rostrum of the replacing avicularium has a triangular mandible, and the rostrum arises below the peristomal collar and bears hooked tips at the ends. In the replacement avicularia in *P. uncinata*, some of the larger avicularia are like the smaller ones, with finely serrate edges and a thin subspatulate mandible (fig. 5B, lower left zooecium.) However, in some zooecia, another type of avicularium originates on the side of the peristome, and angles down over the frontal, ending in rostral tips that are hooked strongly up (fig. 5C). The mandible has a strong triangular sclerite, and the blade is a narrowed spatula. When the avicularium is opened fully, the mandible curves around behind the peristome distally, suggesting the ability to clean off the peristome or extended tentacles.

In addition to the lateral avicularia, there are numerous tiny, pointed or rounded avicularia which originate at the areolar pores or other frontal pores. In older zooecia about to become submerged in calcification, the apertures are almost surrounded by tiny avicularia. No median, suboral or frontal, avicularia are seen, such as are occasionally found in *Parasmittina areolata*, but distal oral avicularia are often present.

Developing zooecia are raised distally, and the primary calcified frontal wall is smooth and thin. It becomes secondarily calcified with a coarsely beaded, glassy appearance. Two or three spines may be found on the distal margins of some zooecia. The distal peristome remains low in zooecia that will develop ovicells, with the other zooecia forming peristomes raised in distal and lateral peaks, curving around to a strong sinus notch proximally. In others the peristome is a tubular collar, with a deep sinus notch proximally. The primary aperture is round, with a narrow, acute or truncate denticle and paired lateral cardelles; the aperture becomes deep set with age. The operculum is horseshoe-shaped,

with a rim sclerite, and the proximal edge is incurved slightly. The denticle is formed by the fusion of the upper part of the primary apertural rim; a suture line can still be seen in the center of some mature denticles.

The ovicell develops as a bifurcation in the distal wall. A thin, two-layered calcareous hood is laid down on the next distal zooecium, but is supported by buttresses. The ovicell frontal fills in with a smooth surface that has a variable number of irregular pores, from a few central ones in some ooecia to those in which the entire frontal is porous.

The peristome fills in distally to form a proximal lip or brim on the ovicell on some zooecia and may bear a small avicularium directed up the brim. The frontal encroaches both proximally and distally, leaving only a small crescentic portion with pores exposed. The ovicells are similar to those of *Parasmittina areolata*, which appears to be a closely related species. The two species are difficult to separate in young colonies, but in older colonies, the larger, coarsely granulated zooecia with the hooked, curved large avicularia of *P. uncinata* are more distinctive.

Waters (1909, p. 174, pl. 17, fig. 13) noted the presence of an ovicell operculum in his *Smittia tropica*, semicircular in shape and about half the size of the zooecial operculum. Such an operculum is found in *Parasmittina uncinata* in ovicells containing large ova, but it is difficult to isolate. It is seated almost vertically, distal to the rim of the zooecial operculum, and is thus hidden by the ovicell hood.

Colonies of *Parasmittina uncinata* were extremely common at Pokai Bay, Oahu, forming extensive crusts on shell, coral, and concrete pipes used to construct an artificial reef. Colonies are colorful, with yellow ectocyst and bright pink ova, but they are not so deeply multilayered as some smittinids, although crusts were thickened even when composed of only a few multiple layers. Older areas of the colonies showed numerous marginal avicularia, and it is perhaps not coincidence, as hydroids and worms commonly infest the colonies, lying along the lateral walls and areolae.

It seems important to note that the colonies from Oahu all show the presence of the narrow denticle on most zooecia and the large uncinate avicularia. On the material from Maui, particularly Station 613, and the specimens from Station 707 on Hawaii, the denticle is almost entirely missing on the colonies with large hooked avicularia.

TABLE 10
MEASUREMENTS (IN MICRONS) OF *Parasmittina uncinata*

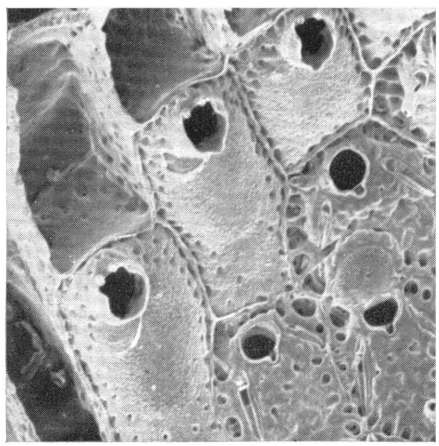
	Minimum	Maximum	Average	Number
Zooecium length	580	720	660	10
Zooecium width	420	560	492	10
Aperture length	110	160	133	10
Aperture width	100	140	115	10
Ovicell length	200	200	200	10
Ovicell width	210	260	259	10
Avicularia (long spatulate)				
Length	240	320	290	10
Width	40	60	58	10
Avicularia (hooked)				
Length	260	420	334	10
Width	110	130	119	10
Avicularia (short)				
Length	180	220	202	4
Width	30	40	38	4
Avicularia (long thin)				
Length	400	420	407	3
Width	100	100	100	3

Specimens apparently closely related to *Parasmittina uncinata* taken from Molokai, between Oahu and Maui, seem to require treatment as a separate species. On these the zooecia are invariably much smaller, the hooked avicularia are dwarfed, and the denticle is consistently absent. This form is discussed as *P. parviuncinata*, new species. As the Mauian population of *P. uncinata* is consistently like the Oahu form in all characters except for the absence of the denticle in the adults, we shall refer to it as form *edentata*, without implying taxonomic standing at this time.

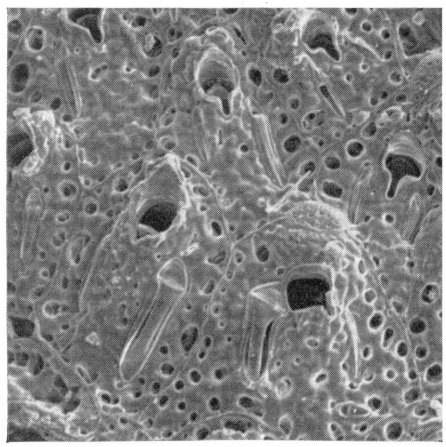
Parasmittina parviuncinata, new species

Figure 5D–F

DIAGNOSIS: Yellowish, incrusting species, with multilaminar, irregular growth. Zooecia small, with coarsely granular frontal, and with one or two rows of areolar pores. Aperture at first nearly circular without median denticle, but moderate-sized cardelles formed by the lower apertural rim. Two spines commonly visible on young specimens. Peristome becoming raised

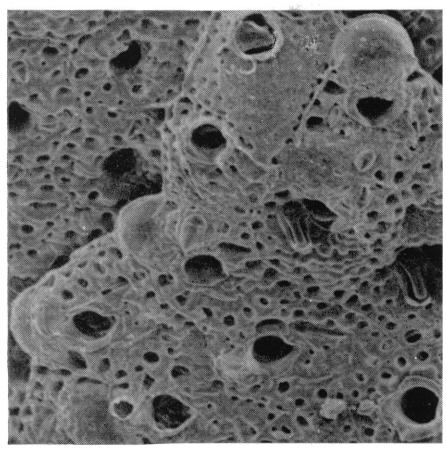


A



B

C



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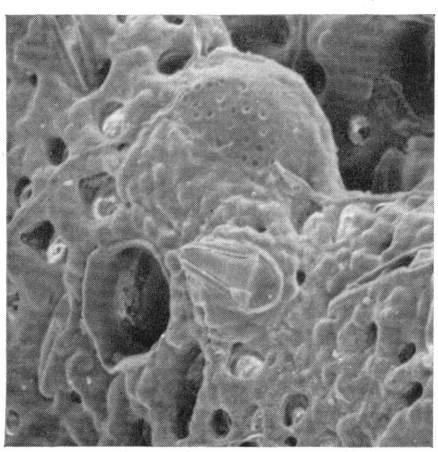

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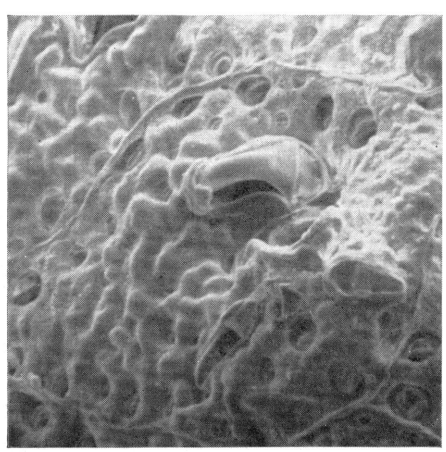


F

into lateral and distal peaks, or possibly becoming tubular, somewhat flaring. Avicularia long or short, paired or single, slim lateral frontal avicularia, directed proximally. In some zooecia, very short, subspatulate avicularium originating on side of peristome and curving across frontal. Rostrum with hooked points at distal ends. Additional small acute marginal avicularia possibly occurring. Ovicells recumbent, with numerous fine pores; encroaching frontal usually covering proximal portion of ovicell, and possibly carrying small, raised, acute avicularium onto ovicell.

ETYMOLOGY: Named for the small avicularium with hooked rostral tips.

HOLOTYPE: AHF Bryozoan no. 166.

TYPE LOCALITY: S-907-67, from Kaunakakai, Molokai; 14 m.

DISTRIBUTION: This species was found only on the island of Molokai at S-905-66, S-907-67, S-908-67, S-910-67, S-911-67, S-912-67; 80 specimens in all.

DESCRIPTION: *Parasmittina parviuncinata* is very similar to *P. uncinata*, new species; the most noticeable common feature is the curved, subspatular avicularium which originates on the side of the peristome and curves over the frontal proximally. Its rostrum has raised, smooth edges and these terminate in two hooked tips. However, in *P. parviuncinata* the hooked avicularia are only about half as large as those in *P. uncinata* (compare avicularia in fig. 5C of *P. uncinata* photographed ×116, with fig. 5F of *P. parviuncinata* photographed ×174). The paired, slim, frontal avicularia may be short or long, but are never widened into larger avicularia as in *P. uncinata*. There are usually many small acute marginal avicularia. Zooecia are small to medium in size, and numerous other pores are found in the area of the avicularia and beside the areolar pores.

The aperture is at first rounded, with the lower part of the rim forming the cardelles. The proximal rim is thin and no denticle is formed, except for an occasional needle-like tip or a bump. The peristome becomes raised either as a tubular collar with a channeled sinus, or into lateral and distal peaks which may flare somewhat.

Ovicells are recumbent, small, and have numerous small pores. They are not much raised and rapidly become immersed in frontal which encroaches across the proximal region, leaving only a small crescent of distal area of pores exposed (fig. 5D). The peristome becomes complete, tubular, in front of the ovicell. Small acute marginal avicularia may be carried onto the ovicell by the advancing frontal (fig. 5E).

Although this species is very similar to *Parasmittina uncinata*, intermediate forms seem to be lacking, and the distributions do not overlap. Forms of *P. uncinata* mentioned, from Maui, lack a denticle but are otherwise like that species in size and avicularian forms.

TABLE 11
MEASUREMENTS (IN MICRONS) OF *Parasmittina parviuncinata*

	Minimum	Maximum	Average	Number
Zooecium length	540	700	617	10
Zooecium width	380	480	421	10
Aperture length	160	200	172	10
Aperture width	120	140	128	10
Ovicell length	220	220	220	4
Ovicell width	220	260	240	4
Avicularia (long spatulate)				
Length	360	420	390	7
Width	90	110	101	7
Avicularia (hooked)				
Length	140	180	160	5
Width	60	80	66	5
Avicularia (short)				
Length	100	120	110	6
Width	40	60	47	6

FIG. 5. A–C. *Parasmittina uncinata*, new species. A. Developing edge of colony with wall folds, zooecia with primary calcified frontals, developing avicularia, denticles; ovicell with superficially calcified granular frontal. B. Immersed ovicells, peristomal peaks and deep sinus notches. Left foreground, long subspatulate avicularium; right foreground angular avicularium with hooked rostral tips. C. Developing ovicell, large avicularia with hooked rostral tips. D–F. *Parasmittina parviuncinata*, new species. D. New layer of colony overgrowing old. Ovicells immersed, no denticles, hooked avicularia small. E. Ovicell immersed in encroaching frontal. F. Tiny hooked (uncinate) avicularium surviving after overgrowth of aperture. Compare size with avicularia in figure 5C.

Parasmittina decorata, new species

Figure 6A–C

DIAGNOSIS: Colonies incrusting, white to tan in color. Zooecia rectangular and oriented in young, unilaminar condition, but disoriented, heaped, greatly varied in size in older, multilaminar colonies. Aperture round, or wider than high; peristome low except for small oral lappets at sides. Denticle medium wide, shallow set, and cardelles formed as acute tips of inner apertural rim. Operculum arch-shaped, with marginal sclerite ending at cardelle articulations; proximal margin straight or curved inward, unreinforced. One, two, or three spines possibly present in low distal peristomal space.

Primary calcified frontal smooth and finely granular, becoming glassy and rugose in older zooecia. Areolae small, and lateral walls thin. Avicularia various; numerous single or paired, tiny acute lateral frontal avicularia present with rostral tips raised and directed proximally and slightly toward one another. Small rounded, shoe-shaped avicularia possibly replacing one or both paired frontal avicularia, and other rounded avicularia possibly present on frontal. Giant spoon-shaped avicularia arising either distally or distolaterally along body wall beside aperture, and spread over much of frontal. Ovicells huge, erect, buttressed, bearing numerous large pores. Adjacent frontal encroaching proximally and distally, rising in frills, from which the name *decorata* is derived. Lozenge-shaped ovicell operculum present, separated from zooecial operculum, and placed in opening almost vertically, beneath forward curve of ovicell globe.

ETYMOLOGY: Latin, *decoro-atus* referring to the ornamented ovicell.

HOLOTYPE: AHF Bryozoan no. 167.

PARATYPE: BPBM K444.

TYPE LOCALITY: AuAu Channel, between Lahaina, Maui, and Lanai Island; Station S-605-67, 58 m. depth. Harvested with black coral by Mike King and John Lawson, of a commercial Scuba diving group; collected by the Soules from the black coral.

DISTRIBUTION: *Parasmittina decorata* was collected frequently from the south coasts of Maui and Molokai; it was first found on the black coral stems (*Antipathes grandis*) harvested by divers from beds in the AuAu Channel, at depths of 50–60 m. Also collected in quantity from areas where the bottom was a mixture of rock, coral patches, and sand, 3–16 m., and from a coral seamount in Kealaikahiki Channel at 120 m. Stations S-601-66, S-605-66, S-606-66, S-607-66, S-608-66, S-609-66, S-610-66, S-612-66, S-613-66, S-615-67, S-616-67, S-619-67, S-650-67, off Maui. S-703-66, Hawaii; and S-905-66, S-907-67, S-911-67, S-908-67, from Molokai. BPBM Lots 406, 408; specimens labeled Sand Island, Oahu, no other data.

DESCRIPTION: This species forms white, cream-colored or tan incrustations on black coral stems, arenaceous and calcareous worm tubes, reef corals, other bryozoans, and conglomerated sand. Unilaminar young colonies are regular, oriented, with subrectangular zooecia; older multilaminar colonies are heaped, little oriented, and the zooecia are varied in size and shape. Colony edges are often raised and free, and by budding upward, are apparently able to surround foreign material and overgrow it. No indication was found that erect tubular colonies are formed, such as are seen in *Parasmittina delicatula* (Busk).

Zooecia have convex, finely granular frontals, which may become glassy, beaded, or rugose in older zooecia. Areolae are small, with a few additional frontal pores found. Lateral walls are thin, but remain clearly marked in older areas where the areolae may be larger. The aperture may be circular, but is usually wider than high, and the peristome is mostly little raised, except for small lateral oral lappets on some zooecia. There is no sinus, and the denticle is medium to wide, sometimes anvil shaped, or truncate, and shallow set. The cardelles are distinct, moderate-sized, directed somewhat proximally.

The operculum is shaped to the primary aperture, and is edged with a marginal sclerite. The proximal edge is straight or slightly incised at the denticle, without a basal sclerite. The ends of the marginal sclerite rest on the cardelles. A single strong spine or spine scar is present on the flat peristomal space distally; occasionally there are two or even three spines (fig. 6C).

Lateral and distal walls form at the growing edges of the colony by upward folding of the doubled basal lamina so that both walls appear to be double. In older areas, it is difficult to distinguish between lateral and distal walls because of the random orientation of frontally budded zooecia. Zooecial walls are thin in the lower half, and perforated by a row of 10 to 20 small pores, plus a few small pores placed higher

up. The upper part of the wall is quite heavy where the frontal invests the original lateral wall folds. Distal walls bear scattered tiny pores, with larger openings at the lower corners.

Where additional layers of zooecia are forming above the old, the lateral walls grow upward like boxes. Other partitions are contributed, however, from upward growth of peristomal lappets, or the margins of the giant avicularia, or from the frills on the ovicell cover. Thus the new lateral walls are not restricted to those directly below them, and many oddly shaped spaces are seen. These spaces furnish pathways for algae, hydroids and worm tubules to permeate the colonies.

The zooecial bud apparently grows upward to the newly forming layer of zooecia, and the polypide originates from one lower corner pore of the new zooecial proximal wall. The polypide is thus diagonally set in the zooecium, which probably accounts for the random orientation of the upper layers. The primary calcified frontal originates proximally with lateral and distal growth around a single row of marginal pores. Before the frontal is closed, the apertural arch is complete from the distal spine area to the cardelles. The upper apertural rim grows proximally and centrally as the frontal fills in. The denticle is formed by the tips of the apertural arch which flank a small flap from the frontal. The secondary frontal calcification also proceeds in an oval from the sides.

Avicularia are numerous and varied. Small acute or rounded frontal avicularia are usually present, lying proximolaterally to the aperture on one or both sides well below the peristomal area. Acute rostra appear to originate from distal areolar pores and are directed proximally and centrally ("pigeon-toed"). When one or both small avicularia are replaced by oval, shoe-shaped avicularia, they appear to originate from lateral areolar pores (fig. 6C). Other small avicularia may be found on the frontal or at the areolae.

Large or giant avicularia with spoon-shaped mandibles are frequently found either distal or lateral to the apertures (fig. 6B). At the growing edges of young colonies, such avicularia lie transversely across the distal margin of the zooecia. The rostral cavities lie entirely along the distal wall of the zooecium and usually do not descend to the basal wall, although they sometimes do so in the initial layer of zooecia in the colony. The body wall forming the partition between the rostrum and the zooecium bears pores like those of distal walls. In older zooecia, the spoon-shaped avicularia originate disto-laterally and lie more or less longitudinally on one side of the supporting zooecium, sometimes extending beyond it proximally. Several instances of twinned giant avicularia were seen, one coming from each side of the zooecial aperture and covering the entire frontal.

The giant avicularia might be considered interzooecial as they originate between transverse walls. The shallow rostral chamber appears to lie on top of the zooecial frontal, but it is confluent with a larger vertical distal tubular chamber. In older, multilaminar colonies, the tube can sometimes be seen to come from the layer beneath as an independent chamber; in other cases, the chamber does not reach the level of the basal wall, lying entirely against the distal wall of the zooecium. The zooecium and avicularium usually arise at the same time, as though by twinning, but occasionally large, apparently functional avicularia exist where the sister zooecium has been overgrown.

The rostral opesium is pyriform, not large, and the rostrum becomes heavily calcified, with the margins turned upward. Small communication pores can sometimes be seen between the rostral wall and the zooecium. In one instance an enormous avicularium was found which bore a complete large avicularium on the rostral frontal area where the mandible of the giant avicularium had rested.

The ovicells of *Parasmittina decorata* are a most distinctive feature (fig. 6A). They stand erect, globose, compressed somewhat disto-proximally and wider transversely; they overhang the distal portion of the aperture as well as the adjacent zooecia. The ooecial cover formed by encroaching frontals appears to be contributed in three or four sections. The proximal portion comes from the peristomal region; the triangular lateral and distal flaps come from the frontals of adjacent zooecia. Buttresses support the ovicell, for it is so large that it extends to the apertures of the adjacent zooecia. The proximal cover of the ovicell does not fuse with the lateral and distal flaps, leaving an irregular area of numerous large pores exposed through which one or two orange ova can sometimes be seen. The edges of the coverings become thickened, and may be raised into a ruffled crest or erect finger-like projections.

There is a heavily chitinized, lozenge-shaped, ovicell operculum in ripe ovicells; it is placed in an erect position, curved inward beneath the ovicell globe. Dissection is necessary to see it.

Parasmittina decorata is probably closely related to *P. delicatula*, but seems to be adapted to living in shallower water, and in sandy areas. The erect, branching colony of *P. delicatula* has few avicularia, and the larger spoon-shaped forms are rare. Its ovicells are recumbent, following the slope of the frontals to present a streamlined effect (fig. 6D). The incrusting, multilaminar colonies of *P. decorata* bristle with avicularia, presumably adapted to their shifting substrata, numerous epizoites, and water-borne sand grains. Large avicularia have been observed to hold sand grains firmly in their rostra. Ovicells are erect, probably to keep them more free of sand. Current flow is minimal in the habitats frequented, perhaps permitting the ovicells to be erect without undue pressure.

Parasmittina decorata resembles *P. unispinosa* (Waters, 1889b, p. 15) from Australia, in the presence of a single spine, in the shape of the aperture and the operculum, and in the position of the ovicell. Waters found one vicarious spatulate avicularium larger than a zooecium, but he figured (pl. 3, fig. 2) a mandible of a round avicularium such as is not found on the present material. Brown (1952, p. 327, figs. 248–252) selected a lectotype for Waters's species. Brown described the avicularia as paired or single, often absent, spatulate or rounded, variable in size, usually placed as a rounded chamber on the frontal wall proximally to and on one side of the orifice, the rostrum somewhat raised directed more or less proximally. He did not figure the avicularia, and remarked that the large avicularia developed mostly where opposing edges of colonies meet. In our material small triangular avicularia are numerous; rounded ones are scarce. The larger avicularia are also numerous, widely distributed on the colonies, and the largest occur where frontal budding has produced multiple layers of zooecia. Powell (1967b, p. 330) described and figured *Parasmittina unispinosa* with large or small spatulate avicularia only. The apertures he figured (text-fig. 82) are virtually identical with the new species, but the ovicell resemblance is questionable.

Levinsen (1909, p. 64) stated that the ooecial cover of *Smittina unispinosa* was single, originating from the cryptocyst of the distal zooecium. This is clearly not true in *Parasmittina decorata*. Waters (1889b, pl. 3, figs. 1–3) figured markings on the ovicell of *Smittia unispinosa* which he compared with the stigma of Levinsen's material. Powell (1967b) did not figure the ovicell cover.

Waters originally described *Smittia unispinosa* from New South Wales, and Livingstone (1929, p. 90) reported it from New Zealand. Brown (1952) gave its Recent distribution as both of the above, and Port Phillip, Victoria, as well as an Upper Pliocene fossil from Castlecliff, New Zealand. Powell (1967b) gave three locations in northern New Zealand, and noted the subtropical marine climate that prevails in north New Zealand waters (p. 207).

Harmer did not seem to have identified *Parasmittina unispinosa* in the *Siboga* Expedition collections. His *Smittina subtubulata* (1957, p. 927, pl. 63, figs. 26, 30) has one or two spines, but the peristome has a raised proximal area, and the ovicells are not erect or large. Harmer's description of *S. fistulata* (1957, p. 925) is very similar to *P. unispinosa* except for the distinctive, erect colony form, narrower denticle, deeper peristome, and lack of the peristomal portion of the ooecial cover. Harmer included Kirkpatrick's *Smittia spathulata* (1890b, p. 619, pl. 17, fig. 1)

TABLE 12
MEASUREMENTS (IN MICRONS) OF *Parasmittina decorata*

	Minimum	Maximum	Average	Number
Denticle width	40	60	45	10
Zooecium length	520	700	630	10
Zooecium width	360	520	436	10
Aperture length	120	180	154	10
Aperture width	140	180	162	10
Ovicell length	340	380	358	9
Ovicell width	400	420	407	9
Avicularia (giant spoon-shaped)				
Length	440	580	493	9
Width	210	260	232	9
Avicularia (short triangle)				
Length	80	100	83	6
Width	40	40	40	6
Avicularia (short oval)				
Length	100	120	110	6
Width	40	60	64	6

from Torres Straits in his synonymy of *S. fistulata*, based on its elaborate tubular colony. It now appears that there are a number of species which produce erect colonies however.

Thornely's *Smittia glomerata* (1912, p. 152, pl. 8, fig. 12) shows very similar ovicells, but has a dentate apertural rim. Harmer's illustrations (1957, pl. 64, figs. 18–20) of Thornely's species show the ovicell to be more immersed and the apertures somewhat tubular as compared with *Parasmittina decorata*. The spatulate avicularian mandibles in Harmer's figure 20 are similar to ours, but in his text he referred to triangular avicularia (*op. cit.*, p. 934) and showed them oriented much differently (fig. 18) from those in Thornely's illustration. Thus it does not seem possible to characterize *S. glomerata* accurately.

Parasmittina delicatula (Busk), 1884

Figure 6D–F

Busk described (1884, p. 156, pl. 18, fig. 2, 2a, b) as *Mucronella delicatula* the tubular erect colonies collected "off Honoruru, Sandwich Islands, 20 to 40 fathoms." He noted the serial, subquadrangular zooecia, the granular frontal with a single row of border pores, the orbicular orifice with a "wide, expanded median mucro" and the "articular tooth" on each side. Busk found some triangular avicularia at one side of the zooecia, pointed downward, but he did not find ovicells or the large spatulate avicularia, which are rare.

Busk's figure 2a shows well the denticle and the wide triangular avicularia so typically seen in our Hawaiian material, which was found in the Bernice P. Bishop Museum collections. Lots 248 and 249 were taken from Pailolo Channel, between Molokai and Maui, and Lot 264 was taken off Waikiki, with no further data recorded. Presumably they were taken by dredging, as was Busk's *Challenger* material. Some material with limited data was given us by Vernon Brock, late director of the Hawaii Institute of Marine Biology. It was taken off Maui between 100–200 fathoms, probably from the Pailolo Channel. One colony of this material had a heavily calcified base, incrusted with coralline algae and foraminiferans. Colony stems are hollow, and branches occur in twos and threes, with some fusing of branches in distal areas.

The type of *Mucronella delicatula* Busk is in the British Museum (Natural History); slide 1887.-12.9.620, from which Busk's figure 2 was drawn, is about 10 rows of zooecia in width. The zooecia switch from linear arrangement to diagonal positioning at the areas of branching. Some frontal budding has occurred so that part of the colony is multilaminar.

In the Bishop Museum material ovicells are plentiful. They are similar to those of several smittinids that have a globose chamber with large pores in the frontal area. The encroaching frontal from the distal region may cover the ovicell to the center, and may have a frilled edge. The peristomal area contributes a proximal cover which is usually flat and does not meet the distal cover, leaving an irregular area of pores exposed. Ovicelled zooecia sometimes occur in long rows. The zooecial frontal slopes upward toward the aperture, and the ovicell hood is raised at about the same degree of slope. It is raised above the frontal of the next distal zooecium, but is partly immersed, or recumbent upon it. When the distal zooecia are arranged in alternate rows, the cover seems to be composed of two or three flaps; the globose ovicell then rests on two distal zooecia and buttresses rise from the lateral walls to support the large structure.

The triangular avicularia are distinctive in having a raised rostrum with a rather large premandibular area, semicircular in shape. The hinge bar is complete, but slender. The mandible is almost an equilateral triangle (fig. 6F), and the pointed rostral tip curves up like a spout. The avicularium originates from the lateral margin, either high or low on the frontal and directed proximally. It occasionally appears to be interzooecial, lying equally on adjacent zooecia.

A very few of the triangular avicularia are replaced by spatulate (spoon-shaped) avicularia, which originate from separate basal wall folds (fig. 6E). They become placed in a lateral or distal marginal position, depending on the orientation of the rows. The rostral chamber can sometimes be traced to the basal wall. A very few small oval avicularia, such as those reported by Harmer in *Smittina fistulata* (1957, p. 924) were found. Many zooecia have no avicularia, especially in the unilaminar areas, but the small triangles are numerous in older, multilaminar areas. Older zooecia are smaller, almost hexagonal, and not oriented.

The frontals of young zooecia are finely

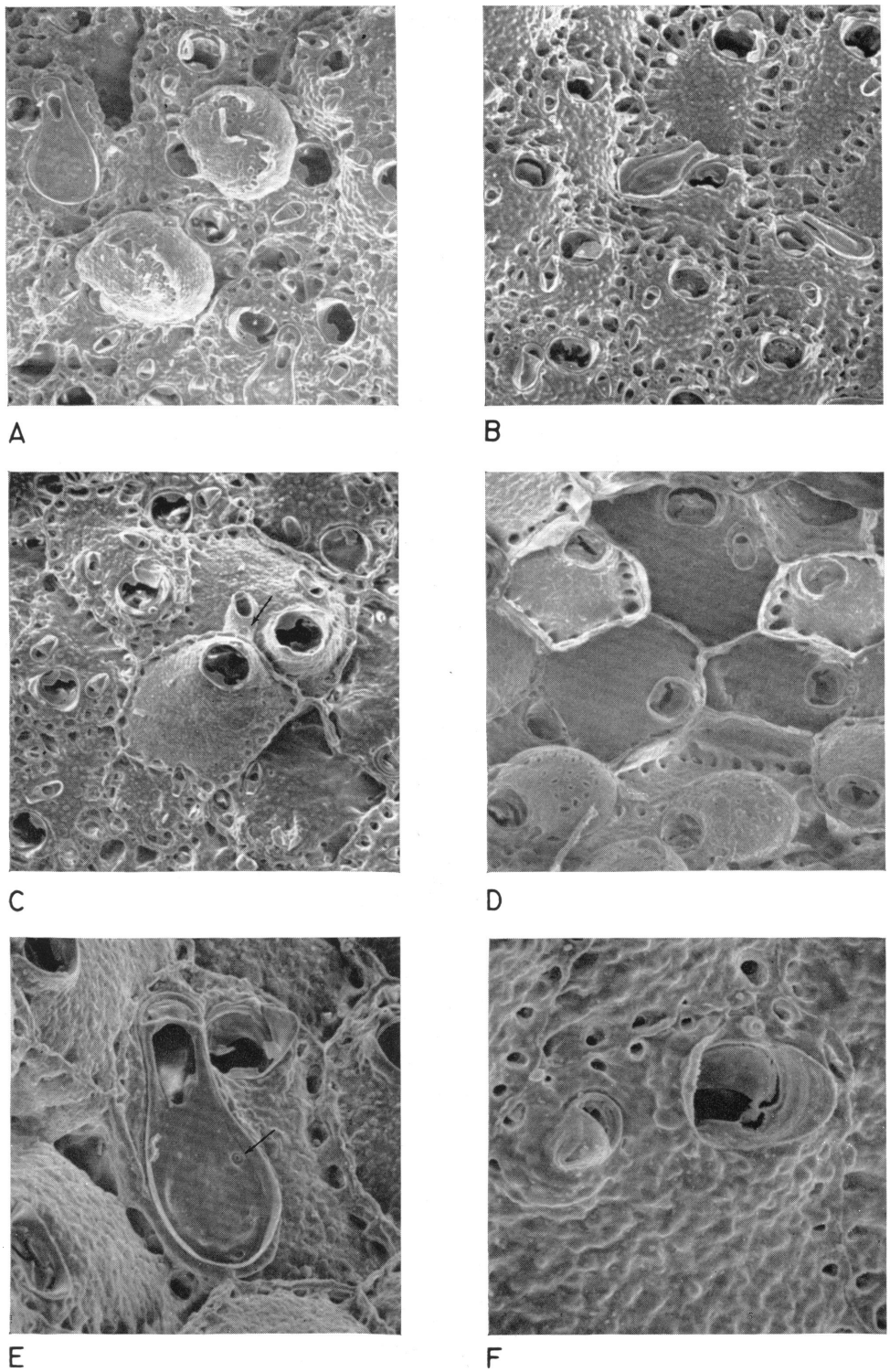


FIG. 6. A–C. *Parasmittina decorata*, new species. A. Giant avicularia, erect, giant ovicells with overgrowth of frontals. B. Orientation of giant avicularia with lateral or distal walls; note numerous small avicularia. C. Frontally budded developing zooecia showing origin of frontal avicularium (arrow). D–F. *Parasmittina delicatula* (Busk). D. Colony with developing walls growing upward for frontal budding. Note recumbent ovicells, few avicularia. E. Giant avicularium in contact with basal wall, communication pore (arrow) in submandibular rostral area. F. Aperture with single spine, lateral oral lappets, wide denticle, acute, raised avicularium.

granular, smooth, and not much inflated. Areolar pores are small. Even in early stages, the lateral walls begin to extend above the frontal level, and apparently continue growing upward well before a new layer of zooecia is formed (fig. 6D). Frontal budding appears to proceed from the distal area of the lower zoid to the proximal area of the new upper zoid.

The longitudinal rows of zooecia split readily, and show the zooecia to have a thick basal wall which is folded upward in distal areas in at least some zooecia. The lower part of the translucent lateral wall, formed from basal wall folds, has a row of many small pores across the middle level. This is topped by an opaque layer with a few, widely spaced, small pores, and capped by a dense, irregular layer contributed by the frontal. The distal walls have a row of pores across the bottom plus small pores completing an irregular circle around the margins of the wall.

The zooecial aperture is subterminal, elevated, and round, or wider than high. The peristome is not much raised, but may have small lateral lappets on some zooecia. Distally there are one or two tall spines on young zooecia. No sinus is present, and the moderately wide denticle is near the surface. The cardelles are hooked, small, set slightly below the level of the denticle opposite its tips. The operculum is arched, with a marginal sclerite, and may be straight across proximally or curved distad. It is inserted beneath the denticle and above the cardelles, as is the case in this group of species.

Smittina fistulata was described by Harmer (1957, p. 925, pl. 63, figs. 18–22) for a branching, tubular colony first described by Kirkpatrick as *Smittia spathulata*, from Torres Straits. Harmer also included in that species Canu and Bassler's (1929, p. 349) *Smittina nitida*, but not their *S. nitida delicatula*, from the Philippine Islands. Harmer described the species as having unilaminar tubes, zooecia distinct, in longitudinal rows. He gave the aperture as being circular, transversely oval, or pyriform, with a narrow denticle and sometimes with a denticulate margin, while Canu and Bassler gave the aperture as suborbicular with a broad denticle. Harmer described the peristome as moderately deep, slightly produced laterally and with two distal spines; Canu and Bassler described the peristome as little salient, thin, complete with two distal spines. Both gave the ovicells as large, globose, with pores. The avicularia were reported by them as small, oval, uncommon. Harmer's plate 63, figures 18 and 19 resemble *P. delicatula* greatly, although spatulas are very rare in Hawaiian material. No apertures were found like those in his figure 20, which shows a denticulate rim. The avicularia in figure 20 are similar to those in *P. decorata*, new species, which also lack a denticulate rim.

According to Patricia Cook (personal commun.) of the British Museum, the type of Harmer's *Smittina fistulata*, 45A, Station 77, is very much like the type of Busk's *M. delicatula*; the Harmer specimen has narrow denticles and the spatulas are rare, but the two might be synonymous. The Harmer specimen with the denticulate aperture (292B, Station 273), she agrees, is of a different tubular species. Tubular colonies are not apparently uncommon among parasmittinid species.

Harmer stated that one of Canu and Bassler's specimens in the British Museum has the tubular colony, and another has a giant spatulate avicularium. Specimen 129, examined by us at the British Museum, is like *P. delicatula*, but Specimen 128 is not.

Canu and Bassler's figure of *Smittina nitida* (1929, p. 349, pl. 42, fig. 4) resembles *P. delicatula* but no avicularia are shown and the ovicell pores are obscured. Their figures of "*S. nitida delicatula* Busk, 1883" (pl. 42, figs. 5, 6) show diagonally placed zooecia as contrasted to the linear arrangement in figure 4. The outer rim of the ovicell is clearly shown but again no avicularia can be seen. As both linear and diagonal zooecia occur in Busk's type, and in our material, on a single colony, the distinction is not definitive.

The identity of *Smittina nitida* (Verrill), 1875 has been greatly confused. Osburn (1912, p. 246, pl. 27, fig. 66a–e) described Verrill's species as a variety of *S. trispinosa* (Johnston), which has also been widely cited. Neither the oval nor triangular, spatulate and subspatulate avicularia on the material figured by Osburn approach in size the spoon-shaped avicularia on *P. delicatula*.

Hincks (1881a, p. 159, pl. 9, fig. 5) described and figured a specimen which he called *Smittia nitida* Verrill, giving its location as North America and Africa. He mentioned the "remarkable modification of the avicularium not noticed by Verrill," meaning the large spatulate avicularium. Harmer (1957) placed Hincks's African specimen in *Smittina aegyptiaca* (Waters), 1909. Yet Waters, in the paper describing

Smittia aegyptiaca as new (1909, p. 157), also cited *S. nitida* (Verrill) and figured it, as taken from the Red Sea (1909:173, pl. 17, figs. 19, 20). At the same time, he placed the *S. nitida* of Hincks in Thornely's *S. protecta*, from Ceylon.

Altogether, the synonymies present a very confusing picture. Our examination of material identified by Harmer as *Smittina aegyptiaca* in the British Museum indicates that much of it is not that species. Hastings (1927, p. 342), who gave a detailed description of that species from the type locality, agreed with us (personal commun.).

Canu and Bassler (1929) cited Osburn's material from the type locality as *Smittina trispinosa* var. *nitida* (Verrill) Osburn, 1912, and also cited as a separate species the *S. nitida* (Verrill) Waters, 1909. In addition, they cited separately the *S. trispinosa* var. *nitida* Hincks, 1881. Examination of USNM 8119–8124, labeled as Hincks's species, indicates that two or more species are included, and all the specimens are rather worn. It is doubtful that any of these could be included in *S. aegyptiaca* Waters. The lack of good comparative material precludes synonymizing them with any accuracy, but USNM 8119, 8121, and 8123 are similar to *P. decorata*, new species. USNM 8122 has an erect tubular colony like that of *P. delicatula*, but the avicularia are lateral oral, directed up the oral lappets. USNM 8124 seems to resemble *S. obstructa* Waters (the *S. parsevalii* of Harmer).

The Canu and Bassler specimen of *S. nitida*, USNM 8128, resembles Harmer's *S. fistulata*. The chief difference appears to be in the proportion of the types of avicularia present; their specimen contains one, somewhat raised, triangular avicularium, numerous small spatulate avicularia, and some large spatulate avicularia that arise distally and perhaps extend to the basal wall. Canu and Bassler's USNM 8129, labeled *S. nitida delicatula*, consists of tiny fragments, some with paired lateral oral avicularia, and some plain, but with no spatulas or complete ovicells. These are probably not the *P. delicatula* of Busk.

Maturo and Schopf (1968, p. 41) reviewed the status of the Verrill specimens of his *Discopora nitida* and designated as lectotype a specimen that they called morphotype A, which bears only a single acute avicularium directed proximally. No giant avicularia are present on it, or on their morphotype B, which has both small ovals and small acute avicularia, the form emphasized by Osburn. In Osburn, 1912, his plate 27, figure 66b resembles Maturo and Schopf's morphotype A, whereas figure 66 resembles their morphotype B (*op. cit.*, fig. 13A, B for morphotype A; fig. 12D for morphotype B).

TABLE 13
MEASUREMENTS (IN MICRONS) OF *Parasmittina delicatula*

	Minimum	Maximum	Average	Number
Denticle width	40	60	53	4
Zooecium length	500	540	511	10
Zooecium width	310	480	373	10
Aperture length	120	150	130	10
Aperture width	170	190	180	10
Ovicell length	300	310	301	10
Ovicell width	340	380	348	10
Avicularia (giant spoon-shaped)				
Length	660	—	—	1
Width	280	—	—	1
Avicularia (short triangle)				
Length	100	110	107	3
Width	60	70	63	3
Avicularia (short oval)				
Length	120	120	120	2
Width	50	60	55	2

From Hawaii, the material most closely resembling *P. nitida* (Verrill) morphotype A, is the material collected by A. E. Verrill in Hawaii, and never described. It is described herein, as *P. emersoni*, new species. Maturo and Schopf indicate that the distribution of *P. nitida* is apparently limited to the western Atlantic. It seems probable that morphotype A represents the *P. nitida* of Verrill, while morphotype B is a distinct, undescribed species.

Parasmittina emersoni, new species

Figure 7A, B

DIAGNOSIS: Colonies heaped, multilaminar, incrusting on arenaceous and calcareous worm tubes. Zooecia very small, quadrate or hexagonal, with medium-sized areolar pores. Frontal area reduced, heavily calcified, mammillate. Body walls strong, possibly extending above level of frontal. Aperture round, or wider than high, without sinus. Peristome not raised, but mammillae of frontal possibly encroaching on

apertural area. Two spine scars rarely seen. Denticle wide, cardelles being strong hooks located slightly distal to denticle tips and lower in aperture. Small, lateral frontal avicularium present on some zooecia. Avicularium short, triangular, directed proximally, with rostrum either low or level, or raised in rounded eminence. Ovicells large compared with small zooecia; raised, supported by buttresses from lateral and areolar walls. Frontal of ovicell with numerous large pores; distally frontal encroaching to form covering possibly rising in peaks and frills at top of ovicell, leaving pores mostly exposed until next layer of zooecia forms above.

ETYMOLOGY: Named for Dr. William K. Emerson, Chairman of the Department of Living Invertebrates of the American Museum of Natural History.

HOLOTYPE: AHF Bryozoan no. 168.

PARATYPE: AMNH 570.

TYPE LOCALITY: The label reads "Hanalei Beach" (north Kauai) "Mch 26.1926."

Parasmittina emersoni was found only in a collection made by A. E. Verrill, in Hawaii. It remained unidentified at the American Museum of Natural History, until forwarded to us by William K. Emerson, for whom it is named. The specimens are badly worn. The label was initialed, handwritten "A.E.V."

This species was not collected at our stations S-801-67 or S-805-67, which are near Hanalei. No large worm tubes were collected by us in that area however, and it is possible that the tubes were thrown up on the beach by one of the storms which strike the north coast so violently. Another possibility is that the tubes were removed from mollusk shells from deeper waters, which were identified by Dr. W. H. Dall at the National Museum of Natural History according to the accession labels at the American Museum. This species was not found at any other location in Hawaii; 22 specimens in all.

DESCRIPTION: Colonies are heaped, with up to eight layers of zooecia; found only on calcareous and arenaceous worm tubes. Zooecia are quite small, irregularly oriented, quadrate or hexagonal. The frontal area is quite reduced, with medium-sized areolar pores. The frontal is coarsely granular, thick, and often mammillate calcareous deposits are present. The body walls are prominent, apparently growing upward rapidly, and serving to protect the zooecia while budding the next superposed layer. The mammillate deposits also strengthen the structure of the colony. Some of the colonies have a honeycomb appearance due to the multiple layers, the small zooecia, and the relatively large apertures (fig. 7A). Apertures are mostly round, but some may be wider than high, and others may be higher than wide. There is no sinus, and the peristome is not raised into lappets, except where the mammillate deposits are built up. The aperture has a medium wide denticle, shallow set and truncate, and strong curved cardelles situated just distal to the tips of the denticle and slightly below them.

Avicularia are not common, but seem to occur in certain areas of colonies. A single, triangular, lateral frontal avicularium is placed below the peristome, directed proximally. The rostrum may be level, or raised onto a spout, or inflated to a rounded eminence. The rostral edges are low, the premandibular area is small, semicircular, and the submandibular opesium is rounded. The avicularia are similar in size and position to the acute avicularia in *P. delicatula*, but in that species the rostral edges are raised. The avicularium of *P. emersoni* apparently originates from a lateral pore and does not seem to connect with any peristomal pores. However, the developmental stages are difficult to see on the present material.

Development must proceed very rapidly in this species, as new lateral walls are under way while the underlying layer of zooecia is being completed. The size of the sand grains of the arenaceous worm tubes frequently exceeds the size of one or more zooecia. In developing zooecia, the secondary calcification of the frontal appears to advance as a thickened fold, forming an oval opening continuous with the apertural rim, which is a wide open arc. The rim ends at the cardelles, which are strong, acute, and wide set so that they mark the juncture of the frontal fold and the apertural rim. The two structures form an oval resembling the cryptocyst of an anascan. The apertural rim moves inward somewhat, but does not seem to contribute to the denticle, which seems to be formed entirely by the primary frontal layer.

The ancestrula is calcified, smooth, and semierect; it has a rounded, subterminal aperture with an almost straight proximal border. There are 10 spines placed around the aperture, except at the center of the proximal border. Two spines are very rarely seen on other zooecia.

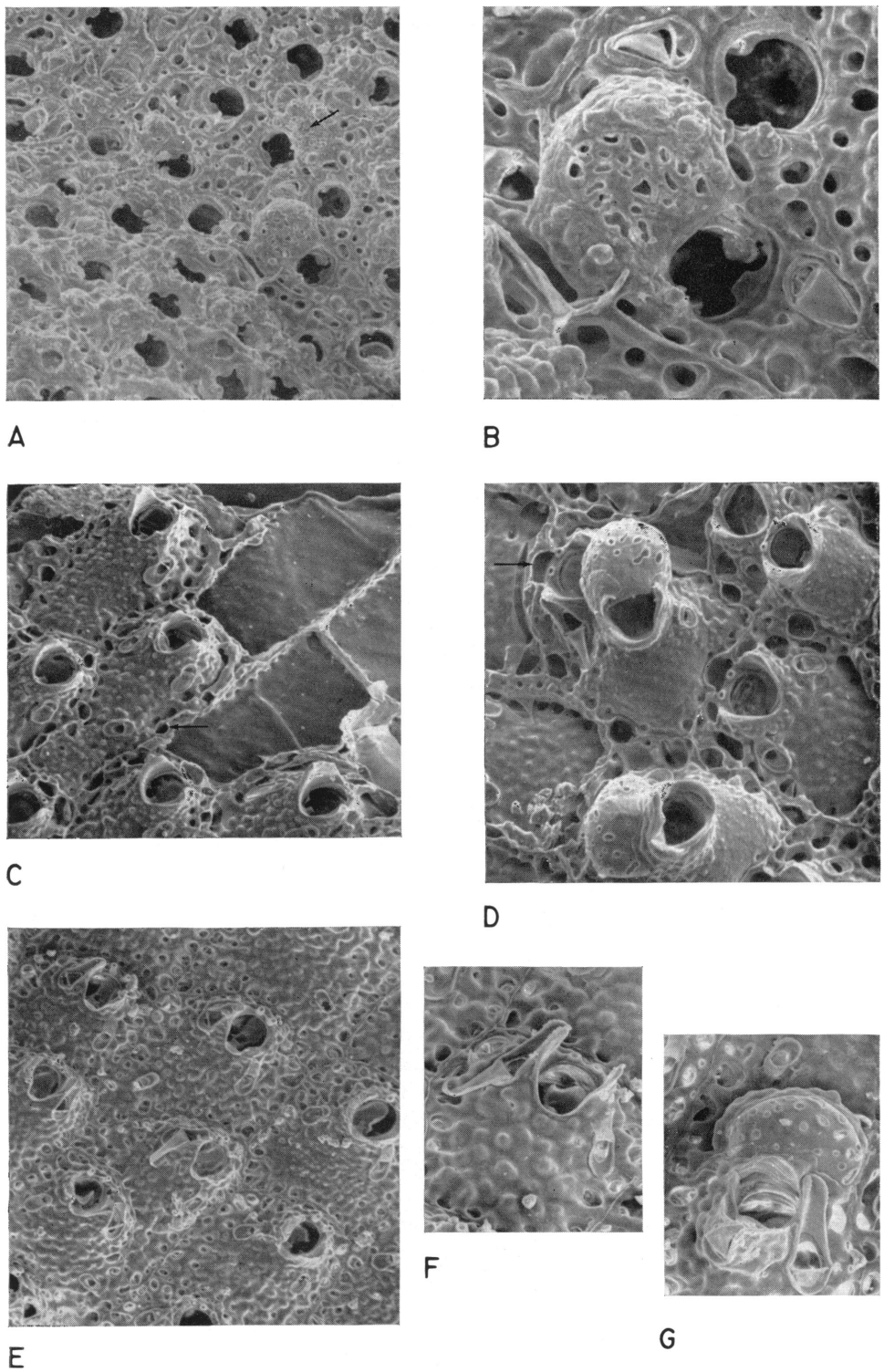


FIG. 7. A, B. *Parasmittina emersoni*, new species. A. Colony, with submerged ovicell (arrow). B. Ovicell, apertures with denticle, cardelles at surface. C, D. *Parasmittina marsupialis* (Busk). C. Developing edge of colony with lateral, transverse walls; tubular with opening (arrow). D. Marsupial ooecia frontally budded, with aborted ovicell opening back of parent zooecium (arrow). E–G. *Parasmittina leviavicularia*, new species. E. Colony showing avicularia directed up peristome or proximally on frontal. F. Raised oral lappet and avicularium. G. Ovicell with many pores, raised avicularium, and extra avicularium near center of proximal peristome.

Few ovicells were found, except for those which could be dissected from superposed layers. They are large in comparison to the small zooecia, but are about one-quarter the size of the ovicells of *P. decorata*, which they resemble somewhat. The ovicell is raised but recumbent, with a central area bearing many large pores (fig. 7B). Distally, the encroaching frontal forms a cover which may rise in peaks or frills along its edge. There are usually several buttresses rising from the lateral walls or areolar partitions, to support the ovicell. When the next layer upward is formed, the ooecial cover usually participates in forming new body walls. The peristome area contributes only a thin layer to the proximal face of the ovicell. A small ovicell operculum was found in a few ooecia that bore ova.

The lateral walls are so heavy that it is difficult to see the communication pores. On the basal colony layer, one, two, or three rows of tiny lateral pores were found. On upper layers, one or two rows of six to 10 pores may occur. Distal walls have a circle of larger pores, sometimes additional central pores, and there are almost invariably larger corner pores. The budding pattern seems to be similar to that in *P. decorata*, where the new polypide apparently originates by diagonal growth upward into the new layer, through one or the other corner pore.

In vertical sections through the colony, the chambers of the avicularia can sometimes be seen to form a triangular space across the corner, between the upper lateral wall and the frontal. The frontal is equally thick above and below the avicularian chambers, suggesting an interzooecial origin for the avicularia.

Both *P. emersoni* and *P. decorata* appear to be adapted to sandy substrata, and to have similarities in the shape of the apertures and the ovicells. They in turn share the characteristics of aperture and ovicell shape with *P. deliculata*, which shows a much different growth form and habitat. It is possible that these species share a common ancestral form, such as the Pliocene *P. unispinosa*. The distributions of the Hawaiian species do not overlap in the present collections.

The resemblance of *P. emersoni* to *P. nitida* (morphotype A) is striking, especially because Verrill himself collected both. The differences are slight, the size of the ovicell pores and the width of the denticle being greater and the cardelles more acute in the Hawiiaan specimens. Dr. Frank Maturo compared SEM photographs of both specimens with us and agreed that the two are different species (personal commun.).

TABLE 14
MEASUREMENTS (IN MICRONS) OF *Parasmittina emersoni*

	Minimum	Maximum	Average	Number
Denticle width	40	50	43	6
Zooecium length	400	600	453	10
Zooecium width	240	390	325	10
Aperture length	80	120	104	10
Aperture width	80	120	114	10
Ovicell length	180	200	190	2
Ovicell width	220	220	220	2
Avicularium length	100	120	112	10
Avicularium width	60	70	63	10

The new species resembles somewhat the species of *Hemismittoidea* in having a single avicularium placed almost medially. It differs in that the avicularia of *P. emersoni* originate only from the lateral areolar area and are not apparently ever connected to the sinus. It seems possible that parasmittinids having only a single avicularium are distinct from those that generally have paired avicularia, even though in the latter these occur singly in some zooecia in a colony.

Parasmittina marsupialis (Busk), 1884

Figure 7C, D

Smittia marsupialis was described by Busk (1884, p. 151, pl. 18, fig. 1), from *Challenger* Station 260, off Honolulu, Hawaii, at 20–40 fathoms. The species seems not to have been recognized since that time, although its ovicells are distinctive and Busk's description is quite accurate. The type specimen is in excellent condition (BMNH Slide 87.12.9.601.). It was also reported by Busk from *Challenger* Station 313, which is in South America, opposite the Straits of Magellan, off Cabo Virgenes. USNM 9234 of the Busk Collection, from Cabo Virgenes, and the British Museum material from Station 313 do not seem to be the *S. marsupialis* of Hawaii, but resemble the *S. trispinosa* var. *munita* of Marcus (1937, not 1938).

The colonies of *P. marsupialis* form large patches of yellowish crust on shell, worm tubes, and coral. The zooecia are subquadrate, with the mature frontal raised, granular, and imperforate. The aperture is elevated, rounded or pyri-

form, higher than wide, and there is no sinus. The denticle is narrow, usually tall, and anvil-shaped, and the moderately strong cardelles lie opposite and slightly below the level of the tips of the denticle. The peristome is low, with lateral oral lappets raised. There may be two spines, and a small crescentic space lies distal to them with the appearance of separation in the distal body wall (fig. 7C, D). The frontal wall slopes upward to the low proximal part of the aperture. The operculum is fragile and horse-shoe-shaped, with a marginal sclerite around distal and lateral edges. In older zooecia, the operculum is sometimes reinforced with chitinous bars across the base where it articulates with the denticle.

Avicularia are numerous; small, short triangular, or rounded, shoe-shaped ones may be paired or single. These may point up the oral lappets of the peristome or they may lie outside the peristome, directed proximally. Other, slightly larger, oval avicularia lie on the proximal frontal, directed either toward the center or toward the margins. Additional triangular frontal avicularia may occur. Occasionally one of the shoe-shaped avicularia is enlarged to about one-half the frontal length, but no "giant" avicularia are found.

A remarkable feature of *P. marsupialis* is the placement of the ovicells (fig. 7D). A smaller ooecium grows upward entirely within the frontal area of the parent zooecium. A transparent primary frontal first forms, inflated above the parent frontal but not covering the parent aperture. Calcification proceeds in an arc from proximal and lateral walls, forming a conical upright ooecium which may be oriented in the same direction as the parent, or be transversely or diagonally placed. Its peristome also bears two spines, and a free-standing ovicell hood forms distal to the spine scars. With the addition of ova, the hood sags over, and may even rest on the parent zooecium, without blocking its aperture. Both parent and daughter zooecia appear to have functional polypides at the same time. The ovicell aperture is pyriform and the peristome is tubular. A small ovicell operculum can be found in hoods containing ova; it is placed high up and slanting in the hood.

The distal marginal space behind the spines in the parent zooecia appears to represent the area that would produce ovicells in other species. Ovicells were never seen in this position on the more than 50 specimens collected, but the marsupial ovicells were numerous.

Another peculiarity of this species concerns the form of the lateral walls. Lateral walls are formed by folding upward of the basal wall, but there is usually little evidence of this in unsectioned mature zooecia. In *P. marsupialis*, the lateral folds appear to rise above the level of the frontals, expanding into tubulae that run along the tops of the lateral walls. There are many openings in the tops of the tubulae, similar in size to areolar pores, which are adjacent to the tubulae. The frontal wall seems to contribute to the tubule surface, giving a frilled appearance to the tubule in places (fig. 7C). There are also very tiny pores in the bottoms of the tubulae, which suggest that the layers of the lateral wall are incompletely fused, leaving a few minute vertical passages to the exterior basal surface. Dye introduced into the tubulae quickly courses through these channels without entering the body cavities, and occasionally penetrates in minute amounts to the basal surface. This structural peculiarity may be associated with the production of the buds for the ooecia. Internally, the lateral walls present the usual pattern of thinner lower wall penetrated by a row of small communication pores, plus an upper portion that is thicker where the frontal descends around the areolae.

Many smittinids appear to be infested with algae or worms that weave strands or tubules through the areolae or along the tops of the lateral walls. However, the tubulae on the walls of *P. marsupialis* seem definitely to be produced by the bryozoan. No organic material was found inside them, such as might be the case in worm tubules. The tubulae become white with increased calcification, as do the oral lappets, so that the colonies of this species can usually be recognized by the distinctive white gridlike pattern of the tubulae on the yellowish frontal surfaces.

Distal walls also appear to be formed by folding of the basal walls (fig. 7C), and are perforated by a circle or basal arc of pores. Tubulae also occur atop the distal walls, where they lie open and spread out to form the crescent where the ovicell would be formed in other species. The exterior basal wall is smooth and translucent, showing the patterns of the lateral walls, and knobby protuberances are present which act as anchors on irregular substrata. Fine, white cal-

careous tracings crisscross the basal exterior, suggesting that the colony does not adhere tightly to the substrata. The patterns of frontal formation are similar to those of other smittinids discussed in the present paper.

The principal problem in identification of this species is found in those specimens lacking ovicells. In their absence, the lateral tubulae and the distal crescent space are the most distinctive features. Several other species have been described in which paired, acute avicularia are directed up the oral lappets. These include *Smittina tripora* of Canu and Bassler (1929, p. 350), which Harmer (1957, p. 941) tentatively placed in his *S. parsevalii* (Audouin). Harmer also placed *Smittia obstructa* Waters, 1889, in his *S. parsevalii*, tentatively. Waters's species has similar oral lappets, with some pointed, ascending avicularia, and some oral avicularia directed proximally; it also has giant spoon-shaped avicularia. The shape of the aperture and the size of the denticle in Waters's species are similar to those of *Parasmittina marsupialis*. Thornely's *Smittia ornata* (1912, p. 152) also has the pointed lateral oral avicularia directed upward. All of the above species have occasional giant spatulate avicularia, which are not seen in *P. marsupialis*.

DISTRIBUTION: Primarily found in Pokai Bay, Oahu: S-514-67, S-515-67, S-516-67, S-521-67, S-522-67, S-525-67. Also at Kaunakakai, Molokai, at S-911-67; 54 colonies in all.

TABLE 15
MEASUREMENTS (IN MICRONS) OF *Parasmittina marsupialis*

	Minimum	Maximum	Average	Number
Denticle width	20	40	32	10
Zooecium length	520	600	572	10
Zooecium width	380	510	424	10
Aperture length	130	160	142	10
Aperture width	120	160	139	10
Ooecium length	280	320	298	5
Ooecium height	280	310	302	5
Ovicell length	180	200	182	10
Ovicell width	220	260	234	10
Avicularia (oral)				
Length	100	120	106	5
Width	40	60	48	5
Avicularia (acute)				
Length	180	220	203	6
Width	80	100	85	6

Parasmittina leviavicularia, new species

Figure 7E–G

DIAGNOSIS: Incrusting species forming yellowish crusts on rock and coral. Primary aperture higher than wide, oval or pyriform, with oral lappets placed laterally. Paired lateral oral avicularia ascending lappets, and rostra prolonged into curved, serrate tips; or paired small oval avicularia placed laterally and directed proximally, or with possibly one ascending and one descending lateral oral avicularium. Peristome low distally when two spines present. No sinus notch or groove, but narrow, anvil-shaped denticle deep set. Frontal granular, sloping upward to raised apertural area. Ovicells recumbent, with about 14–24 pores. Two rows of areolar pores, possibly merging into one surface opening in older areas. Small oval areolar avicularia common; no giant avicularia.

ETYMOLOGY: The species is named *leviavicularia* for the raised position of the lateral oral avicularia.

HOLOTYPE: AHF Bryozoan no. 169.

TYPE LOCALITY: S-707-67, Mahukona Beach Park, Hawaii; collected July 16, 1967, at 13 m.

DISTRIBUTION: On Kauai: S-803-67; on Molokai: S-907-67, S-908-67, S-911-67; on Maui: S-600-66, S-601-66, S-610-66, S-613-66, S-615-67, S-650-67; on Hawaii: S-707-67, S-710-68; 45 specimens in all.

DESCRIPTION: Colonies are heaped, multilaminar, forming a yellowish crust on coral and rock. Zooecia are oriented in rows and nearly rectangular in shape in young colonies, rounded distally and with apertures somewhat elevated. The primary aperture is rounded, wider than high, becoming pyriform with the growth of lateral oral lappets (fig. 7E). The denticle is narrow, anvil-shaped with pointed tips. The cardelles are small, acute, and placed slightly distal to the tips of the denticle. Two spines may be present distally. The proximal portion of the peristome occasionally forms a projection, merging with the lateral oral lappets to form a spout. The operculum is horseshoe-shaped, reinforced with a marginal sclerite around the curved edge; the base is straight or slightly incised, not reinforced.

The paired lateral oral avicularia originate from a lateral frontal pore and a peristomal pore located at the level of the cardelle. When present, the lateral avicularian rostra ascend the oral

lappets, which become elongated, and raised into a lip with serrate edges (fig. 7F). The premandibular area is semicircular, and the mandible is a long triangle or may widen slightly before it forms a hooked tip. Some rostral chambers are much inflated.

One or both ascending avicularia are sometimes absent, or may be replaced by small oval or shoe-shaped avicularia directed proximolaterally. These are also connected to a frontal pore and a peristomal pore, and the rostrum retains a tubular connection with the peristomal pore in the premandibular area. The three upper zooecia in figure 7E show this. The oval avicularia are sometimes enlarged but they never approach the size of the giant spoon-shaped or bilobate avicularia seen in *P. parsevaliformis*, new species. The giant avicularia in the latter species appear to originate interzooecially.

An additional ascending avicularium is sometimes present on peristomes which fill in proximally, particularly on ovicelled zooecia. On other zooecia where the apertures are sufficiently elevated, there is occasionally a hatchet-shaped avicularium descending the frontal, on the distal side of the aperture.

The ovicell arises as an irregularly margined hood, with small projections which merge around the pore spaces to complete the globe. The peristome may grow across the proximal part of the ovicell, forming a projecting brim or lip, and the encroaching frontal may also move in behind the brim in a thin strip. A heavier rim is formed round the distal base of the ovicell, but the pores remain exposed. No avicularia were seen to encroach on the ovicell itself, as is the case in the *Smittina parsevalii* of Harmer (1957 p. 942). There are from 14 to about 24 pores in *P. leviavicularia* (fig. 7G).

There are a number of species in the literature which have acute, ascending, lateral oral avicularia; several of these also have the spatulate or spoon-shaped avicularia. The *Smittina tripora* of Canu and Bassler (1929, p. 350) from the Philippines is not, according to Harmer, the same as the *Smittia tripora* Waters, 1904, from the Antarctic. Canu and Bassler's specimen is similar to *S. obstructa* (Waters, 1889b, p. 18), but the spatulas are much smaller.

Kirkpatrick (1888, p. 80, pl. 10, fig. 3) described and figured *Smittia latiavicularia* as having acute, paired, ascending avicularia, as well as the small oval avicularia seen in the present new species. No large spatulate avicularia were found on that species, but Harmer (1957, p. 944) in his section on *Smittina parsevalii*, mentioned it as being similar to Thornely's *Smittia ornata* (1912, p. 152), though without the "bosses" on the ovicells. Thornely's species has large spatulas however. The *S. trispinosa* var. *i* of Hincks (1884b, p. 361, pl. 13, fig. 7) shows acute lateral oral avicularia, but they are usually not elevated, and sometimes frontal avicularia typical of *Smittina trispinosa* are present. The *Smittia rostriformis* of Thornely (1905, p. 123) resembles *Parasmittina leviavicularia*, but is probably the *S. latiavicularia* of Kirkpatrick (1888, p. 80) rather than his *S. rostriformis*. Kirkpatrick's *S. rostriformis* resembles our *P. serrula*, new species, or the *Smittina areolata* of Canu and Bassler. Examination of a number of specimens rather than the types alone is needed before conclusions can be drawn on synonymizing any of the above-mentioned species.

Kirkpatrick (1888, p. 80) also described *Smittia murarmata*, with a single avicularium ascending the lateral oral margin. This may be related to the *Smittina projecta* of Okada and Mawatari (1936, p. 66), from Izu Peninsula, Japan, which has one long elevated avicularium with serrate rostrum, a moderately wide denticle and ovicells with many pores. This is probably the *Smittina trispinosa* var. *applicata* of Canu and Bassler (1929, p. 345). We have examined their holotype, USNM 8127, also from Japan. It is a small, worn colony, and shows only the single

TABLE 16
MEASUREMENTS (IN MICRONS) OF *Parasmittina leviavicularia*

	Minimum	Maximum	Average	Number
Denticle width	20	40	31	10
Zooecium length	520	620	568	10
Zooecium width	400	500	446	10
Aperture length	130	140	139	10
Aperture width	110	120	118	10
Ovicell length	200	220	208	4
Ovicell width	260	300	275	4
Avicularia (acute, up)				
Length	200	240	216	10
Width	80	100	90	10
Avicularia (oval)				
Length	100	220	162	10
Width	40	100	72	10

ascending avicularium. Frontals are white, finely granular, and pearly. The only difference between Okada and Mawatari's illustration and Canu and Bassler's type is in the number of pores in the ovicell. The USNM specimen has few pores. The condition of the material makes determination difficult, but none of these forms appears to be identical with the new species, although they may be closely related. Thornely (1912, pl. 8, fig. 14) illustrated Kirkpatrick's *S. murarmata* as having two ascending avicularia, and described the colonies as red or orange and the ovicells as being rather flat, with a frontal area of irregularly shaped pores. Both Thornely and Kirkpatrick worked on Indian Ocean material.

Parasmittina parsevaliformis, new species

Figure 8A–F

DIAGNOSIS: Yellow to tan incrusting species forming flat, oriented colonies when young; older colonies multilaminar, heaped, disoriented. Zooecia nearly rectangular, with granular frontals and small areolar pores. Primary apertures round, with medium-sized denticle, shallowly set, and with cardelles opposite tips of denticle. Peristomes with raised lateral oral lappets and two or three distal spines, or raised in a distolateral collar. Secondary apertures pyriform, higher than wide. Avicularia with acute, bulbous lateral oral avicularia ascending oral lappets on one or both sides, or paired, acute or oval frontal and areolar avicularia. Large spoon-shaped avicularium arising alongside aperture on many zooecia, directed proximally. Ooecia with few pores, tubular peristome, and often bearing avicularium on distal part of hood.

ETYMOLOGY: Named for its resemblance to *P. parsevalii* (Audouin).

HOLOTYPE: AHF Bryozoan no. 170.

PARATYPE: BPBM K445.

TYPE LOCALITY: S-514-67, Pokai Bay, Oahu, 21 m. Collected July 9, 1967.

DISTRIBUTION: Oahu, Pokai Bay: S-514-67, S-521-67, S-522-67, S-526-68, S-527-68; Mokumanu: S-507-66; Hauula, BM 401. On Molokai: S-905-66, S-907-67, S-910-67. On Maui (scarce): S-610-66, S-613-66. One hundred fifteen specimens in all.

DESCRIPTION: Another of the yellowish to tan incrusting species found abundantly in Hawaii, *Parasmittina parsevaliformis* was collected from a variety of substrata, on rock, cement, coral, and shell. Colonies are flat and oriented in alternate rows in young, unilaminar specimens, becoming heaped and randomly arranged after undergoing frontal budding into multilaminar colonies. Zooecia are elongate, subrectangular, rounded distally (fig. 8A), becoming more varied in shape in older colonies. The primary aperture is at first round, with a narrow to medium-sized denticle that is near the surface. The denticle is anvil-shaped, and the cardelles are set opposite the tips of the denticle, but somewhat deeper. The peristome has lateral oral lappets and two of three spines in the low distal position, or it is raised distally and laterally in a collar when spines are absent. The secondary aperture is rounded or pyriform and is higher than wide. There is no sinus, except in the ooecia, which often have channeled tubular peristomes. The operculum is rounded distolaterally, straight proximally. It is thin in young zooecia, but in older zooecia the operculum may have a heavily chitinized rim and horizontal bar, complete or incomplete, at the level of the denticle, similar to that figured by Waters (1909, pl. 15, fig. 8) for his *Smittia egyptiaca.*

Avicularia are numerous and varied. Acute lateral oral avicularia, if present, ascend the oral lappets on one or both sides. These have a bulbous rostrum, with a semicircular premandibular area, and a triangular mandible, which is sometimes elongated slightly (fig. 8B). One or both of the acute avicularia may be replaced by oval avicularia that are directed down the frontal proximally or proximolaterally. Other oval or triangular avicularia may lie on the frontal, or along the areolae, or on the distal side of the peristome. Large, spoon-shaped avicularia are common; they appear, in mature condition, to belong to zooecia which are modified by the loss of the contiguous oral lappet, and by the distortion of the aperture. They seem to arise alongside the aperture and curve proximally over the zooecial frontal (fig. 8A).

In our Hawaiian material, it can sometimes be seen that the spoon-shaped avicularia actually originate in separate areas of the basal wall on the growing edge (fig. 8C). In older areas, it is possible to dissect and find rounded or narrowly rectangular chambers which suggest simultaneous but independent frontal budding of these large avicularia, distal to the supporting zooecium. Separate lateral walls, complete with

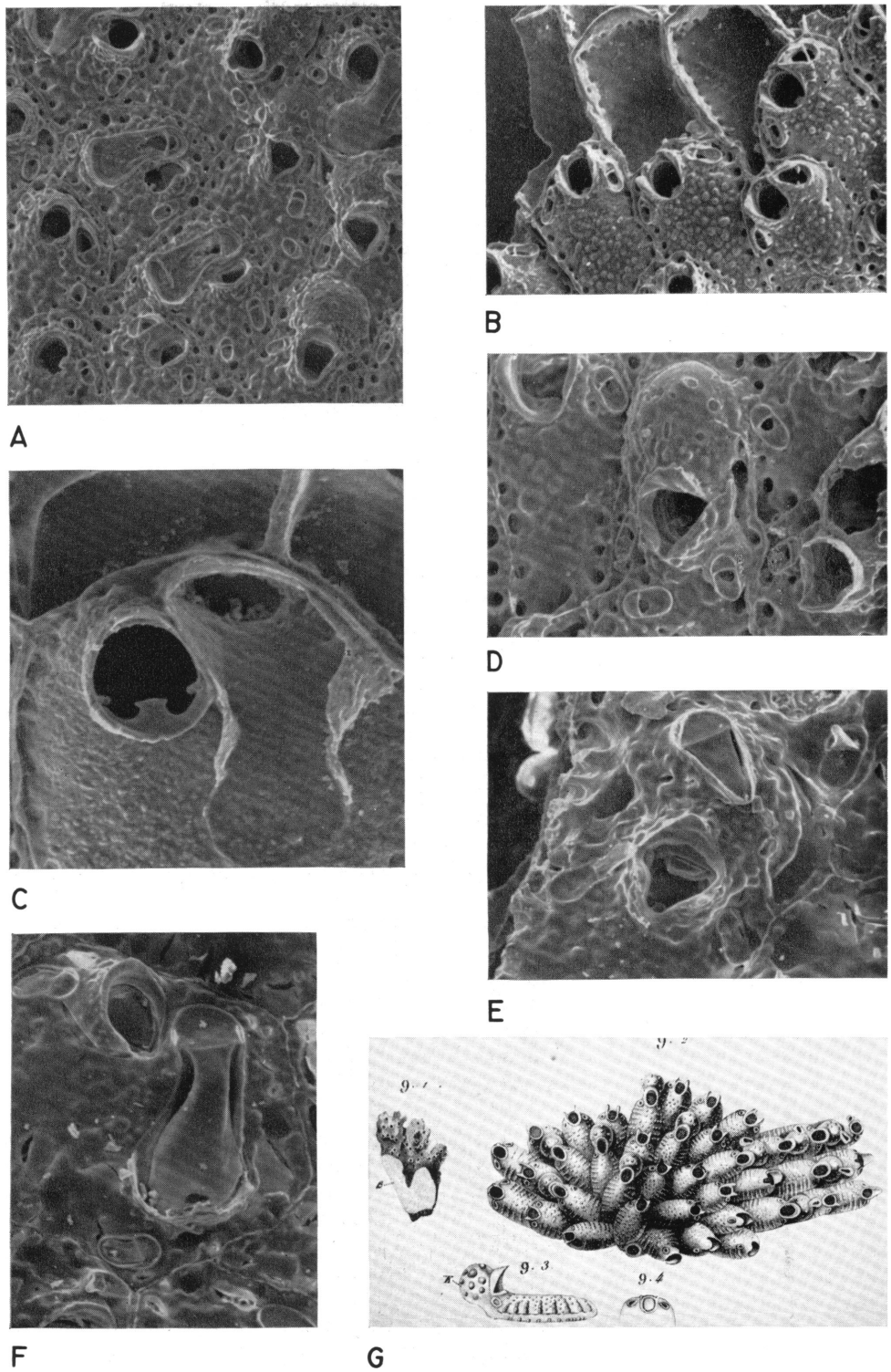


FIG. 8. A–F. *Parasmittina parsevaliformis*, new species. A. Colony with giant avicularia, ovicells with few pores. B. Developing edge of colony, bulbous lateral oral avicularia. C. Development of giant avicularium and host zooecium from separate basal folds. D. Ovicell with pores occluded. E. Ovicell overgrown by encroaching frontal, carrying avicularium onto ovicell. F. Giant avicularium mandible with bilobate tip, trimmed by irregular rostral edge. G. Photograph of Savigny's illustration (?1817, pl. 7, fig. 9) of *Cellepora parsevalii* Audouin (1826, p. 236,) which lacks giant avicularia.

communication pores, can be seen in some cases in the deeper tubular portion of the rostrum. The avicularium and its "host" zooecium invariably seem to arise at the same time, as though in a "twinning" phenomenon. The frontal wall of the host can be seen to be complete, but thinner, beneath the shallow basal portion of the avicularium chamber. The lateral walls between the two are not so thick as they are between two independent zooecia.

The edges of the giant avicularian rostrum become raised around the distal, postmandibular curve, forming an irregular calcareous fringe, which seems to have the effect of trimming and shaping the mandible. The tip of the mandible may be rounded, bilobed, or trilobed, depending on the vertical sculpturing of the rostral edges (fig. 8F). The submandibular area of the rostrum is heavily calcified, with a keyhole-shaped opesial area, and a complete, arching hinge bar. When a new layer of zooecia are formed, the edges of the rostrum grow upward just as the lateral walls do.

Lateral wall structure is similar to that in other species reported, with a single row of pores on the lower portion, and a palisaded appearance on the upper portion where it is invested by frontal, around the areolar pores. Formation of lateral walls appears to be by a double fold; distal walls may be formed by folding or by curving of lateral walls (fig. 8B). Larger pores are found at the basal corners of the zooecial walls. Frontal formation is usual, but the denticle appears to be formed entirely by the frontal, without contribution by the apertural rim.

Ovicells are moderate-sized and recumbent, becoming immersed in surrounding frontal. The ooecial peristome is at first U-shaped, with a distal gap for the spines. The ovicell globe grows upward distally, with finger-like projections on the free edge of the hood. These fingers grow around the pore positions, fusing to complete the globe. Older ovicells show the peristome filled in distally and proximally, forming a tubular structure with a pyriform aperture and sometimes with a vertical sinus fold. There are only six to 10 ovicell pores, which appear to be closed (fig. 8D).

The surface of the ovicell hood is at first granular, but the encroaching frontal rapidly covers all or most of the hood. Large triangular avicularia, which seem to originate from the distal areolar area, are carried up the ovicell especially in older areas of the colony. Their chambers are separate from the chambers of the adjacent zooecia, and some can be seen to be in contact with the same basal layer as the ooecia, namely, the frontals of the zooecia beneath, in multilaminar colonies.

The Hawaiian material might be considered the same species as the *Cellepora parsevalii* of Audouin (1826, p. 238), which Harmer classed as *Smittina parsevalii*. In the present paper (fig. 8G), our copy of the Savigny illustration (?1817, pl. 7, fig. 10) shows that small lateral oral avicularia were present, presumably placed in an ascending position, but there is no suggestion of the large spoon-shaped avicularia which are so characteristic of the Red Sea, Atlantic, and Pacific material ascribed to that species (Harmer, 1957, p. 942; Powell, 1967a, p. 172; Cook, 1968, p. 215). Audouin's description was, of course, not a description at all, but simply the applying of a name to a drawing previously published by Savigny (?1817). Harmer justified the use of the Audouin name because of the similarity of his material from Ghardaqa (Red Sea), although it is not known whether the Savigny material came from the Red Sea or the Mediterranean coast of Egypt. There is no type specimen, nor any description of type material, so far as we know.

In the Savigny illustration (?1817, pl. 7, fig. 9), the ovicells can be seen to have few pores, and to have the triangular avicularia encroaching on the ovicells from adjacent frontals. In the Hawaiian material, the colonies that have ovicells with few pores and encroaching avicularia also have the giant spoon-shaped avicularia. In contrast, the very similar form described herein as *Parasmittina leviavicularia*, new species, has ovicells with many pores, and without encroaching ovicell avicularia, and spoon-shaped giant avicularia are never present. The distribution of these two forms overlaps only at three stations, at Kaunakakai, Molokai, and on western Maui nearby. Harmer included forms similar to both of the above in his *Smittina parsevalii* from the Indo Pacific.

Harmer (1957, p. 942) also tentatively placed Waters's *Smittia obstructa* (1889b, p. 18) from New South Wales in synonymy with *S. parsevalii*. Waters's illustrations (pl. 3, figs. 7, 8) suggest that his material is very similar to our *P. parsevaliformis*; were it not for the lack of good comparative material of Waters's species, this portion of the Hawaiian material might well be

placed in *Parasmittina obstructa* (non-*parsevalii*).

Waters's species has ovicells with few pores and with encroaching avicularia, lateral oral lappets, and large spoon-shaped avicularia which he referred to as being vicarious. Hastings (1932, p. 431) remarked, concerning her specimen of *Smittina obstructa* from New South Wales, "In this specimen, unlike that described by Waters, the large spatulate avicularia are not vicarious, but are on the frontal wall, with their proximal end beside the orifice of the zooecium. The only one visible on the specimen [of Waters] lent me is, however, similar, though the orifice of the zooecium can only be discerned clearly when the specimen is wet."

Both Hastings and Waters probably referred to the same type of avicularium. Harmer concluded that the avicularia were not interzooecial, and referred to Waters's figure 7 as having a distally directed spatulate avicularium. The avicularium illustrated by Waters actually appears to be separate from the apertures of the randomly oriented adjacent zooecia; the aperture to which the spatula is probably related would be outside the field illustrated, and perhaps calcified over, as Hastings's comments suggest.

Harmer (1957, pl. 65, fig. 6) showed a colony with all spatulas directed distally, and it is questionable if this should not be a separate species, because all our material is quite consistent in having the spatulas directed proximally. Harmer's other illustration (pl. 65, fig. 5) shows a colony in which the ovicells have numerous small pores in place of the few larger ones which occur in our material having spatulas, and in the Savigny illustration without spatulas.

Further work obviously needs to be done on this complex to determine whether environmental factors can produce the various phenetic types which are found. The fact that the distribution of our two forms resembling Harmer's *S. parsevalii* differs within the islands negates the suggestion that the form lacking the spatulas represents a recessive genetic character, even though the comparative numbers of the two forms found suggest this. Also, the ages of the colonies do not seem to be significant, as the ovicells differ, whether in unilaminar or multilaminar colonies.

Thornely's *Smittia ornata* (1912, p. 152, pl. 8, fig. 13) has all the features of *Parasmittina*

TABLE 17
MEASUREMENTS (IN MICRONS) OF *Parasmittina parsevaliformis*

	Minimum	Maximum	Average	Number
Denticle width	30	40	36	10
Zooecium length	500	700	600	10
Zooecium width	320	480	385	10
Aperture length	110	160	127	10
Aperture width	100	110	106	10
Ovicell length	200	240	215	4
Ovicell width	240	260	245	4
Avicularia (giant)				
Length	310	390	360	10
Width	120	200	174	10
Avicularia (acute, ascending)				
Length	140	200	168	10
Width	80	100	92	10
Avicularia (ovals)				
Length	80	140	111	10
Width	40	60	53	10

obstructa (Waters) but has peculiar raised "bosses" on the ovicell, according to Harmer (1957, p. 944). Harmer examined a paratype of *S. ornata*, described from the Indian Ocean, and reported that the bosses were short, rounded tubules, apparently chitinous. Cook examined the Thornely specimen and thought it might belong to Harmer's *S. parsevalii*, although the zooecia of *S. ornata* are somewhat larger (personal commun.).

Cellepora raigii Audouin, 1826

Figure 9E

The *Smittina raigii* (Audouin) of Harmer (1957, p. 938, pl. 65, figs. 1–3) is an Indo-Pacific form, or group of forms, with a wide range of variation. The original *Cellepora raigii* of Audouin (1826, p. 238), illustrated by Savigny (?1817, pl. 7, fig. 10) is shown in a photographed copy in the present paper (fig. 9E) as having a pyriform aperture with lateral oral lappets, a moderately large denticle shallowly set, and 2–4 spines. Giant interzooecial avicularia are placed more or less on the proximal frontals and directed distally. No other zooecial avicularia are present, no areolae are shown, nor are ovicells illustrated. However, some of Harmer's material has very large lateral oral avicularia,

similar to those in *Smittia trispinosa* form *bimucronata* Hincks (1884b, p. 362, pl. 13, fig. 6). Such avicularia are also present in some of the Hawaiian material (see *Parasmittina hastingsae*, new species).

Among the nearly 200 specimens which resemble Harmer's *Smittina raigii* to varying degrees taken from the five major Hawaiian Islands, some 12 combinations of variations are distinguishable. These can be grouped into four different forms that are similar to certain portions of Harmer's material. It is difficult to place any of these forms definitely in Audouin's species, and probably not in Harmer's species either. Harmer confused their identities by including a very wide range of variation. He also indicated that he doubted the vicarious nature of the large avicularia, so clearly figured in Savigny (?1817), and he interpreted them as being large lateral oral avicularia. Both kinds of avicularia clearly occur and on the same colony (fig. 9C) in some Hawaiian specimens. These specimens resemble most Harmer's Victoria specimens C and D, which Harmer (1957, p. 940) placed only provisionally in *S. raigii*. He remarked on the numerous avicularia, some very large, and the paired, proximally directed lateral avicularia. Hawaiian material shows the presence of tubules of commensals (fig. 9C), as did Harmer's material.

There are three forms having a moderately wide denticle, comprising 80 percent of the specimens, and one form having a narrow denticle (20 percent of the specimens) in Hawaiian material. They have in common a pyriform aperture with lateral oral lappets and, usually, numerous avicularia of various sorts. Ovicells are covered to varying degrees by encroaching frontal. Distribution patterns overlap to some extent and one form is limited to one area of a single island, apparently.

As it is not possible to establish experimentally the bearing environmental influence has on these forms, they are treated herein as a group of separate species according to Mayr's (1969, p. 47) definition of species group. Each form is well represented by a number of specimens. The form most closely resembling *Smittina raigii* (Audouin) is named *Parasmittina raigiformis*, new species. It might well be that this species group represents a center of diversification that is still in transition.

Edward R. Long of the United States Naval Oceanographic Office has recently sent a specimen of a very young colony, collected on a settling plate in Hawaii, which looks very much like Savigny's illustration, with only a few small frontal avicularia and no ovicells. The giant avicularia are clearly separated from the autozooecia as kenozooecia or interzooecial avicularia.

Parasmittina raigii, sensu lato

If all the forms observed in Hawaiian material were grouped under *P. raigii*, a very wide range of variations would have to be included in the species. The following specimen variations, with station data and numbers of specimens (in parentheses), are distinguished:

Narrow Denticle

1. 2 spines, short triangular and long triangular shoulder avicularia, no interzooecial avicularia, ovicell pores small; 805 (5), 802 (9), 803 (2), 513 (1).
2. 3–5 spines, medium and large shoulder avicularia, no interzooecials, no ovicells; 802 (1), 803 (1), 805 (1).
3. 2 spines, medium shoulder avicularia, large short interzooecials; 800 (1), 803 (3). See *Parasmittina kauaiensis*.
4. 2 or 3 spines, long and short shoulder avicularia, small interzooecials; 802 (1), 803 (2), ?BPBM 328 (1, Waikiki, Oahu). Specimens with peristomal projections; 910 (2), 905 (2), 903 (7), probably belong with number 10.

Medium Denticle

5. 2 spines, no avicularia; 910 (1), 512 (1).
6. 2 or 3 spines, long and short shoulder avicularia, no interzooecials; BPBM 329 (1), 512 (6), 513 (6), 705 (1).

Wide Denticle

7. 2 spines, long shoulder avicularia, no interzooecials; 500a (1), 500b (1), 601 (15), 610 (3), 701 (1), 707 (2), 900 (6).
8. 3–6 spines, a) with medium shoulder avicularia, small interzooecials, 522 (1); b) plain, 610 (1).
9. 2 spines, no shoulder avicularia, huge interzooecials; 514 (1), 610 (1); most like *Cellepora raigii* Audouin.
10. 2 spines, a) few small shoulders, no interzooecials, flabellate peristomal projections, 905 (3), 910 (1); b) denticle variable, larger shoulders, no interzooecials, varied projections, 910 (4), 903 (1) no projections, 905 (2); c) denticle variable, peristome bimucronate, small shoulders, small interzooecials, 905 (1), 910 (1), 601 (1). See *Parasmittina ilioensis*.
11. 2 spines, ovicell pores large, small shoulders, large

long interzooecials, many small triangular avicularia; 600 (2), 601 (11), 610 (7), 613 (10), 910 (1), 500b (1). Second most common form. Peristomal projections on some from 610. See *Parasmittina raigiformis*.

12. 2 or 3 spines, ovicell pores large, very large shoulders, large triangular interzooecials; 601 (40), 610 (8), 613 (8), 703 (1), 705 (4), 500b (3), 513 (1), 905 (5), 910 (1). Most common form. Peristomal projections on some from 601. See *Parasmittina hastingsae*.

If only those localities having more than three occurrences are considered, the narrow denticle forms are limited to Kauai (802, 803, 805) and Molokai (903, 905, 910). Wide denticled forms are concentrated mainly along western Maui (601, 610, 613) and northern Molokai (905, 910) with only two stations on Oahu (500b, 513) and one on Hawaii (705) represented. The north side of Molokai seems to be the area of distribution common to both (see distribution map 8). Approximately 20 percent of the nearly 200 *raigii*-like specimens have a narrow denticle; 80 percent have predominately medium-to-wide denticles. About 37 percent of all specimens have no interzooecial avicularia, 8 percent have small interzooecials, and 55 percent have large interzooecials. However, within the narrow denticled forms alone, 55 percent have no interzooecials, 37 percent have small interzooecials and only 8 percent have large short interzooecials. Among medium-to-wide denticled specimens only 33 percent have no interzooecials, 1 percent have small interzooecials, and 65 percent have large interzooecials. Thus it would seem that denticle width is a valid criterion for distinguishing the groups.

TABLE 18
OCCURRENCE OF INTERZOOECIAL AVICULARIA

	% with None	% Small	% Large or Giant
All *raigii*-like forms	37	08	55
Narrow denticled forms	55	37	08
Medium-wide denticled forms	33	01	65 short and long

Parasmittina sp.

In distinguishing species within the group of *raigii*-like forms, the few specimens with 3–6 spines must remain unidentified for the present because of the lack of comparative material. The zoaria are young, mostly in coral cups, with small zooecia. The primary aperture is round, surrounded by six long, slender, telescope-shaped spines. The peristome is wide, with a deep sinus flanked by irregular lappets, and usually with a medium to wide denticle. Avicularia were absent in one specimen from Maui, scarce in others. From Oahu, one colony had shoulder avicularia and tiny interzooecials. From Kauai, specimens had large shoulder avicularia, no interzooecials, and narrow denticles. Although the colonies were all small, they were easily distinguishable from the young stages of the other forms with 2 or 3 spines. In the list of *raigii*-like forms, page 415, numbers 2, 8a, and 8b are placed in the category with 3–6 spines.

Parasmittina kauaiensis, new species

Figure 9A, B

DIAGNOSIS: Incrusting species with granular frontals and small areolae. Apertures rounded, without a sinus, with two spines and lateral oral lappets. Denticle shallow set, narrow, and anvil-shaped. Cardelles acute, situated distal to denticle tips. Tiny oval or acute frontal or marginal avicularia possibly present; few medium-sized subspatulate avicularia arising beside oral lappet, extending along distolateral zooecial margin. Acute, equilaterally triangular avicularia present on proximal zooecial border, directed distally. Ovicells raised, flattened, with few small pores. Ooecial peristome gradually closing distal peristomal gap, and frontal encroaching on ovicell hood distally.

ETYMOLOGY: Named for the type locality, the island of Kauai.

HOLOTYPE: AHF Bryozoan no. 172.

TYPE LOCALITY: S-803-67, Kukuiula Harbor, south side of Kauai, July 3, 1967, 13–16 m.

DISTRIBUTION: S-800-67, S-803-67, S-805-67; ?S-513-67.

DESCRIPTION: One of the forms in the *raigii*-like groups of species, *P. kauaiensis* is also an incrusting species with granular frontals and small areolae. Frontal budding gives multi-layered colonies their randomly oriented zooecia. Apertures are rounded, with lateral oral lappets that slope proximally without a distinct sinus. The narrow denticle is anvil-shaped and shallowly

TABLE 19
MEASUREMENTS (IN MICRONS) OF *Parasmittina kauaiensis*

	Minimum	Maximum	Average	Number
Denticle width	20	30	25	10
Zooecium length	500	600	548	10
Zooecium width	300	420	364	10
Aperture length	110	130	125	10
Aperture width	100	110	101	10
Ovicell length	200	210	201	10
Ovicell width	240	280	260	10
Avicularia (shoulders)				
Length	180	280	223	6
Width	60	100	83	6
Avicularia (acute interzooecials)				
Length	100	140	120	4
Width	80	100	85	4
Avicularia (ovals)				
Length	80	100	90	2
Width	40	60	50	2

set, and cardelles are acute, placed distal to the denticle tips (figs. 9A, B). Two spines occur in the distal peristomal gap.

Tiny, oval, or acute frontal avicularia occur adjacent to the aperture, or along the marginal areolae, or randomly oriented on the frontal. A few medium-sized subspatulate avicularia occur, extending from beside an oral lappet along the distolateral zooecial margin in a proximal direction (fig. 9A, bottom central zooecium). The rostral edges are raised, very finely serrate, and the mandible widens slightly and narrows to an acute or subacute tip. Somewhat larger acute triangular avicularia, which may be interzooecial, are usually located along the proximal margins of the zooecia, and directed distally (fig. 9B; the right avicularium belongs to an adjacent zooecium directed opposite to the ooecium). These marginal, or possibly interzooecial, avicularia never attain the size seen in the other species figured in the group.

Ovicells are raised, recumbent, and somewhat flattened on the face of the hood (fig. 9B). Pores are smaller and fewer than the other species in figure 9. Lines between pores are sometimes present. Frontal encroaches on the distal part of the hood, and the peristome gradually closes across the forepart of the hood in an arch shape. Peristomal projections occasionally are found. The species is based on form 3, plus form 1.

Parasmittina hastingsae, new species

Figure 9C, D

DIAGNOSIS: Yellowish, incrusting species with numerous varied avicularia, including medium-sized lateral frontal shoe-shaped avicularia, directed proximally, large subspatulate or long triangular avicularia placed beside aperture and along zooecial margin, plus short triangular interzooecial avicularia which appear to be on proximal frontal, directed distally. Primary apertures round with two or three spines, becoming pyriform with growth of lateral oral lappets. Sinus wide and shallow, descending to wide denticle. Ovicells raised, with medium-sized pores. Oral lappets close across hood to form tubular peristome, encroaching frontal gradually submerging ovicell.

ETYMOLOGY: Named for Dr. Anna B. Hastings who contributed greatly to the knowledge of tropical bryozoans.

HOLOTYPE: AHF Bryozoan no. 173.

TYPE LOCALITY: S-601-66, Napili Bay, Maui, 3 m., August 6, 1966.

DISTRIBUTION (number of specimens in parentheses): S-601-66 (40), S-610-66 (8), S-613-66 (8), S-703-66 (1), S-705-67 (4), S-500b-66 (3), S-513-67 (1), S-905-66 (5), S-910-67 (1).

DESCRIPTION: The most common form of the specimens similar to *Parasmittina raigii* in the Hawaiian Islands, *P. hastingsae*, is yellowish and incrusting. The primary apertures are rounded, but become pyriform with the growth of lateral oral lappets. In the distal gap of the peristome, two or three spines may occur. The sinus is wide and shallow, sloping laterally into the lappets. The denticle is usually wide, although there is intracolony variation. Cardelles are strong and acute.

Some colonies contain numerous avicularia, especially those penetrated by worm tubes and other commensals. Whereas *Parasmittina raigiformis* has mostly small triangular frontal avicularia, *P. hastingsae* has mostly larger oval frontal avicularia, as well as much larger shoulder avicularia, which seem to arise beside the peristome (but not as a part of the peristome, as is the case in *P. serrula*, fig. 3D). The shoulder avicularia extend proximally along the zooecial wall. On the extreme left, in figure 9C, can be seen such an avicularium with serrate rostral edges and a subspatulate mandible. The central avicularium (fig. 9C), with an open acute

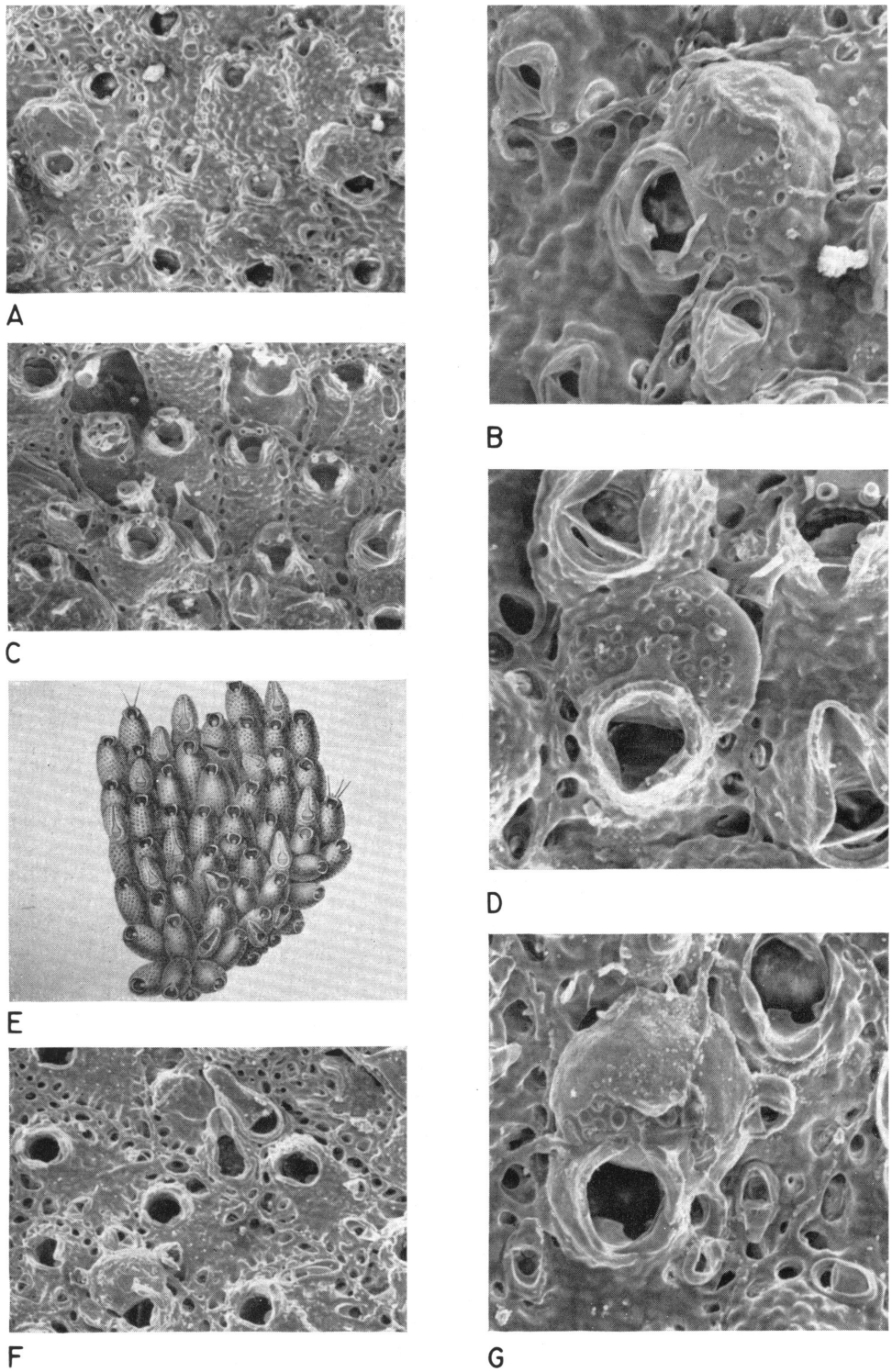


FIG. 9. A, B. *Parasmittina kauaiensis*, new species. A. Colony with small acute and oval avicularia, narrow denticles. B. Ovicell with small pores, narrow denticle, distal cover. C, D. *Parasmittina hastingsae*, new species. C. Colony with long shoulder avicularia, short triangular or subspatulate interzooecial avicularia. Note calcareous commensal tubes infesting colony. D. Ovicell with wide denticle, larger pores. E. *Cellepora raigii* Audouin, 1826; plate 7, figure 10 photocopied from Savigny, ?1817. F, G. *Parasmittina raigiformis*, new species. F. Colony with large distally directed interzooecial avicularia. G. Ovicell, medium wide denticles.

TABLE 20
MEASUREMENTS (IN MICRONS) OF *Parasmittina hastingsae*

	Minimum	Maximum	Average	Number
Denticle width	20	40	34	10
Zooecium length	410	510	479	10
Zooecium width	280	400	361	10
Aperture length	120	140	131	10
Aperture width	100	120	114	10
Ovicell length	200	200	200	8
Ovicell width	220	250	240	8
Avicularia (shoulders)				
Length	140	180	170	4
Width	60	80	70	4
Avicularia (acute interzooecials)				
Length	300	380	347	3
Width	140	140	140	3
Avicularia (ovals)				
Length	60	90	80	9
Width	40	60	57	9

mandible may be an interzooecial one. The common interzooecial avicularia (figs. 9C, D) are short and triangular, with a raised rostrum, tiny serrations, and a central suture. These avicularia originate mostly along transverse walls and lie on the proximal frontals, directed distally. They appear to rise as small conical chambers after secondary calcification of the underlying frontal has taken place. This is similar to the manner in which frontal budding of a new layer of zooecia occurs in a number of parasmittinids, such as in *P. decorata*. In one instance the submandibular area appeared to consist of two halves underlain by the double transverse wall, with the opesial area contributed by distal frontal from the base of the peristome, suggesting similarities with ovicell formation (D. Soule, 1973).

Ovicells are raised, with numerous pores that are slightly smaller than those of *P. raigiformis*. The peristomal lappets grow across the hood, leaving a labellar area within the tubular peristome. A tiny ovicell operculum can sometimes be isolated by dissection. Encroaching frontal covers distal portions of the hood irregularly, gradually submerging the ovicell. Differences in the ovicells of the two species are difficult to discern with the light microscope.

This species most resembles the *Smittina raigii* (Audouin) of Harmer (1957, pl. 65, fig. 1) of specimen 295A[3] from Station 273. It differs from Savigny's original figure, shown herein (fig. 9E) in having numerous very large lateral oral avicularia, directed proximally, and in the presence of numerous other frontal avicularia. Specimens in variation number 12, of *P. raigii, sensu lato,* comprise this species.

Parasmittina raigiformis, new species

Figure 9F, G

DIAGNOSIS: Incrusting species having pyriform aperture with lateral oral lappets, two spines. Denticle medium to wide, cardelles acute. Zooecium frontal coarsely granular, with single row of areolar pores. Numerous small acute and subacute avicularia present placed adjacent to aperture, on frontal, along areolae. Giant interzooecial avicularia present mostly along transverse walls, oriented toward next distal aperture. Ovicells at first raised, with large pores, becoming immersed, almost covered by incroaching frontals.

ETYMOLOGY: Named for its resemblance to *Parasmittina raigii* (Audouin).

HOLOTYPE: AHF Bryozoan no. 174.

TYPE LOCALITY: S-601-66, Napili Bay, Maui, 3 m.; August 6, 1966.

DISTRIBUTION (number of specimens in parentheses): S-601-66 (11), S-610-66 (8), S-613-66 (10), S-905-66 (5), S-910-67 (1), S-500b-66 (1), S-514-67 (1).

DESCRIPTION: Colonies are incrusting, mostly on coral, yellowish in color. Zooecia have coarsely granular frontals with a single row of medium-sized areolar pores. Apertures are rounded or pyriform, with small lateral oral lappets, and a wide, shallow sinus. The denticle is medium to wide in size, truncate, and set near the surface. Cardelles are usually acute, situated opposite the denticle tip or slightly more distally. Two spines may be present.

Small avicularia are numerous; they are triangular or rounded (figs. 9F, G), and may occur on the frontal, or along the marginal areolae, beside the aperture (but not on the lappets) and sometimes on older, immersed ovicells. A few small subspatulate shoulder avicularia rarely occur, originating beside the aperture and following the curve of the zooecial margin proximolaterally.

Giant interzooecial avicularia also occur, especially in areas with many ovicells, and

TABLE 21
MEASUREMENTS (IN MICRONS) OF *Parasmittina raigiformis*

	Minimum	Maximum	Average	Number
Denticle width	20	40	34	10
Zooecium length	420	500	479	10
Zooecium width	280	440	361	10
Aperture length	120	140	114	10
Aperture width	100	120	114	10
Ovicell length	200	200	200	8
Ovicell width	220	260	240	8
Avicularia (short interzooecial)				
Length	140	180	170	4
Width	60	80	70	4
Avicularia (long interzooecial)				
Length	300	380	347	3
Width	140	140	140	3
Avicularia (ovals)				
Length	60	90	80	9
Width	40	60	57	9

where symbiont tubules are common. They appear to be formed at the transverse walls in a manner similar to frontal budding, and may be oriented so that they are directed toward the next distal aperture, from the proximal area (fig. 9F). This is not always the case however, expecially where multiple layers of colony are formed. In one case, the open aperture of the zooecium below was clearly visible beneath the avicularium opesium, as though the avicularium had been formed by frontal budding.

The giant avicularia are of two sizes; some are short triangular and some are long, but both have a duck-billed rostrum. There is a median suture in the submandibular area and a tiny pore at the end, which appear to indicate the areas of fusion and divergence in the body walls. The mandible is either acute, or labellar, widened somewhat before it narrows to a tip.

Ovicells form as a double layer distal to the peristomes, which bear two spines in the low distal area. The hood is at first much raised, with large pores, and the peristome gradually grows from the oral lappets across the hood in an arch (fig. 9G). Encroaching frontal forms distal flaps which later submerge the older ovicells almost completely. Tiny frontal avicularia have been carried onto some of the submerged ovicells by the encroaching frontal. Forms 9 and 11, page 415, are included in this species.

Parasmittina ilioensis, new species

Figure 10A–F

DIAGNOSIS: Incrusting species forming regular rectangular zooecia in primary colony layer. Frontal budding producing heaped, irregular multilaminar colonies. Primary apertures rounded, with two or three distal spines and small lateral oral lappets. Median denticles variable within a colony, mostly medium wide; cardelles acute, with tips directed toward denticle. Older peristomes producing curls and projections around spines and lappets. Lateral frontal avicularia arising beside oral lappets and extending proximolaterally or proximally. These may be tiny, acute or oval, or longer subspatulate avicularia. Ovicells large, erect, with large pores, and with distal flaps and curls. Ooecial peristome becoming tubular, with proximal projections and distal arch above labellar area.

ETYMOLOGY: Named for the type locality, Ilio Point, Molokai.

HOLOTYPE: AHF Bryozoan no. 176.

TYPE LOCALITY: S-903-66, Ilio Point, Molokai; August 21, 1966, 9–12 m.

DISTRIBUTION: S-903-66, S-905-66, S-910-67, S-601-66.

DESCRIPTION: Young colonies are unilaminar, regular, with rounded or squarish apertures bearing small lateral oral lappets. The denticle is anvil-shaped, usually medium to wide, but narrower ones may occur within a colony. No sinus is found until peristomes become deepened or tubular. Cardelles are acute, opposite the tips of the denticle, shallow set. Distal spines number two or three (fig. 10A).

Lateral frontal avicularia arise from a frontal pore beside the oral lappets and an areolar pore, but they do not seem to be connected to the peristome. Such avicularia may be small ovals or triangles, directed proximally, or larger subspatulate shoulder avicularia with raised rostra (fig. 10A, C).

The most distinctive feature of *P. ilioensis* is the formation of flabellate curls and projections around the spines and apertures in older colonies (fig. 10C–E). Projections apparently break off and the colonies may be littered with fragments.

Ovicells are at first erect, with large pores. The ooecial peristome becomes tubular, gradu-

ally closing across distally in a peak or brim which leaves a labellar area below it. Distally, thick flaps of secondary calcified frontal form a cover with curled edges (fig. 10B; parts of peristome projections broken off).

The fully developed colonies with elaborate projections are rare and restricted in distribution. It is difficult to determine the exact distribution of the species because some young, unilaminar colonies do not show the projections. In the list of *raigii*-like forms, those of number 10, page 415, are the basis of the species. Others possibly include numbers 6 and 7, with medium to wide denticles, and possibly some of numbers 1 and 4 from Molokai, with narrower denticles. The narrow denticle forms seem more closely related to *P. kauaiensis*, new species.

A presumed ancestrula of *Parasmittina ilioensis* (fig. 10F) shows a primary zooecial opesia surrounded by long spines and shortened proximally (upper portion of photo). The first distal zooecium has five distal spines (bottom of photo) and a larger opesia. The surrounding basal pad shows ridges for five potential zooecia; the single distal zooecium present, plus two potential distolateral positions and two proximolateral positions separated by a center proximal keel. Because the ancestrula settled on a parent colony in a coral colony it had no room for expansion.

TABLE 22
MEASUREMENTS (IN MICRONS) OF *Parasmittina ilioensis*

	Minimum	Maximum	Average	Number
Denticle width	40	40	40	10
Zooecium length	440	680	554	10
Zooecium width	280	360	311	10
Aperture length	120	140	132	10
Aperture width	100	120	117	10
Curls[a] height	120	190	165	10
Ovicell length	200	220	203	10
Ovicell width	240	280	256	10
Avicularia (shoulders)				
Length	200	340	270	12
Width	80	120	103	12
Avicularia (ovals)				
Length	80	120	107	10
Width	50	60	57	10

[a]The erect, calcareous twists of frontal between the spines.

Parasmittina dolabrata, new species

Figure 11A–D

DIAGNOSIS: Species forming solid, multilaminar, erect and branching colonies. Zooecia very irregular in size, shape, and orientation; bordered by areolar pores and separated by distinct lines. Apertures rounded, higher than wide, with narrow truncate median denticle. Cardelles set slightly distal to tip of denticle and hooked proximally. Irregular lateral oral lappets possibly occurring flanking 1–3 spines in distal gap of some zooecia. Avicularia varying in number and shape. Small lateral oval avicularia, paired or single, on frontal near peristome, directed proximally. One may be replaced by large, hatchet-shaped blunt avicularium with pronged mandible, arising beside or below aperture and extending proximally along margin of zooecium. Single, large acute interzooecial avicularia arising along lateral areolae and mostly directed toward oral lappet distally, but possibly being directed otherwise. Small oval areolar avicularia possibly occurring. Ovicells large, immersed, becoming covered with encroaching frontal so that only few of numerous pores remain open. Larger areolar pore penetrating ovicell hood on each side.

ETYMOLOGY: *dolabrata* in Latin means hatchet, after the shape of the avicularium rostrum.

HOLOTYPE: AHF Bryozoan no. 177.

TYPE LOCALITY: AHF 167-34, Post Office Bay, Charles (Santa Maria) Island, Galapagos Islands.

DISTRIBUTION: Specimens in the Hancock collections labeled *Parasmittina crosslandi* by Osburn: AHF 170-34, Stephens Bay, Chatham (San Cristobal) Island; AHF 317-35, off Gordon Rocks, Indefatigable (Santa Cruz) Island; AHF 311-35, off Bindloe (Marchena) Island; AHF 167-34, Post Office Bay, Charles (Santa Maria) Island. From James Bay, James (San Salvador) Island, a specimen collected by C. Angermeyer, June 13, 1969.

The "*Smittina trispinosa* Johnston 1838 variety" of Canu and Bassler (1930, p. 27) belongs to the new species, in our opinion, following examination of USNM type 8498 from station 2813, east of Santa Cruz Island, and USNM 8499 from Station 2815 between Santa Cruz and San Salvador Islands in the Galapagos. Some of the Hancock specimens labeled *P. trispinosa* from the Galapagos must be placed in the new species;

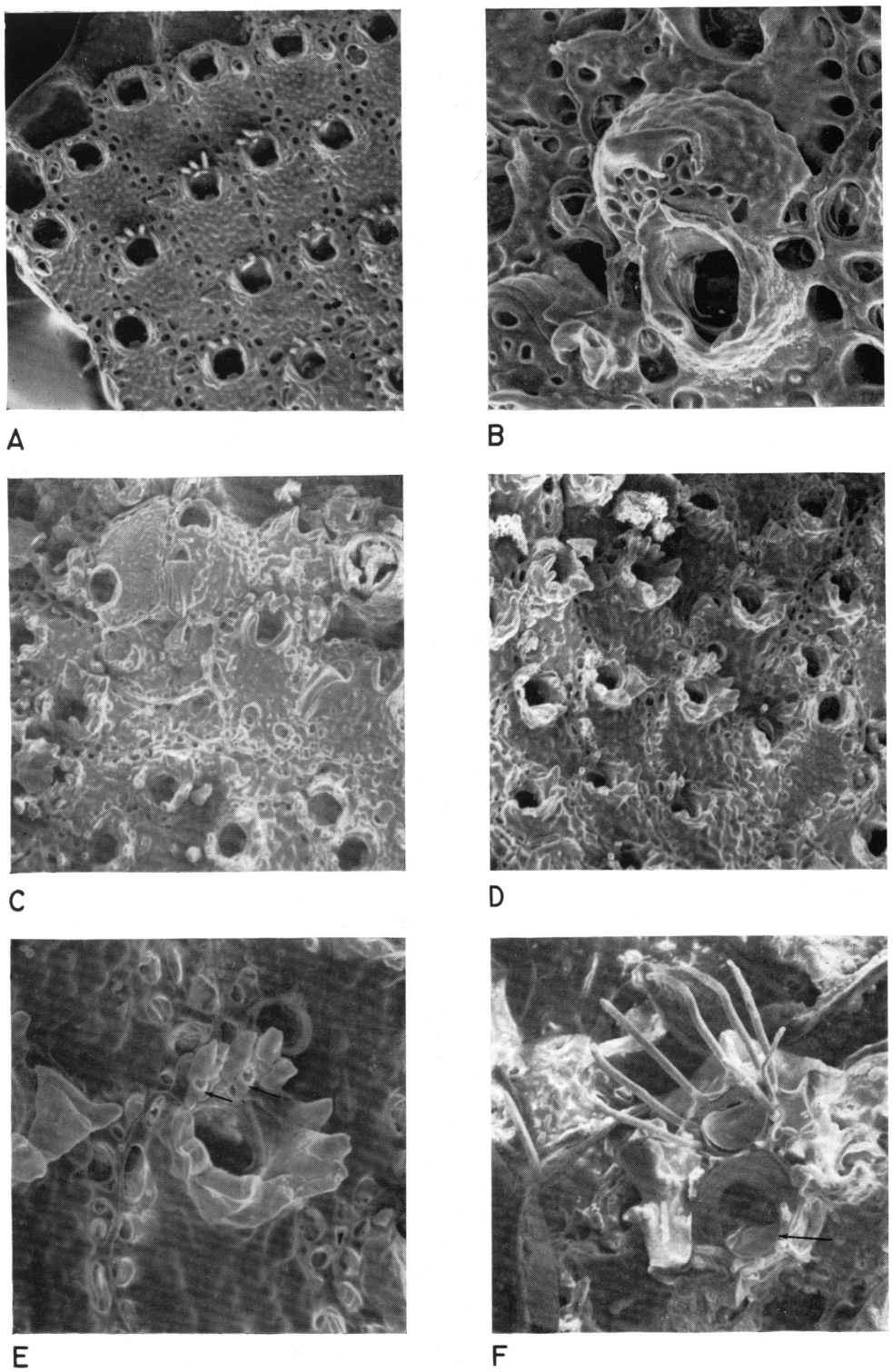


FIG. 10. A–F. *Parasmittina ilioensis*, new species. A. Developing edge of colony. B. Ovicell with large pores, decorative cover. C. Colony with many projections, some broken off, and large shoulder avicularia. D. Colony with apertural projections. E. Apertural projections curled between and around spines (arrow). F. Ancestrula with spines, and first distal zooecium (lower individual, arrow).

included are AHF 352-35, between Wreck Bay and Stephens Bay, Chatham (San Cristobal) Island; AHF 173-34, off S. Seymour Island; and AHF 143-34, off Wenman Island.

All of Osburn's (1952, p. 415) "*Parasmittina spathulata* (Smitt), 1873" from the Galapagos Islands (AHF 143-34, 55-33, 201-34 and 446) belong to the new species. *Escharella jacotini* var. *spathulata* as figured by Smitt 1873 (pl. 10, fig. 200) resembles much more closely *P. areolata* (Canu and Bassler).

Specimens that seem to belong to the new species but differ only in size include those from AHF 277-34, off Isabel Island, Mexico; AHF 450-35 from Secos Island, Panama; and AHF 253-34 from Port Culebra, Costa Rica, all labeled *Parasmittina trispinosa*, by Osburn.

DESCRIPTION: Colonies consist of solid, branching, erect stems formed of multilayered zooecia that are heaped and irregular in size and shape. Frontals are coarsely granular with a single row of areolar pores. Apertures are rounded or higher than wide, with or without lateral oral lappets. The medium wide denticle is set at the surface like a large frontal granule, or slightly recessed in a wide shallow sinus. Cardelles are strong, hooked proximally, and may have a burred appearance. The operculum is curved distolaterally and incised in the denticle area proximally.

Avicularia are numerous on most colonies and of various sorts. Small single or paired oral oval avicularia are directed proximally; one or both of these may be replaced by small acute avicularia which are usually directed up the oral lappet (fig. 11A). One of these may be replaced by a large hatchet-shaped avicularium with a squared rostral tip. The mandible may have a two-pronged tip (fig. 11C). This avicularium is similar to the "twinned" avicularia of *Parasmittina parsevaliformis* in that it arises from a separate basal fold beside the "host" zooecium. It may crowd the aperture and survive after the zooecium is closed over. This type of avicularium may be situated distolateral to the aperture (fig. 11C) or proximal to it (fig. 11D). Although small acute avicularia may occur on oral lappets, much larger acute avicularia, which seem to be interzooecial in origin, may occur beside the aperture or on the frontal, mostly directed distally (fig. 11D). Ovicells are immersed, with the pores becoming rapidly covered over until only a few tubular ones remain open (fig. 11B; in 11D the upper aperture is an ooecium with 3–4 open pores). Avicularia also encroach on the ovicell hood from all directions. Areolar avicularia can also be seen frequently.

The specimens from Panama bore the same variety of avicularia, but the hatchet-shaped ones were considerably longer in Galapagos specimens measured. The Panama zooecia were longer, however. Variation in the size of the triangular lateral oral avicularia occurs throughout this species as well as in the *Parasmittina trispinosa*, *P. californica*, and *P. alaskensis* from the eastern Pacific.

Parasmittina dolabrata is allied with *P. obstructa* and *P. parsevaliformis* in the nature of the lateral oral avicularia coupled with more or less blunt large avicularia. Neither of these latter two species have the large interzooecial triangles, however. The nature of the frontal and denticle is similar to Canu and Bassler's *Smittina trispinosa granosa* (1929, p. 345), USNM 8126 from Station 5478 in the Philippine Islands. In that specimen the lateral oral lappets are tiny and the oral avicularia small but the large avicularium is longer and spatulate.

Canu and Bassler (1930, p. 27, pl. 4, figs. 1–4) compared their *Smittina trispinosa* variety, from the Galapagos, to *Smittia nitida* Verrill of Hincks, 1881a, p. 159. Waters put Hincks's form in Thornely's *S. protecta*, and Harmer put it in Waters's *S. egyptiaca*.

Examination of specimens of *Smittina egyptiaca* (BMNH 26.9.6.180, 26.9.6.181, 1489–399J, 1388–399B, 1485-295E, 1385, and 1962.2.20) indicates that there are superficial similarities to *Parasmittina dolabrata*, but there are a number of differences among those specimens placed in *Smittina egyptiaca* by Harmer and others. Of Harmer's *Siboga* Expedition material, specimen BMNH 1388 from 399B seems closest to the new species.

Maturo and Schopf (1968, p. 41) discussed the two forms of *Discopora nitida* Verrill, 1875, and concluded that the originally described form contained only a single, acute frontal avicularium. Osburn, 1912, included a form with oval, triangular, and giant avicularia. It is this form that most authors considered typical until Maturo and Schopf published their study of the types. It seems possible that Morphotype B, the form emphasized by Osburn, might belong to *Parasmittina dolabrata*. However, the colony form differs. The zooecia are well sepa-

TABLE 23
MEASUREMENTS (IN MICRONS) OF *Parasmittina dolabrata* (PANAMA)

	Minimum	Maximum	Average	Number
Denticle width	40	40	40	10
Zooecium length	680	980	864	10
Zooecium width	460	680	562	10
Aperture length	110	140	131	10
Aperture width	120	150	135	10
Ovicell length	240	300	264	5
Ovicell width	300	340	314	5
Avicularia (hatchets)				
Length	200	260	222	10
Width	90	140	106	10
Avicularia (triangles)				
Length	120	140	130	6
Width	70	80	77	6
Avicularia (ovals)				
Length	100	130	115	10
Width	60	60	60	10
Avicularia (interzooecials)				
Length	100	110	105	2
Width	60	60	60	2

TABLE 24
MEASUREMENTS (IN MICRONS) OF *Parasmittina dolabrata* (GALAPAGOS)

	Minimum	Maximum	Average	Number
Denticle width	40	40	40	10
Zooecium length	500	740	607	10
Zooecium width	380	510	451	10
Aperture length	120	140	134	10
Aperture width	110	130	119	10
Ovicell length	220	260	244	5
Ovicell width	300	310	304	5
Avicularia (hatchets)				
Length	320	420	352	10
Width	100	120	107	10
Avicularia (triangles)				
Length	100	140	124	10
Width	70	100	86	10
Avicularia (ovals)				
Length	100	130	111	10
Width	60	60	60	10
Avicularia (interzooecials)				
Length	180	240	203	10
Width	100	140	112	10

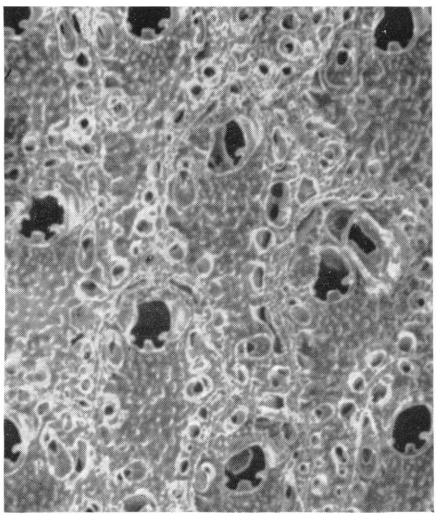
rated by grooves, and the ovicells are more erect with many pores in Morphotype B according to Maturo and Schopf's illustration, figure 12D. Osburn's illustrations (1912, pl. 27, figs. 66, 66a–e) give several forms included by him. None of these show the largest blunt avicularium, however.

Parasmittina trispinosa (Johnston): Osburn
and
Parasmittina californica (Robertson): Osburn

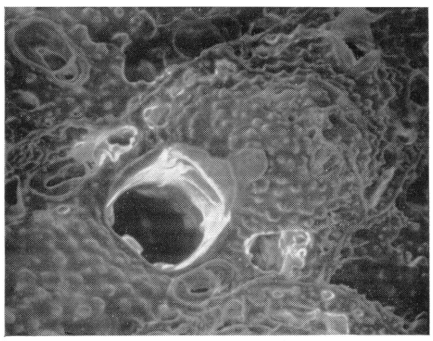
In reviewing the status of the eastern Pacific *Parasmittina*, we have reexamined many of the Allan Hancock Foundation specimens of "*P. trispinosa*," *P. californica*, *P. jeffreysi*, *P. spathulata*, *P. collifera*, *P. crosslandi*, and *P. fraseri*. As has been explained previously, some of the specimens of *P. crosslandi* have been removed from that species and placed in *P. triangularis*, new species, or in *P. dolabrata*, new species. The *P. spathulata* from the Galapagos Islands has been placed in *P. dolabrata* also.

There has been much difficulty in separating specimens into "*Parasmittina trispinosa*" and *P. californica*, and it is doubtful that any of the eastern Pacific material actually belongs to *P. trispinosa* (Johnston). Brown (1952, p. 332) selected as lectotype the specimen of *P. trispinosa* figured by Busk (1854, pl. 85, figs. 1, 2) with a small acute frontal avicularium directed distally. Osburn (1952, p. 412) indicated his doubts about the exceedingly wide distribution and range of variation in specimens attributed to that species. Various authors have contributed to the confusion by placing almost any parasmittinid with

FIG. 11. A–D. *Parasmittina dolabrata*, new species. A–C. Specimen from Panama. D. Specimen from the Galapagos Islands. A. Colony with surface denticles, large and small avicularia. B. Ovicell with most pores occluded, shallow denticle and burred cardelles. C. Giant avicularium originating from basal wall beside aperture; mandible bifurcate. Remains of operculum lying on frontal below aperture. D. Ovicell with pores (arrow), giant hatchet avicularium displaced proximally, large acute interzooecial avicularia. E–G. *Smittina kukuiula*, new species. E. Developing edge of colony. F. Aperture with denticle and rostrum. G. Ovicells, with pores open on left, closed on right.



A



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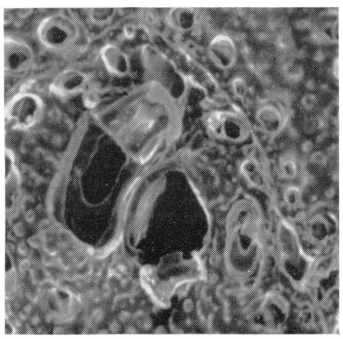

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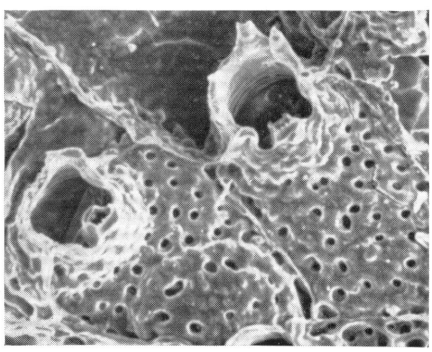
D



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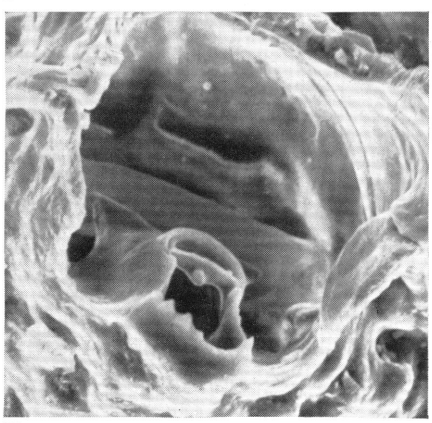

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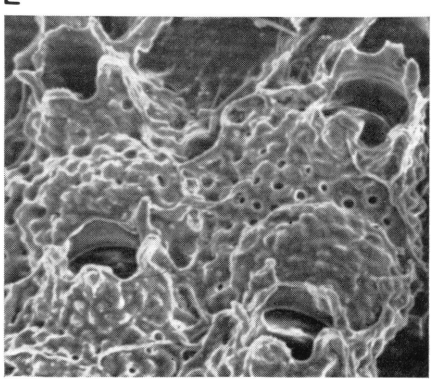


G

3 (and sometimes 2 or 4) spines and with an acute avicularium in *P. trispinosa*.

The form from Puget Sound has either a tubular peristome or oral lappets and usually two spines in the distal gap. The aperture is rounded with a medium-sized denticle and in some cases cardelles seem to be absent. The marginal sclerite of the operculum then ends on either side of the denticle instead of the usual termination at the cardelles. A few zooecia have a single large acute avicularium ascending one oral lappet. These are connected to areolar pores and a peristomal pore, with the rostrum forming a pedestal on the zooecial frontal. There are many small acute frontal or areolar avicularia but small oval avicularia are rare. There are, on some zooecia, huge acute avicularia that arise in the lateral wall or from the basal wall and extend distally with a raised, keeled rostrum directed toward the proximolateral part of the peristome. Occasionally they extend beside the peristome distad. The mandibles are wide triangles, not curving, with a short triangular sclerite based at the hinge.

The forms from the California Channel Islands vary considerably also, with most of them having a single bulbous acute avicularium ascending the oral lappet or tubular peristome. Areolae are sometimes large and extend over the frontal to the base of the rostrum or near the peristome. Cardelles are present, but small. Ovicells are varied, with pores few to many, small to large. In the Temperate forms neither the large oval nor hatchet-shaped avicularia, such as are found in *P. dolabrata* are present.

Three Allan Hancock Foundation samples that Osburn labeled *Smittina californiensis* were collected at Pt. Fermin, off Redondo Beach, and at Smugglers Cove, Santa Cruz Island, all southern California locations. In these specimens, huge, equilaterally triangular avicularia are situated on high, moundlike rostra, which appear to originate at the proximal zooecial margin. Ovicells are set high, and the globe has many large pores. Material recently collected by Michael Foster from Coches Prietos Cove, Santa Cruz Island, is of the same description.

Robertson (1908, pls. 22, 23) illustrated *Smittia trispinosa* and *Mucronella californica* with large avicularia which encroach on the oral area, arising somewhat proximally and extending distally. Both have other small frontal avicularia, and the ovicells shown have a few large pores. The aperture of Robertson's *S. trispinosa* has lateral oral lappets, a deep set denticle, and a sinus notch, whereas her *M. californica* has a round aperture with the denticle set at the surface.

In *Parasmittina californica* (Robertson) the peristome may be low, or raised on the sides, or tubular. The giant avicularium is longer, slimmer, and curves around the base of the peristome without ascending it. It appears to originate at lateral areolae. The rostrum is not raised, and thus Osburn's illustration of "*P. californica*" (1952, pl. 57, figs. 8–11) may not actually be of that species, but of "*P. trispinosa*" instead.

Examination of Soule's Puritan-American Museum Expedition Collections from Baja California and the Gulf of California shows both the typical *P. californica* (Robertson) and the *P. trispinosa* of Osburn, plus *P. dolabrata*, new species. Although Robertson collected *P. californica* in southern California according to her records, the species appears to be limited in more recent years to the San Diego area, Baja California, and the Gulf of California.

The range of "*Parasmittina trispinosa*" *sensu lato* appears to extend from Puget Sound south and into the Gulf of California. It may be that these two supposed species consist, in fact, of several as yet unrecognized species, or that there are population differences. A thorough collecting, such as was done in the Hawaiian material, is necessary in order to clarify this situation.

It is of interest to note that, of the three Hawaiian species with acute avicularia that ascend the oral lappets (*Parasmittina marsupialis*, *P. parsevaliformis*, and *P. leviavicularia*), none are associated with large or giant acute frontal avicularia. In *P. obstructa* (Waters) and *P. parsevalii* (Harmer, part), the largest avicularia are rounded, blunt, or bifurcate, as in *P. dolabrata*. The colony form of *P. dolabrata*, with large interzooecial acute avicularia, burred cardelles, and tubular ovicell pores, differentiate that species from the others mentioned; also distinguishing it from the "*P. trispinosa*" complex is the hatchet-shaped avicularium.

SMITTINA NORMAN, 1903

Smittina kukuiula, new species

Figure 11E–G

DIAGNOSIS: Species forms small incrusting colony with tiny zooecia. Frontals perforate,

areolae small, but becoming overlain by larger secondary pores in older zooecia. Apertures formed by separation of transverse wall into proximal and distal arches. Distal portion forming irregular peristome with spinous projections; proximal portion curving forward into peristome with bilateral sinuses flanking avicularium. Denticle wide with flaring tips and oval avicularium sitting atop denticle, directed outward. Rostrum elevated with finely serrate tip. Hinge bar straight with tiny median ligula. Ovicells immersed, with 8–12 pores, bordered by roll of frontal or covered completely.

ETYMOLOGY: Named for the type locality, Kukuiula Harbor on the Island of Kauai.

HOLOTYPE: AHF Bryozoan no. 178.

TYPE LOCALITY: S-803-67; Kukuiula Harbor, Kauai. Collected July 3, 1967, McVey and Swerdloff, divers. No other known distribution.

DESCRIPTION: The single colony found was incrusted on coral and is the only specimen of the genus *Smittina* in the Soule collections from Scuba and snorkel diving zones. The zooecia are small with finely perforate frontals and small areolar pores. Larger pores appear to be formed in superficial calcification along the margins so that several small pores may be visible beneath the larger ones. Apertures seem to be formed by separation of the two layers of the transverse wall, and the distal portion rises as a peristome with irregular spinous processes (fig. 11E, G). The wide denticle is apparently formed by the primary frontal, after which the proximal peristome advances proximally and medially to form blunt cardelles and a peristomal collar, with a sinus on either side of the denticle. The median avicularium is connected to distal areolae on either side of the peristome and forms a central, diamond-shaped chamber from which the rostrum arises (fig. 11F).

The avicularium is small, with a blunt-tipped, tonguelike mandible. The hinge bar is straight, with a tiny median ligulate spur. The rostral tip is finely serrate or denticulate.

Zooecial distal walls curve into the next distal zooecium, and the peristome rises above the frontal. The walls bear tiny communication pores at the basal level, plus larger corner pores.

Ovicells are immersed and bear 8–12 small pores placed in two arcs. The more distal arc is bordered by a roll or ridge of frontal (fig. 11E); both pores and ridge become covered over (fig. 11G). Formation of the ovicell may be associated with the transverse slotlike structure seen on the distal peristomal wall in figure 11F.

This little species resembles some of the specimens in the Hancock collections from the Galapagos Islands, placed in *Smittina smittiella* by Osburn. Osburn (1947, p. 39) originally described that species from Florida and the Caribbean. Osburn's type AHF Bryozoan no. 7, from A505, shows a smooth peristome without spinous processes, and frontals are finely porous with reticular lines which form the larger pores in older specimens. Ovicells have many small evenly scattered pores, becoming reticulate but not generally closed. Ovicells are recumbent but remain raised and distinct from adjacent frontals, and they lack the roll or ridge appearance of the Hawaiian material.

In the Galapagos material and the Hawaiian specimen frontal pores become infundibuliform but seem to lack the early reticular appearance. Ovicells of Galapagos specimens are similar to the Atlantic material, however, rather than to the Hawaiian specimen.

Osburn allied his species to Smitt's *Escharella landsborovi* var. *minuscula* (1873, p. 60). Smitt's illustrations are purported to be *E. landsborovi* but figure 202 has a raised rostrum atop the denticle similar to that of *Smittina smittiella*.

Hincks (1884b, p. 361, pl. 13, fig. 5) described *Porella malleolus* from India (coast of Burma) as having a hammer-shaped avicularium mandible within the lower lip, and sometimes with a frontal avicularium directed distally. His figure is not sufficient to distinguish it from several other species, such as those described by Powell (1967b) from New Zealand, except for the frontal avicularium, and the presence of the ligula on the mandible hinge bar in *S. malleolus*.

In *Smittina protrusa* Powell (1967b, p. 380, pl. 17, fig. a), the ligula is longer and spinelike, as illustrated by the *Smittia malleolus* of Waters (1889b, p. 16, pl. 3, figs. 14, 15), which Powell placed in *S. protrusa*. Harmer (1957, p. 921, pl. 63, figs. 7–10) figured *Smittina malleolus* (Hincks) with a small ligula and the long acute frontal avicularium which is directed distally toward the aperture.

Marcus (1953, p. 302, figs. 63–65) placed his "*Smittina* – species" (1938, p. 44, fig. 25) in Osburn's *S. smittiella*, although he noted (fig. 63) the occurrence of tiny lateral oral avicularia on some peristomes. The figure (65) of the avicularian mandible indicates that it is much wider

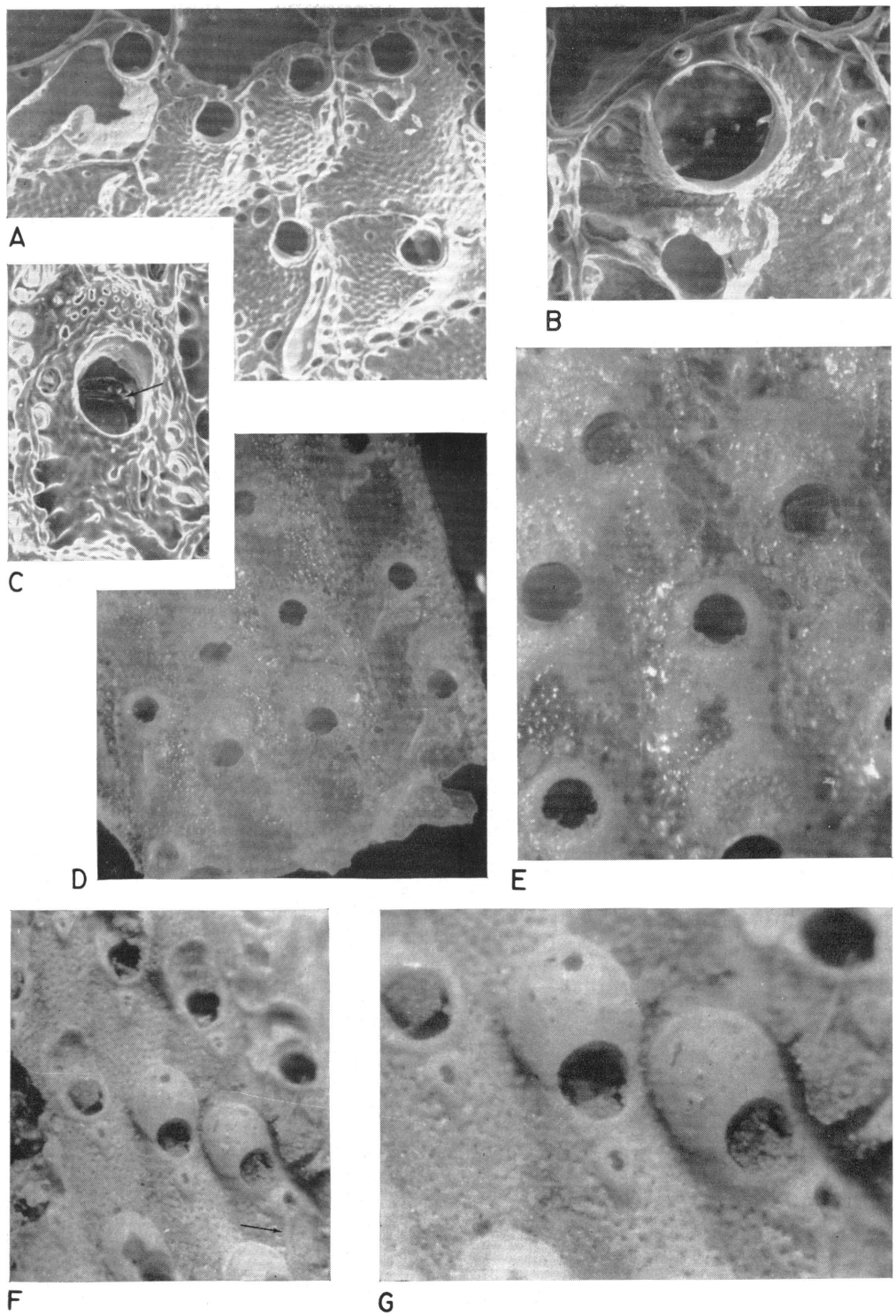


FIG. 12. A–C. *Pleurocodonellina lahainae*, new genus, new species, S.E.M. micrographs. A. Developing edge of colony, with giant avicularium chamber forming. B. Aperture, developing acute frontal avicularium; no denticle. C. Ovicell, with ovicell operculum (arrow) open above zooecium operculum. D, E. Light micrographs. D. Colonies showing pleurocyst frontals, areolae, frontal avicularia. E. Apertures with sinuses and ovicells with crescent of tiny pores. F, G. *Codonellina anatina* (Canu and Bassler), photograph of National Museum of Natural History type specimen. Note part of giant spoon-shaped avicularium on lower right of colony (arrow).

than that found on eastern Pacific material identified by Osburn as *S. smittiella*, or on the new Hawaiian species.

Powell (1967a, p. 170, pl. 3, fig. 12) placed his material from the Red Sea, plus the *S. smittiella* of Osburn, in *Smittina malleolus* (Hincks) even though he found no frontal avicularia in his or Osburn's specimens.

There is considerable variation in the Hancock specimens from the Galapagos Islands. Those from Tagus Cove, Albemarle Island (Isla Isabela), have a narrower, truncate denticle. Those from Duncan (Pinzon) Island and Indefatigable (Santa Cruz) Island have a wider denticle with the paired lateral sinuses more like the new species. Ovicells on the specimen from Duncan Island are not immersed or covered. A specimen from Santa Cruz Island, Southern California, differs in having the oval avicularium completely outside the sinus. The denticle is very wide and uncovered, with a median suture; hooked cardelles are present. It should probably not be included in *Smittina smittiella* at all.

In view of the significance which the occurrence and placement of avicularia have shown during the course of the present study, it is considered inadvisable to place the Hawaiian material in *S. smittiella*. It seems doubtful that Marcus's material belongs in Osburn's species, and also unlikely that either of these belong in *S. malleolus* (Hincks).

The type locality of Kukuiula Harbor, pronounced Kookoo-ee-oola, on the south coast of Kauai is also the type locality of *Thalamoporella verrilli* Soule and Soule, 1970. A spicule, probably from that species, appears at the very top of figure 11G on the colony of *Smittina kukuiula*.

PLEUROCODONELLINA, NEW GENUS

DIAGNOSIS: Incrusting colonies; zooecia with pleurocyst frontals, single row of areolar pores. Primary aperture round with wide, curving sinus, one or two sets of lateral cardelles; no median denticle. Secondary sinus narrowing proximally. Operculum shaped to secondary aperture, with rim sclerite; closing both aperture and ovicell. Single frontal avicularium, median or skewed, directed proximally. Ovicell immersed, with crescent of small pores exposed.

TYPE SPECIES: *Pleurocodonellina lahainae*, new genus, new species.

Pleurocodonellina lahainae, new species

Figure 12A–E

DIAGNOSIS: Zooecia with granular, imperforate frontals bordered by single row of areolar pores, and with distinct lateral walls. Primary apertures round, rimmed, with wide arc of proximal sinus. One, sometimes two, pairs of slender cardelles occurring, hooked proximally. No median denticle present. Sinus narrowed in secondary aperture. Operculum with shape of aperture, bordered by marginal sclerite. Operculum possibly creased across midline; closing both aperture and ovicell. Ovicells finely perforate, immersed; sometimes with tiny interior operculum. Small, single, acute avicularium recumbent on lateral frontal directed proximally; rarely paired. Sometimes replaced by huge spoon-shaped avicularium with rostrum covering frontal.

ETYMOLOGY: Named for the type locality, off Lahaina, Maui.

HOLOTYPE: AHF Bryozoan no. 179.

TYPE LOCALITY: S-613-66, AuAu Channel, off Lahaina, Maui; 15 m., on coral. Divers McVey and Wass; glass-bottom boat made available by Chris Rose and Ray Croteau.

DISTRIBUTION: S-613-66, no other stations; 24 specimens.

DESCRIPTION: The colonies are incrusted on coral, in an area where shifting sand commonly occurs. The frontals are granular, bordered by a single row of areolar pores and separated by distinct lateral walls, characters similar to those seen in parasmittinids. Little transverse wall folding seems to occur in development; rather the distal wall is commonly formed by lateral wall extensions (fig. 12A). Apertures are at first round, with a very wide sinus proximally, limited by slender, hooked cardelles (fig. 12B). One or two distal spines rarely occur on marginal zooecia. The secondary aperture develops a narrower sinus, and tiny additional paired cardelles sometimes can be seen. The frontal appears to overgrow the primary aperture slightly (light micrographs fig. 12D, E). The operculum is rounded distally, shaped to the sinus proximally, and has a marginal sclerite. The operculum may be creased across the middle, apparently to effect closure of the raised distal portion of the aperture. The operculum also closes the ovicell, which sometimes has its own tiny operculum (fig. 12C). Ovicells are

immersed, leaving rows of fine pores exposed.

The presence of accessory cardelles or lateral denticles seems to indicate that the developmental sequence seen in smittinid denticle formation does not become completed in *Pleurocodonellina*. This in turn probably affects the angle of closure by the operculum when the median denticle is not present.

The formation of the frontal avicularium is similar to some parasmittinids, originating with a median frontal pore and a lateral areolar pore. The rostrum is inflated, and the avicularium becomes recumbent on the lateral frontal, directed proximally. Some median avicularia are small and acute (fig. 12C), some are longer and acute (fig. 12D), and others infrequently form enormous spoon-shaped avicularia. Rarely, the tiny avicularia are paired. The rostral chamber of the spoon-shaped avicularium is huge, covering most of the zooecial frontal (fig. 12A). Superficial calcification occurs after the rostral chamber is complete.

The new genus is similar to *Codonellina* Bassler, 1934 (emending the *Codonella* of Canu and Bassler, 1927, p. 25), except for the perforate frontal in their genus and the connection of the avicularian chamber to areolar pores on both sides of the aperture. Harmer (1957, p. 1050) remarked, in discussing *Codonellina montferrandii*, that some young colonies of his *Siboga* Station 348 O, and also Thornely's Ceylon *Lepralia mortoni* Haswell, 1881 were hardly distinguishable from his figure 30, plate 69, except that they had conspicuous marginal areolae, and the frontal was imperforate. He suggested that they are a variety of *C. montferrandii*.

Harmer also placed *Lepralia acuta* and *L. obtusata* (Ortmann, 1890, p. 41) in *C. montferrandii*; yet Ortmann stated that the frontal and the ovicell of *L. acuta* are granular whereas those of *L. obtusata* are punctured. Ortmann's illustration of *L. acuta* shows a creased operculum. Okada and Mawatari (1936) referred *L. acuta* to *Codonellina*, as having a granular frontal with tiny tremopores.

Hastings (1932, p. 414) noted that a specimen from Ceylon was identified by Waters as *L. montferrandii*, but that Waters also mentioned the marginal areolae, the imperforate frontal, and a somewhat raised peristome. Waters (1909, p. 171) in his Red Sea paper said that material from Manaar had the triangular avicularium, sometimes replaced by a large spathulate avicularium, a raised peristome, and large pores around the border instead of uniform perforations. Waters said, "This form, which may have to receive another generic name, also occurs from New Zealand (A.W.W. coll.)."

One specimen of Thornely's collection from Ceylon examined by us at the British Museum (slide 1936.12.13.40) is labeled "not" *Lepralia mortoni* Haswell, 1881. It has quite large areolae, an acute suboral avicularium and the creased operculum, such as is seen in the new species. Haswell's species is uniformly punctate.

Okada and Mawatari (1936, p. 69) described and figured *Smittina elongata*, which has the characters of the new genus. It has small, slender, acute median avicularia but lacks the large spatulate avicularia, and the zooecia are quite elongate. They obtained only one colony of it, and so might have missed the occasional large avicularia, if present.

It is difficult to determine from Savigny's (?1817, pl. 9, fig. 14) illustration of *Flustra montferrandii* Audouin, 1826, whether the frontal is porous or coarsely granular. Waters (1909) and subsequent authors have recorded it as porous. Brown (1952, p. 325) reported on *Smittina flexuosa* Hutton as a foliaceous species without median lyrula, and with prominent lateral cardelles. It is imperforate with only large marginal areolae. The median avicularium is small and oval, and the ovicell is immersed, perforate. This may belong to the new genus, or to *Hippomonavella*. Thus it seems advisable to erect a new genus for those codonellinid-like forms having a granular frontal, as the nature of the frontal seems to be a valid character. The distinction is in keeping with Osburn's effective separation of *Smittoidea*, *Parasmittina*, and *Smittina* along such lines.

Smittia signata Waters (1889b, p. 17, pl. 3, figs. 4–6) may belong to the new genus. Waters shows a sinus, probably formed, he said, by the two lateral teeth. The sinus appears to be much narrower than in our material; Waters related it to a schizoporellid sinus. Canu and Bassler (1929, p. 308) placed Waters's species in *Lacerna* Jullien, 1888, but according to Jullien's description and figure (p. 48, pl. 1, fig. 2), there are no avicularia, the spines are not transient, and the ovicells are granular except for a row of basal pores.

Hastings (1932, pp. 429–430, fig. 12) reported *Smittina signata* from Tizard Bank, and showed a

TABLE 25
MEASUREMENTS (IN MICRONS) OF
Pleurocodonellina lahainae

	Minimum	Maximum	Average	Number
Zooecium length	600	980	738	10
Zooecium width	280	400	328	10
Aperture length	110	140	123	10
Aperture width	120	160	140	10
Ovicell length	280	340	307	10
Ovicell width	280	340	242	10
Avicularia (long acute)				
Length	220	280	242	10
Width	60	80	64	10
Avicularia (small acute)				
Length	110	150	124	10
Width	40	50	43	10
Avicularia (giant)				
Length	360	700	434	10
Width	120	200	152	10

more ovoid ("schizoporellid") operculum, such as is seen on our specimens. Harmer's *Smittina signata* (1957, pp. 928–930, pl. 63, figs. 27–29) has paired or single small avicularia which may have a median origin, and which are sometimes replaced by spathulate avicularia. One specimen was found in the Allan Hancock Foundation Collections from Halape, Hawaii, which Osburn had labeled *S. trispinosa* var. *munita*. We have tentatively identified it as *Parasmittina signata*, but it is in very poor condition. The sinus of *P. signata* is narrower than in *Pleurocodonellina*; the operculum also is shaped to fit the sinus, as it is in *Arthropoma*. *Schizopodrella horstii* Osburn was later transferred by him to *Lacerna*; but specimens in the Allan Hancock Foundation Collections resemble closely the illustrations of *S. signata* mentioned above. Lagaaij (1963, p. 197) agreed with Harmer in placing *L. horstii* in synonymy with *L. signata*, but placed that in *Parasmittina*. The cardelles are deep set in *L. horstii*, whereas in *P. lahainae* they are near the surface. Osburn (1952, p. 362) placed *Lacerna fistulata* O'Donoghue in the Hippoporinidae; its frontal is smooth, veined, without visible areolar pores, but the ovicells are erect, large, and with large pores such as are seen in some of the smittinids.

Both Hastings and Harmer mentioned finding smittinid colonies with a tiny denticle present in a few zooecia but absent in others. We have observed this also, in *Parasmittina parviuncinata* and *P. circularis*, where the acute denticle seems to be on the way to disappearance.

Codonellina anatina (Canu and Bassler), 1927
Figure 12F, G

Described from Hawaii by Canu and Bassler (1927, p. 26), *Codonellina anatina* is distinctive and probably should not be combined in synonymies as Harmer did, placing it in *C. montferrandii* (1957, p. 1049). It appears that *C. spatulata* (Okada and Mawatari, 1936) is a synonym of *C. anatina*, however.

Osburn (1952, p. 422) summarized the characters of the genus, and widened the species description to include Galapagos material. This should probably be excluded, as the spatulas are small in the Galapagos specimens and never approach the Hawaiian form in size, resembling those in *C. montferrandii* more closely. Some Galapagos material has apertural rims with quite pronounced knobs at the lower proximal corners.

The National Museum of Natural History type of *C. anatina* (fig. 12F, G) contains few intact zooecia. Easily seen are the porous frontal, small triangular median avicularium, and the large spoon-shaped avicularium (arrow, fig. 12F), which sometimes replaces the small avicularium. Ovicells have scattered pores, and the apertures are rimmed with strong cardelles and a wide proximal sinus.

The type locality of *Codonellina anatina* is *Albatross* Station 4055, at Pt. Alia on the northeast coast of Hawaii, on recent maps labeled Pepeekeo Pt. The species did not occur in our collections, as they probably were restricted to deeper waters such as the *Albatross* collected in.

The genus *Schizomavella* may be easily confused with the genus *Codonellina*. The chief difference seems to be in the formation of the aperture, which in *Codonellina* has an apparently complete peristomal rim component, sometimes with small knobs at the lower proximal corners. In *Schizomavella*, the peristomal rim component appears to stop at the proximal corners, and the proximal lip which forms the sinus is contributed by the frontal in material we have examined. Dimorphic apertures were found in Hawaiian *Schizomavella*. In both genera, the frontal is perforate, the ovicell is perforate, and the oper-

culum closes both aperture and ovicell. In Osburn (1952, p. 316) there is an error in the key to the Schizoporellidae which indicates that the ovicell is not closed by the operculum in *Schizomavella*.

Similar comparisons can be made with the new genus *Pleurocodonellina* and a superficially similar genus, *Hippomonavella*. In *Pleurocodonellina* the aperture is completed by the peristomal rim, but in *Hippomonavella* the proximal lip and sinus seem to be formed by the frontal. Both genera have imperforate frontals with areolar pores, and the opercula close the aperture and ovicells.

Osburn (1952, p. 365) placed *Schizoporella longirostrata* Hincks (1883) in the genus *Hippomonavella* Bassler, 1934, along with *Hippomenella parvicapitata* of Canu and Bassler, 1930. Canu and Bassler (1930, p. 20) remarked also that there are two groups of species in *Hippomenella* Canu and Bassler, 1917; one with a "mucron" and richly decorated ovicell, and the other without a mucron and with the ovicell finely punctate. The latter group included *H. parvicapitata*.

Schizoporella longirostrata Hincks (1883) from the Puget Sound-Queen Charlotte Islands region has an imperforate frontal with tiny areolae and a heavy ectocyst. The "*S. longirostrata*" from southern California of Robertson (1908, p. 291, pl. 20, fig. 49) has many perforations in the frontal except for the most central (pectoral) area. The avicularia are sometimes skewed far to the side. Osburn (1952, p. 365) placed this species in the genus *Hippomonavella* Bassler (1934) which has as its genotype *Lepralia praeclara* MacGillivray, 1895, with only a single row of areolar pores. Osburn placed *Hippomenella parvicapitata* Canu and Bassler, 1930, from the Galapagos in *Hippomonavella*, yet it clearly has several rows of pores except in the central frontal, as is typical of the genus *Hippomenella*.

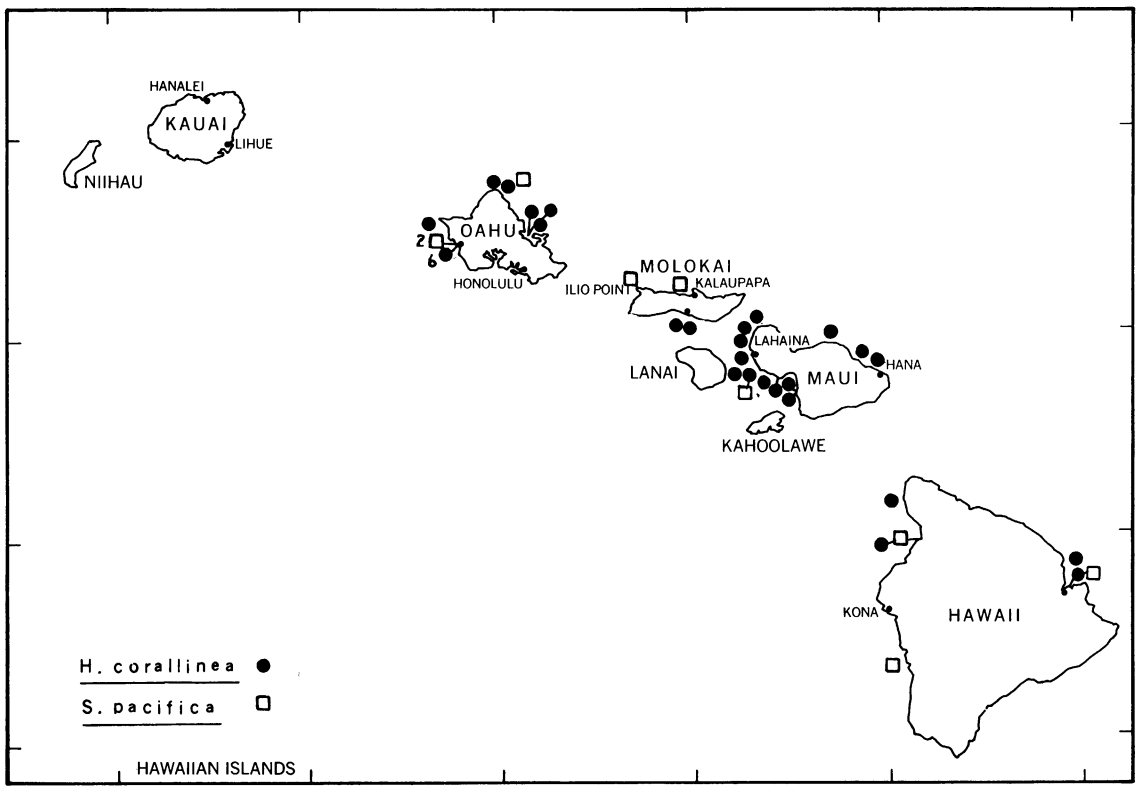
Lagaaij (1963, p. 186) described a new species from the Gulf of Mexico, *Hippopodina bernardi*, which has an imperforate pectoral area, with two rows of marginal pores, and with large, evenly perforate ovicells. This is similar to a species illustrated by Osburn (1952, pl. 46, fig. 16) as *Codonellina cribriformis* (O'Donoghue). The illustration is in error, as the actual AHF specimens so labeled conform to Osburn's description (p. 424) of having a tremocyst frontal and porous ovicell. Osburn did state that in younger stages, the frontal is hyaline, smooth to slightly granular. Further generic distinction may have to be made for those forms with a single row of areolar pores and those with only the pectoral area imperforate. Developmental studies would be most valuable in this question.

Frontal formation in the *Hippomonavella longirostrata* from Puget Sound and southern California is much different from that seen in parasmittinids studied. The margins of the frontal become heavily calcified, leaving a thin, smooth central portion. This morphology is puzzling and also needs further investigation; it is not known whether the type species of *Hippomonavella* shows this character.

CONCLUSIONS

THE TAXONOMIC STUDIES of Smittinidae from the Hawaiian Islands and portions of the eastern Pacific have presented many difficulties in separating species on the basis of subtle differences and in interpreting the complex distribution patterns. It is clear that within the islands distinct isolation processes are occurring or have occurred. These may be due to substrate variations, differences in water mass character or quality, or to differences in localized circulation patterns.

The distribution maps 2–8 indicate that species differences distinguished in the present paper are more than random scatterings. For example, species included in maps 2 through 5 show extensive colonization of the channel between Maui and Lanai Islands; those in maps 6 through 8 show far fewer occurrences at those stations. The island of Kauai offers few areas sheltered from heavy surf and is in contact with the more northern cooler water mass circulation patterns. Furthermore the extensive rainfall on the island (300+ inches per year in some areas) feeds large, fast-flowing streams which transport great quantities of sediment into the few, shallow water, fringing areas. The incidence of bryozoans in Kauai's shallow waters seems much reduced. It is of interest to note that the



MAP 2. Distribution of *Hemismittoidea corallinea* and *Smittoidea pacifica*.

harbor at Kukuiula is the type of locality of several species described by the authors as new: *Thalamoporella verrilli* Soule and Soule (1970), *Smittina kukuiula*, new species, and *Parasmittina kauaiensis*, new species.

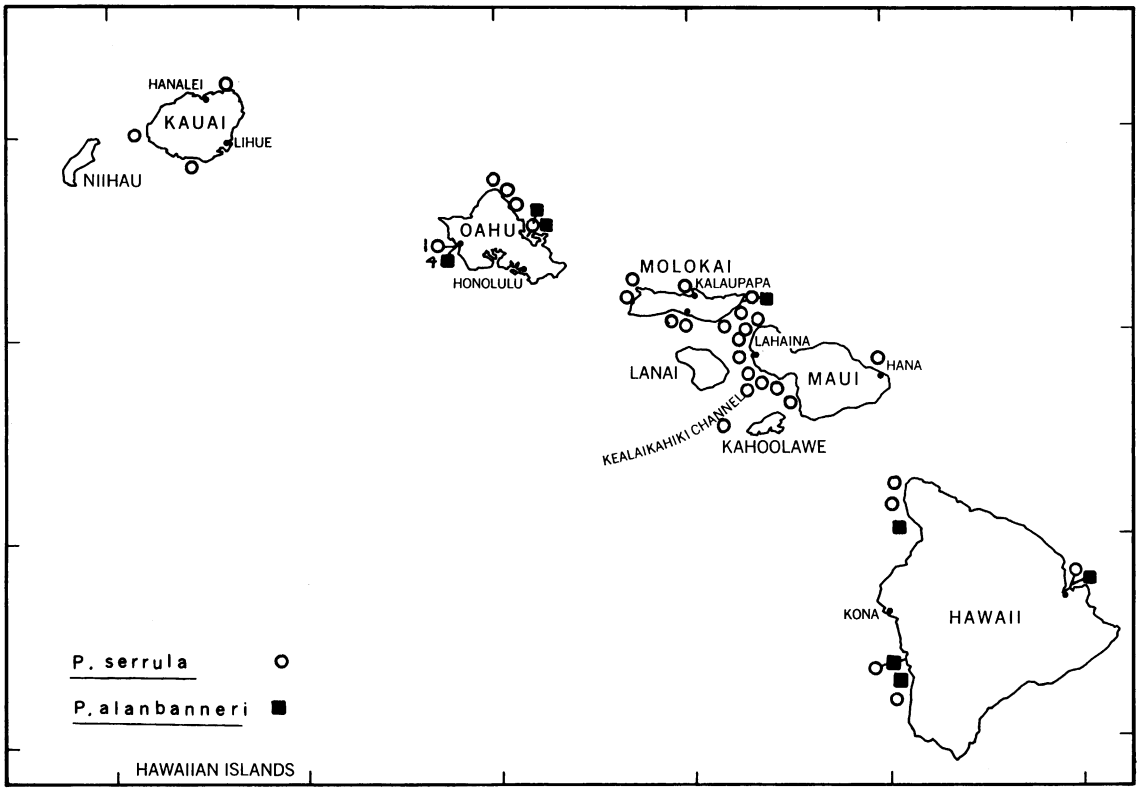
The island of Hawaii also has areas of heavy rainfall runoff on the north and northeast coasts, plus large amounts of sugar cane trash dumped into the sea in those areas. As the island of Hawaii has had numerous recent lava flows, much of the coast slopes sharply into the sea, with little shallow water. The west coast has shallower areas and older lava benches with correspondingly more shallow-water bryozoans. Hawaii is much farther south than the central cluster of the islands of Oahu, Molokai, Lanai, Kahoolawe, and Maui.

The south coast of Molokai is shallow and muddy, but seems to support certain smittinid species (maps 2–6) but not others (maps 7, 8). The northern tips of Molokai, at Ilio Point and Kalaupapa, also host a differing group of species, especially the *raigii*-like forms.

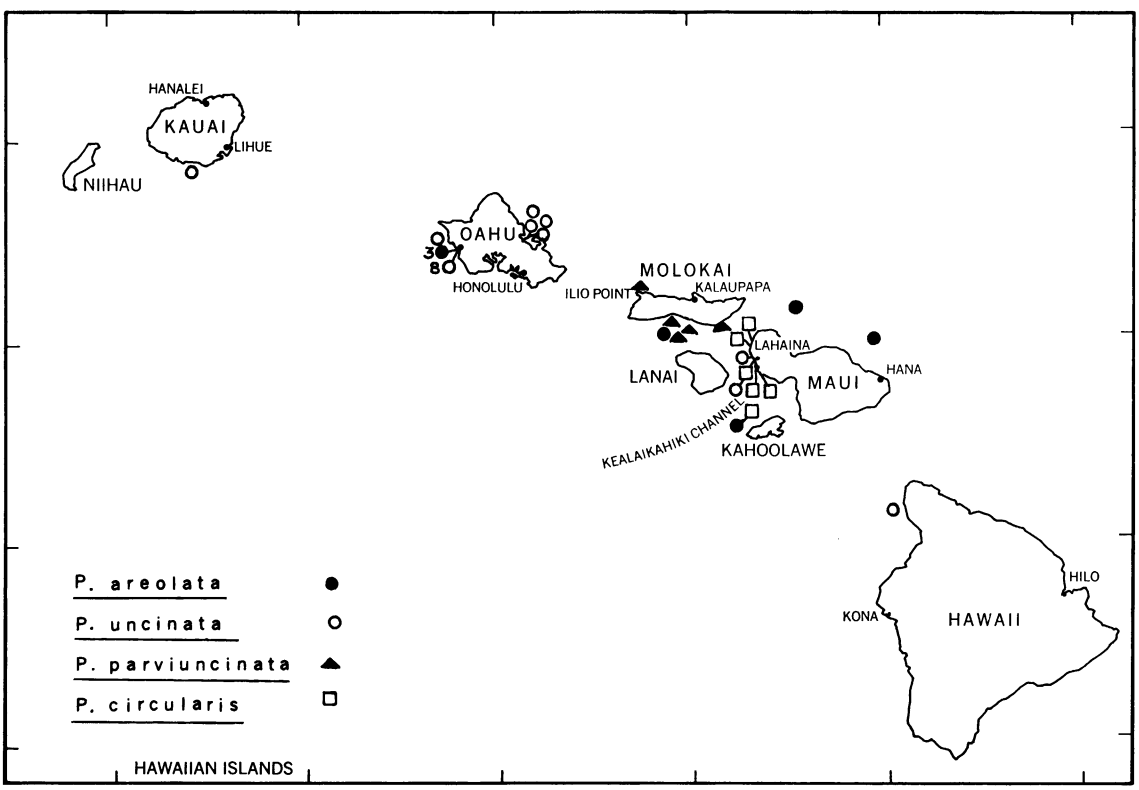
There is little question that the Hawaiian faunae have a strong Indo-Pacific component; it seems to be the principal one in some major invertebrate groups. In the bryozoans also, this appears to be true, at least at the generic level. The present authors (1967) reviewed the pertinent literature in major invertebrate groups, discussing 13 species that were common to Hawaiian and eastern Pacific waters and which were mostly cosmopolitan warm temperate or tropical species.

Among the Smittinidae reported herein, none of the Hawaiian species occurred along the continental coastal waters of the eastern Pacific. The Galapagos Islands appear to share one species of smittinid with Hawaii (*Smittoidea pacifica*) and at least two species with the mainland (*Parasmittina dolabrata* and *P. crosslandi*). The "*P. trispinosa*" of the continental California coast has some similarities to the *P. parsevaliformis-P. leviavicularia* species but is still distinct from them.

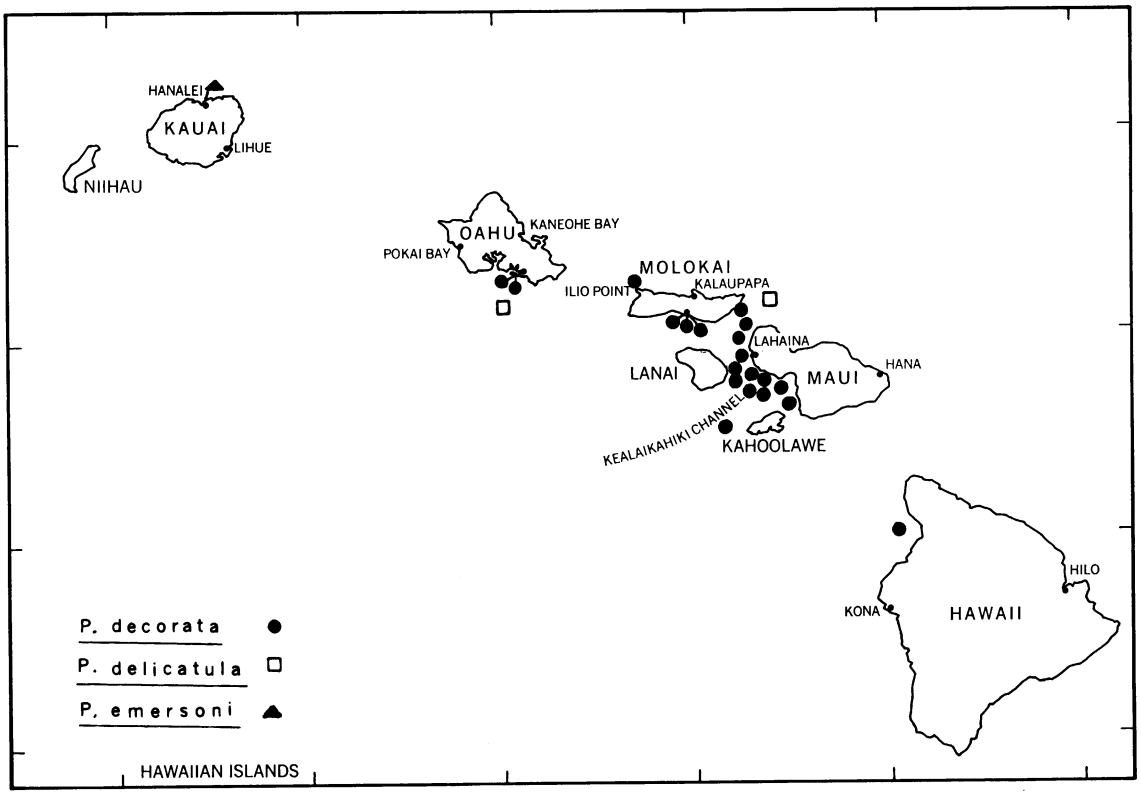
Roger G. Skolmen of the United States De-



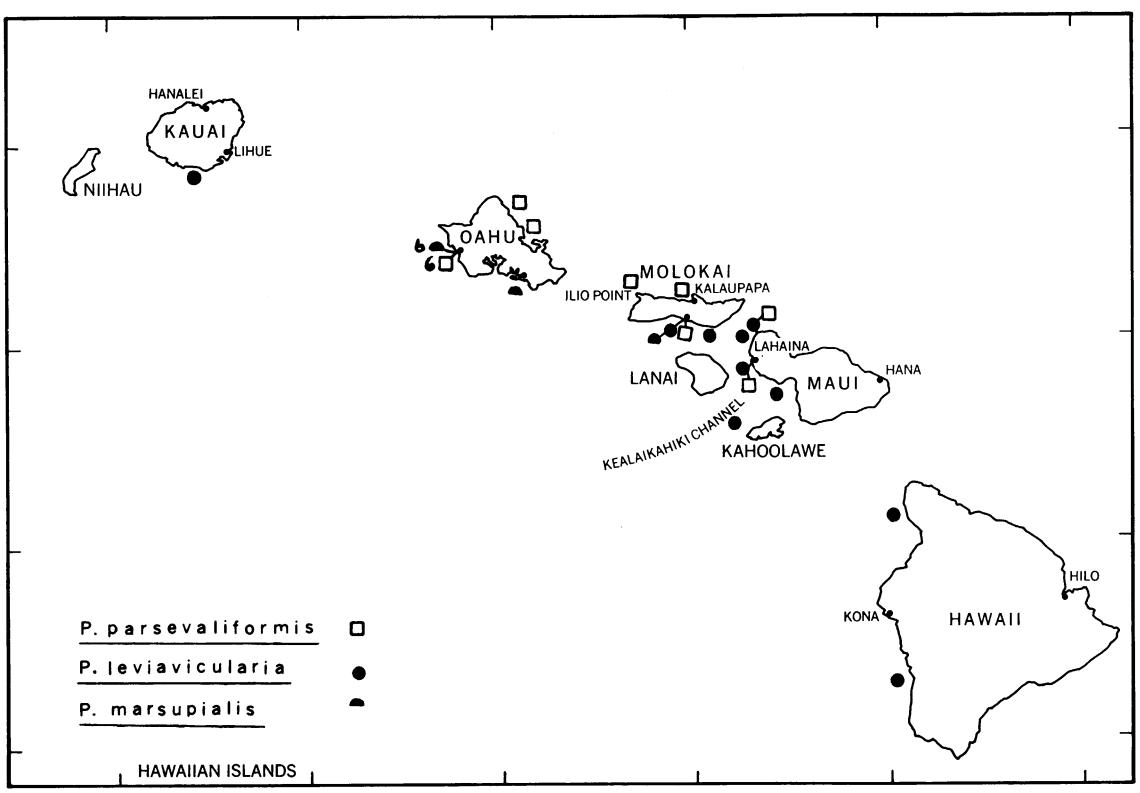
MAP 3. Distribution of *Parasmittina serrula* and *P. alanbanneri.*



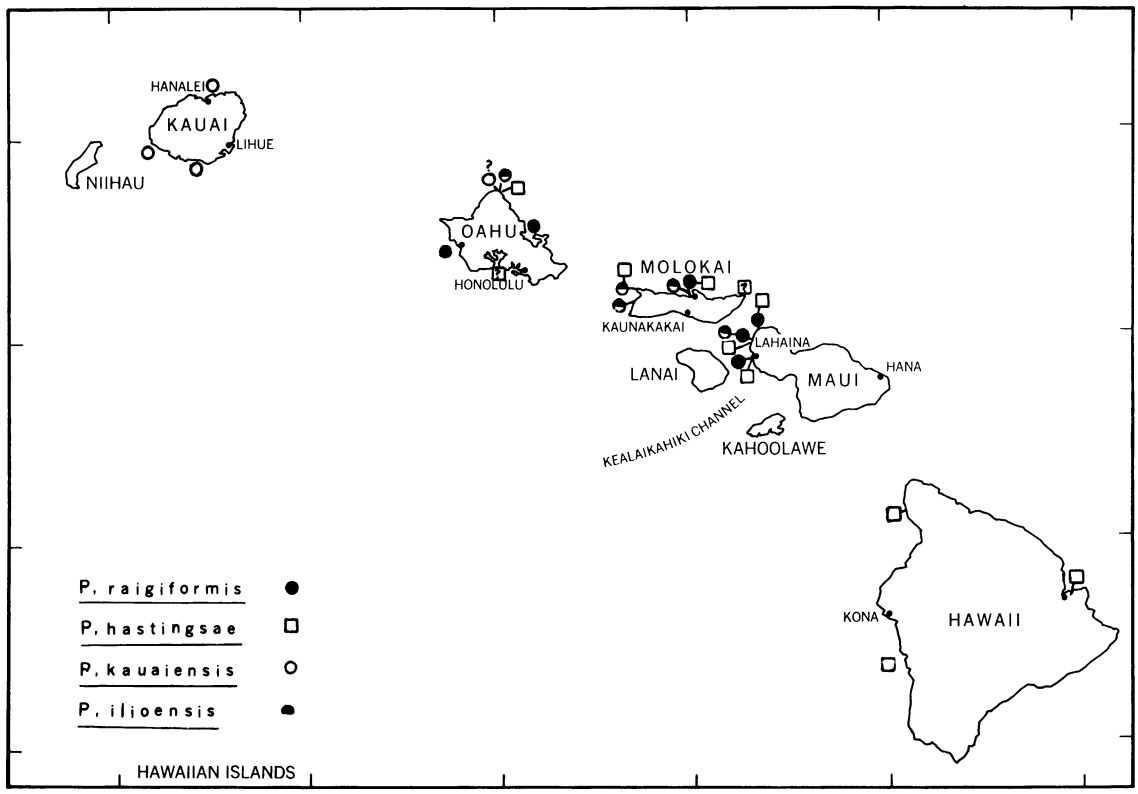
MAP 4. Distribution of *Parasmittina areolata, P. uncinata, P. parviuncinata,* and *P. circularis.*



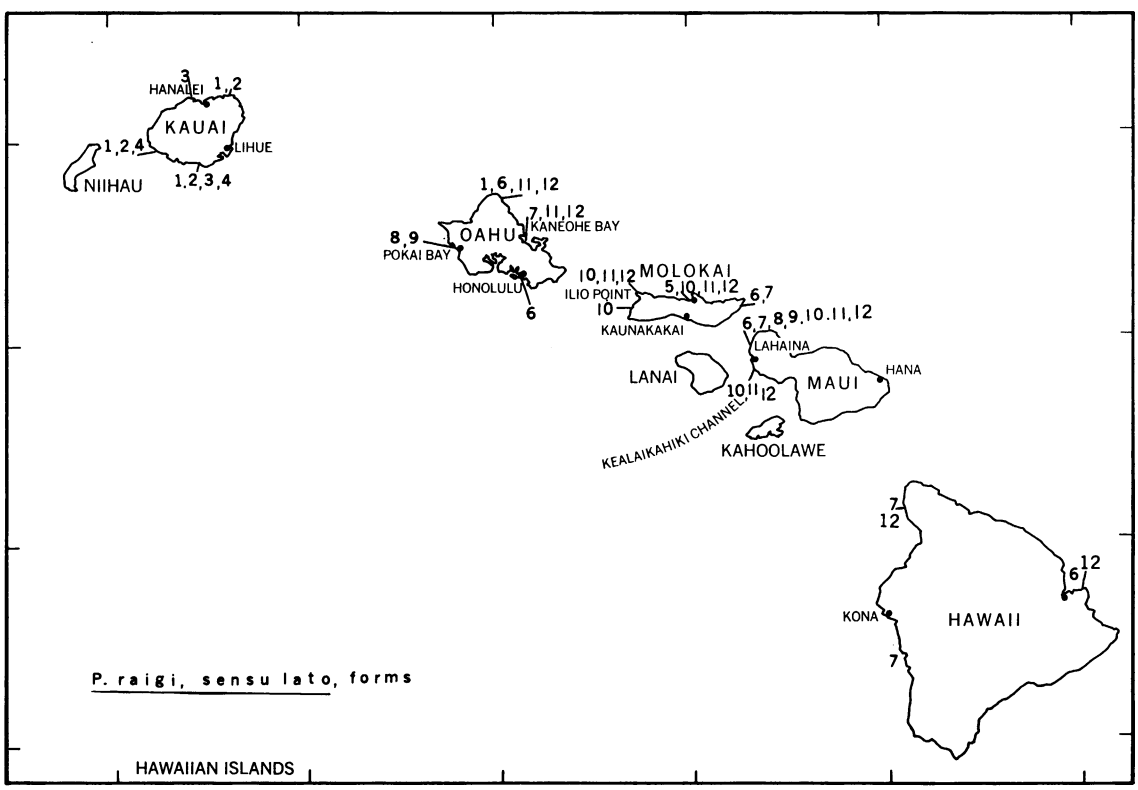
MAP 5. Distribution of *Parasmittina decorata*, *P. delicatula*, and *P. emersoni*.



MAP 6. Distribution of *Parasmittina parsevaliformis*, *P. leviavicularia*, and *P. marsupialis*.



MAP 7. Distribution of *Parasmittina raigiformis*, *P. hastingsae*, *P. kauaiensis*, and *P. ilioensis*.



MAP 8. Distribution of *Parasmittina raigii*, *sensu lato*, forms.

partment of Agriculture Forest Service in Honolulu, provided (personal commun.) the authors with a list of drift logs that had been in the water a long time, recorded by him and Clarence Strong on Hawaiian shores.

North American logs far outnumbered drift logs from Asian or South Pacific waters. The east coast of Kauai, southeast coast of Oahu, north coast of Maui, east side of Kahoolawe, and southeast coast of Hawaii all received North American logs. Heaviest concentrations occurred on the northern tip of Oahu, the northwest tip of Maui, the east bay of Kahoolawe, and exceedingly heavy concentrations on the southeast tip of Hawaii.

Skolmen observed that the logs from the West Coast were more heavily attacked by marine borers than those from Asia. He surmised that the Asian logs were in colder water and travelled more quickly than those from North America.

Hawaii lies at the northernmost fringe of the tropical waters; it is in fact considered only marginally tropical, or subtropical. It is evident that mechanisms exist for water transport from North America, the Indo-Pacific, and Asia; the transport times of course are unknown. Survival, reproduction, and speciation are contingent upon finding a suitable niche within the islands, which seem literally to be at the hub of the Pacific.

The question of whether *Codonellina*, and the new genus *Pleurocodonellina* belong in the Smittinidae is still uncertain. The foregoing discussions will hopefully shed some light on the similarities and differences within the family. Further knowledge of developmental morphology of many groups should ultimately permit revision along stronger biological lines than has previously been possible.

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