FOLIA MALACOLOGICA
Folia Malacol. 34(1): 1–19
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, March 2026
https://doi.org/10.12657/folmal.034.001

OPISTHOTEUTHIS BRUUNI (CEPHALOPODA: CIRRATA: OPISTHOTEUTHIDAE) FROM OFF CALIFORNIA, NORTHEASTERN PACIFIC, WITH POSTHUMOUS DESCRIPTIONS BY ERIC HOCHBERG

TRISTAN JOSEPH VERHOEFF

Invertebrate Zoology, Tasmanian Museum and Art Gallery, Winkleigh Place, 7018, Rosny Park, Australia (e-mail: tristan.verhoeff@utas.edu.au); https://orcid.org/0000-0001-5103-8592

ABSTRACT: *Opisthoteuthis bruuni* is herein recorded from the northeastern Pacific off California, the specimens of this taxon from the northeastern Pacific were previously considered as new species (though never published) by the late F. G. (ERIC) HOCHBERG, whose data and illustrations are posthumously included herein. The specimens are morphologically and genetically comparable to *O. bruuni* from the southeastern Pacific, supporting a range extension of the species from Chile and Peru, northwards to waters off California.

KEYWORDS: flapjack octopus; marine invertebrates; Mollusca; octopus; taxonomy

INTRODUCTION

DR FREDERICK GEORGE (ERIC) HOCHBERG (1941–2023) was a well-known teuthologist who contributed greatly to the descriptions of many cephalopod species and genera, particularly octopods, as well as cephalopod parasite research. HOCHBERG's contributions to research on cirrate octopods (finned octopods of Suborder Cirrata Grimpe, 1916) was more limited, but he added to the FAO catalogue chapters on cirrate octopods (HOCHBERG et al. 2014), a molecular study (PIERTNEY et al. 2003), and described a dicyemid parasite from *Cirroctopus glacialis* (Robson, 1930) (HOCHBERG & SHORT 1983). However he was planning on several descriptions and re-descriptions of cirrate species from the Pacific that never reached the point of publication.

HOCHBERG was curator of invertebrate zoology at the Santa Barbara Museum of Natural History, California (USA) since 1973, but retired from this role in 2016 due to deteriorating health, he passed away 31st May 2023 (age 82) (LILLY et al. 2024, PAUL VALENTICH-SCOTT, personal communication).

Early notes and unpublished manuscript drafts indicate that HOCHBERG was planning on describing several cirrate octopods. Relevant herein are two species he was planning on describing based on material collected off the California coast, northeastern Pacific, allocated to the genera *Opisthoteuthis* Verrill, 1896, or *Grimpoteuthis* Robson, 1932. The first was *Grimpoteuthis* (=*Opisthoteuthis*) *"packardi"*[1] 'nomen nudum' to be described from ~14 specimens along with spawned eggs (collected between latitudes 32°43.8'N to 36°51'N, 285–480 m depth) (HOCHBERG et al. 1996), and secondly was *Opisthoteuthis "berryi"* 'nomen nudum', which later had its proposed specific epithet changed to *"hazardi"*, collected from off Point Conception [34°30'N] to the vicinity of San Diego [32°N], 200–700 m depth (HOCHBERG 2011).

The manuscripts for *Opisthoteuthis "berryi"* and *O. "hazardi"* were last updated ~2011, shortly before ERIC HOCHBERG left the SBMNH due to his declining health. The name change from *"berryi"* to *"hazardi"* was in honour of local drag boat fisherman Mr RALPH W. HAZARD (1916–2003), who had a long history with the SBMNH, donating deep-water octo-

[1] Throughout this paper specific epithets enclosed in quotations "X" are unavailable names (including *nomen nudum*), i.e., "manuscript names" (e.g., *O. "hazardi"*).

pods in the 1960s and early-1970s (and would later invite ERIC to join him on his trawler the "Kildee"). Ralph Hazard passed away in late 2003, and on the 26th December 2003, HOCHBERG wrote to the Santa Barbara Maritime Museum that he was naming the species after RALPH HAZARD (correspondence).

Examination of HOCHBERG's (1990s–2011) description and illustrations of *O. "hazardi"* reveal it to be morphologically indistinguishable from *Opisthoteuthis bruuni* (Voss, 1982) from the southeastern Pacific, with recent re-description of *O. bruuni*, as well as molecular evidence further confirming this identification and also indicating that *O. "packardi"* was in all probability the same species too. While not new species, HOCHBERG's descriptions are a significant northwards range extension for *O. bruuni*, and provide valuable morphological data on this population of the species. HOCHBERG's (1990s–2011) surviving information and illustrations on this material is posthumously published herein.

MATERIALS AND METHODS

HISTORIC COLLECTION OF SPECIMENS

Material attributed to *O. "hazardi"* was collected opportunistically from 1957–1993 by research vessels (RV "Ocean Sentinel" and RV "Velero") as well as fisheries vessels (FV "Kildee", FV "Elsie B", FV "Julie K" and FV "Tammy"), using a range of trawling gear (e.g., 10 foot Tucker trawl, small otter trawls, and 30 foot shrimp trawl). Preservation history of material is uncertain, but much of it was frozen at sea before later formalin fixing and storage in 70% ethanol. The majority of the specimens were accessioned at the Santa Barbara Museum of Natural History, Santa Barbara, California (USA) (SBMNH). Capture locations of material are mapped on Fig. 1.

Terminology, measurements and indices used by HOCHBERG generally agree with that used for opisthoteuthids more recently (see VERHOEFF 2024, 2025). All efforts were made to locate any original tabulated datasets prepared by HOCHBERG for the material examined (raw measurements and sucker counts), but none could be located at the SBMNH. However, raw mantle length measurements were available for all specimens examined, while the rest of the indices were generally available as averages for males and females (sourced originally from multiple specimens) and for some indices a range was available in addition to the average (format e.g., 3.4–4.9–6.0, where the central underlined number is the average, and the flanking numbers are the minimum and maximum for a range of specimens).

REMOTELY OPERATED VEHICLE OBSERVATIONS

Observations of cirrate octopods from remotely operated vehicles operated by the Monterey Bay Aquarium Research Institute (MBARI) and documented on the MBARI Deep-Sea Guide were consulted to compare observations of opisthoteuthids off the California coast (MBARI 2025a, 2025b).

MOLECULAR ANALYSIS

HOCHBERG provided *Opisthoteuthis* tissues for sequencing from the NE Pacific specimens that he was planning to describe as new species. For this material, 16S mitochondrial sequences were generated for the thesis of HUDELOT (2000), and later built upon for PIERTNEY et al. (2003). As is covered in the discussion, *O. "hazardi"* was the *Opisthoteuthis* "sp. 3" of PIERTNEY et al. (2003) (*O.* "sp. 1" of HUDELOT 2000) (from specimen **SBMNH 464912**), while *O. "packardi"* was *Opisthoteuthis* "sp. 4" of PIERTNEY et al. (2003) (from HOCHBERG's proposed type specimen, **USNM 893774**, GenBank sequence AF110100). The sequence for *O. "hazardi"* was designated "AJ252769" according to PIERTNEY et al. (2003) (including supplementary material) but an error occurred resulting in sequence AJ252769 being a *Stauroteuthis* sequence when uploaded to GenBank. The original sequence was retrieved from HUDELOT (2000) for inclusion herein and comparison with *O. "packardi"* (Appendix). While COI sequences are superior for examining the systematics of cirrate octopods (VERHOEFF 2023), the availability of 16S sequences for both *O. "hazardi"* and *O. "packardi"* as identified by HOCHBERG, as well as two 16S sequences for *O. bruuni* from the SE Pacific (near the type location, National Museum of Natural History, Santiago, Chile, specimens **MNHNCL 300138** and **MNHNCL 300139**) result in 16S being utilised herein.

A Maximum Likelihood (ML) analysis was done using the above sequences to assess their similarity to each other and all available opisthoteuthid 16S sequences (sourced from GenBank, www.ncbi.nlm.nih.gov/genbank/), and using grimpoteuthid sequences as the outgroup (see Table 1), in MEGA X (KUMAR et al. 2018). Sequence alignment used MUSCLE for non-coding DNA, model selection used MEGA X's "model selection" tool. The final 16S rDNA dataset for analysis had 467 positions (including sites that were in at least 80% of sequences), tree construction used the Tamura 3-parameter model with discrete Gamma distribution to model evolutionary rate

differences among sites (G parameter = 0.546), allowing for some sites to be evolutionarily invariable (I = 57.28% sites) (T92 + G + I model with Bayesian Information Criterion or 'BIC' score of 3691.9). The phylogenetic tree was tested with the bootstrap method (1000 replications).

Fig. 1. Collection locations for *Opisthoteuthis bruuni* between Monterey Bay and San Diego, California, locations are shown for material originally attributed to *O. "hazardi"* (orange squares), as well as *O. "packardi"* (red circles) which is also referable to *O. bruuni*. Area covered marked at top-right by a red square relative to the rest of the USA and Mexico

Table 1. The 16S rDNA sequences utilized herein. The five sequences for *O. bruuni* are at the top of the table, including sequences from specimens off Chile, SE Pacific, and three sequences from specimens off California, including those identified as *O. "hazardi"* and *O. "packardi"*; NA – not available

Species	Location	GenBank Number	Notes
Opisthoteuthis bruuni	Chile, SE Pacific	MT725733	MNHNCL 300138
O. bruuni	Chile, SE Pacific	MT725734	MNHNCL 300139
O. "hazardi"	Redondo Canyon, California, NE Pacific	NA (see Appendix)	SBMNH 464912, *O.* sp. 3 (PIERTNEY et al. 2003)
O. "packardi"	Monterey Bay, NE Pacific	AF110100	USNM 893774, *O.* sp. 4 (PIERTNEY et al. 2003)
O. sp.	Monterey Bay, NE Pacific	ON367811	USNM 1660928
O. sp. JN-2021	NW Pacific?	MW354513	Details: VERHOEFF (2023)
O. mero	New Zealand, SW Pacific	MT216997	
O. mero	New Zealand, SW Pacific	MT216998	
O. sp. (*?dongshaensis*)	Off California, NE Pacific?	AJ252768	
O. sp.	Off Taiwan, NW Pacific	AJ315375	
O. chathamensis	New Zealand, SW Pacific	MT216982	
O. agassizii	Off Brazil, west Atlantic	AF487303	
O. grimaldii	N Hebrides Terrace, NE Atlantic	ON367812	
O. hardyi	SW Atlantic	AF487302	
O. hardyi	SW Atlantic	FJ785403	
O. hardyi	SW Atlantic	FJ785404	
O. massyae	SE Atlantic	AF299265	
O. massyae	NE Atlantic	AF487297	
O. massyae	NE Atlantic	AF487298	
O. massyae	NE Atlantic	AF487299	
O. massyae	NE Atlantic	AF487300	
O. massyae	NE Atlantic	AF487301	
O. massyae	Off South Africa, SE Atlantic	AJ414702	
O. massyae	Off Namibia, SE Atlantic	AJ315371	
O. massyae	North Sea, NE Atlantic	AJ315372	
O. massyae		AY414502	
O. massyae	Off Namibia, SE Atlantic	AY616970	
O. massyae	S Hebrides Terrace, NE Atlantic	ON367805	
O. massyae	N Hebrides Terrace, NE Atlantic	ON367807	
Insigniteuthis calypso	Off Namibia, SE Atlantic	AJ315374	
I. calypso	Sardinian Channel, Mediterranean	FJ403541	
I. calypso	Sardinian Channel, Mediterranean	FJ403542	
I. californiana	Bering Sea, N Pacific	ON367799	
I. californiana	Bering Sea, N Pacific	AJ315373	
Exsuperoteuthis depressa	Off Japan, NW Pacific	AB191117	
Grimpoteuthis discovery	NE Atlantic	AF487306	
Luteuthis dentatus	New Zealand, SW Pacific	AJ315377	
Cryptoteuthis brevibracchiata	NE Atlantic	MT435502	

ABBREVIATIONS

Morphological: I–IV L/R – arms I–IV left/right, An – anus, AGC – accessory gland complex, AG1–3 – accessory glands 1–3, ASG – anterior salivary glands, AL – arm length, ALI – arm length index (AL%ML, also given as a multiple of ML), BB – buccal bulb, Ca – caecum, Cr – crest, DESF – distal enlarged sucker field, DO – distal oviduct, DOG – distal oviducal gland, Du – hepatic duct, ED – eye diameter, EDI – eye diameter index (ED%ML), FiM – fin muscle, FL – fin length, FLI – fin length index (FL%ML), FW – fin

width, FWI – fin width index (FW%FL), Fu – funnel, FuL – funnel length, FuLI – funnel length index (FuL%ML), FFuLI – free funnel length index, Hd – hood (of beak), Gi-R/L – gill (right/left), HW – head width, HWI – head width index (HW%ML), Int – intestine, ISe – interpallial septum, ML – mantle length, MW – mantle width, MWI – mantle width index (MW%ML), LW – lateral wing (of shell), Oes – oesophagus, OO – olfactory organ, Ov – ovary sac, PA – pallial aperture gape, PAI – pallial aperture index (PA%ML), PESF – proximal enlarged sucker field, PO – proximal oviduct, POG – proximal oviducal gland, Ro – rostrum, Sa – saddle (of shell), SC1–3 – spermatophoric complex parts 1–3, SD – sucker diameter, SDI – sucker diameter index (SD%ML), Sh – shoulder (of shell), SS – spermatophoric sac (Needham's sac), St – stomach, Te – testis, TL – total length, TO – terminal organ, TOLI – terminal organ length index (TOL%ML), WD – web sector depth, WDI – web depth index (web depth%ML).

Institutional: CASIZ – California Academy of Sciences, San Francisco, CDFG – California Department of Fish and Game, MBARI – Monterey Bay Aquarium Research Institute, MNHNCL – National Museum of Natural History, Santiago, Chile, NMFS – National Marine Fisheries Service (La Jolla, California), SBMNH – Santa Barbara Museum of Natural History, SIO – Scripps Institution of Oceanography (California) [BI and RHP referring to 'benthic invertebrate' and 'R. H. Parker' collections], UCSB – University of California, Santa Barbara, USNM – United States National Museum (now Smithsonian National Museum of Natural History).

General: coll – collector, FV – fisheries vessel, max – maximum, NE – north-east, RV – research vessel, SE – south-east.

SYSTEMATICS

Class Cephalopoda Cuvier, 1795

Order Octopoda Leach, 1818

Suborder Cirrata Grimpe, 1916

Superfamily Opisthoteuthoidea Verrill, 1896

Family Opisthoteuthidae Verrill, 1896

Genus *Opisthoteuthis* Verrill, 1883

Opisthoteuthis bruuni (Voss, 1982)

Figs 2–18

Synonymy:

Grimpoteuthis bruuni Voss (1982: pp. 426–433, figs 1–2)

Grimpoteuthis bruuni Voss, 1982 – Vega Petkovic (2007: p. 207, fig. 1)

Opisthoteuthis bruuni – Collins (2003), Cardoso & Hochberg (2012), Pardo-Gandarillas et al. (2021)

Non *Cirroteuthis macrope* Berry, 1911 – Phillips (1934)

Non *Stauroteuthis* sp. juv. – Berry (1912: pp. 274–275, pl. 33, fig. 1)

Non *Opisthoteuthis californiana* Berry, 1949 – Lee & Brophy (1969: p. 221), McCosker & Anderson (1976), Anderson (1978)

Opisthoteuthis sp. A – Hochberg (1976: pp. 14–25)

Opisthoteuthis sp. – Hochberg et al. (1992: p. 219, fig. 238 b,c), Ibáñez et al. (2011: pp. 37–40, fig. 2)

Grimpoteuthis sp. – Hunt (1999: pp. 152–156)

Grimpoteuthis sp. 2 – Norman (2000: p. 182)

Opisthoteuthis sp. 1 – Hudelot (2000)

Opisthoteuthis n. sp. 3 – Piertney et al. (2003: pp. 349–350, fig. 1, Supplementary Information)

Opisthoteuthis n. sp. 4 – Piertney et al. (2003: pp. 349–350, fig. 1, Supplementary Information)

Opisthoteuthis "packardi" – Hochberg et al. 1996 (unpublished manuscript)

Opisthoteuthis "berryi" – Hochberg 1990s–2011 (unpublished manuscripts)

Opisthoteuthis "hazardi" – Hochberg 1990s–2011 (unpublished manuscripts)

Material examined: **SBMNH 45973B** (male, 42 mm ML; Santa Barbara Channel, 34°11'N, 119°35'W, 219 m, FV "Elsie B", 6/X/1957, coll Captain H. Durrah) [Originally proposed holotype of *O. "hazardi"*]; **SBMNH 45973A** (male, 35 mm ML; location per **SBMNH 45973B**) [proposed paratype of *O. "hazardi"*]; **SBMNH 47075** (male, 25 mm ML; 8 miles south of UCSB, 34°18'N, 119°50'W, 382 m, 21/IV/1976, coll S. Anderson) [proposed paratype of *O. "hazardi"*]; **SBMNH 45975** (female, 34 mm ML; off Gaviota, 34°10'N, 120°40'W, 275 m, otter trawl, 24/X/1968, coll P. Brophy & S. Douds [voucher Lee & Brophy 1969]) [proposed paratype of *O. "hazardi"*]; **SBMNH 45964** (female, 36 mm ML; 4–5 miles off Naples Reef, eastern edge of Santa Barbara Basin, 34°10'N, 120°05'W, 255–275 m, 30ft shrimp trawl, FV "Kildee", 27/I/1974, coll Captain R. Hazard) [proposed paratype of *O. "hazardi"*]; **SBMNH 45974** (3 females, 30–36 mm ML; 4–5 miles off Naples Reef, eastern edge of Santa Barbara Basin, 34°10'N, 120°05'W, 255 m, 30ft shrimp trawl, FV "Kildee", 21/X/1974, coll Captain R. Hazard) [proposed paratype of *O. "hazardi"*]; **SBMNH 45970** (female, 41 mm ML; off Goleta, 34°11'N, 119°35'W, 255 m, otter trawl, FV "Elsie B", 1/XI/1968, coll Captain H. Durrah [voucher Lee & Brophy 1969])

[proposed paratype of *O. "hazardi"*]; **SBMNH 45965 & 45968** (6 females, 21–42 mm ML; 4–5 miles off Naples Reef, eastern edge of Santa Barbara Basin, 34°10'N, 120°05'W, 255 m, 30ft shrimp trawl, FV "Kildee", 10/II/1974, coll Captain R. HAZARD) [proposed paratype of *O. "hazardi"*]; **SBMNH 45967** (2 females, 28 & 32 mm ML; 4–5 miles off Naples Reef, eastern edge of Santa Barbara Basin, 34°10'N, 120°05'W, 252 m, 30ft shrimp trawl, FV "Kildee", 4/II/1974, coll Captain R. HAZARD) [proposed paratype of *O. "hazardi"*]; **SBMNH 45966** (2 females, 34 & 37 mm ML; off Naples Reef, eastern edge of Santa Barbara Basin, 34°10'N, 120°05'W, 275 m, 30ft shrimp trawl, FV "Kildee", 3/II/1974, coll Captain R. HAZARD) [proposed paratype of *O. "hazardi"*]; **SBMNH 142824** (2 females, 48 & 60 mm ML; "12 mile finger", 8 miles south of Santa Barbara Harbor, 34°21'N, 119°30'W, 183–255 m, FV "Kildee", 27/V/1982, coll Captain R. HAZARD) [proposed paratype of *O. "hazardi"*]; **SBMNH 62956** (17 males, 33–42 mm, 13 females, 30–36 mm ML; Santa Cruz Island, off China Bay, 34°7.5'N, 119°39.5'W, 255 m, FV "Kildee", 17/VI/1982, coll Captain R. HAZARD) [proposed paratype of *O. "hazardi"*]; **SBMNH 62949** (male, 34 mm ML; off Goleta, 34°21'N, 119°59'W, 497 m, 29/V/1989) [proposed paratype of *O. "hazardi"*]; **SBMNH 62947** (male, 33 mm ML; 12–15 miles SE of Point Dume, 33°52'N, 118°38.5'W, 695–732 m, FV "Julie K", 9/III/1979) [proposed paratype of *O. "hazardi"*]; **SBMNH 464912** (formerly "**CMMLA 93.02.004**") (male, 48 mm, 1 female, 26 mm ML; Redondo Canyon, off South Santa Monica Bay, 33°55'N, 118°36–37'W, 304 m, RV "Ocean Sentinel", station "LASD T-0-1000", 17/XI/1993, coll JAMES LANDESMAN [sequenced by HUDELOT (2000) & PIERTNEY et al. (2003) as *O.* "sp. 1" or "sp. 3"]) [proposed paratype of *O. "hazardi"*]; **SBMNH 47244** (female, 32 mm ML; off Naples Reef, eastern edge of Santa Barbara Basin, 34°10'N, 120°05'W, 234 m, 30ft shrimp trawl, FV "Kildee", 13/XI/1974, coll Captain R. HAZARD); **SBMNH 45997** (female, eggs only; off Santa Barbara Harbor, 33°50'N, 118°50'W, 270 m, -/X/1968, coll P. BROPHY [voucher LEE & BROPHY (1969)]); **SBMNH 51699** (male, 15 mm ML; Santa Barbara Basin, 34°15'N, 120°00'W, depth unknown, 10ft tucker trawl, RV "Velero", 18/XI/1977, coll JAMES CHILDRESS); **SBMNH 42225** (female, 43 mm ML; 5 miles off Naples Reef, eastern edge of Santa Barbara Basin, 34°24'N, 119°56'W, 311 m, trawl, FV "Tammy", 13/IV/1979, coll F. DONAHUE); **SBMNH 142825** (2 males, both 36 mm ML; National Marine Fisheries Service (NMFS) "Tow #1" off San Diego, La Jolla, 32°52'N, 117°16'W, 549 m, 8/II/1981); **SBMNH 142826** (female, 27 mm ML; NE Pacific off California, CDFG Station 63A9-6 (coordinates and depth unknown), 7/XII/1963).

Additional material [Attributed to *O. "packardi"*, though no description of morphology survived in HOCHBERG's notes for accurate comparison to *O. "hazardi"* – this material is listed here to assist future studies]: **SBMNH 345776** (male, 30.0 mm ML (258.5 g), off Moss Landing, head of Soquel Canyon, 36°49'N, 121°59'W, 285–300 m, MBARI ROV, 11/III/1996, coll G. VAN DYKHUIZEN) [proposed holotype of *O. "packardi"*]; **SBMNH 345777** (female, 24.0 mm ML (370.7 g), location per **SBMNH 345776**) [proposed paratype of *O. "packardi"*]; **SBMNH 142121** (2 males, 17 & 20 mm ML, 5 females, 15.5–18 mm ML, off Moss Landing, Soquel Canyon, 36°50'N, 121°58'20"W, 317–359 m, MBARI ROV dive 408, 4/VI/1992, coll G. VAN DYKHUIZEN); **SBMNH 142122** (1 male, 30 mm ML, off Moss Landing, Soquel Canyon, 36°49'53.9"N, 121°58'24.98"W, 374 m, MBARI ROV station OPI #2, 20/VII/1992, coll G. VAN DYKHUIZEN) [proposed paratype of *O. "packardi"*]; **SBMNH 142123** (1 male (mature), 22 mm ML; off Moss Landing, Soquel Canyon, 36°50'01"N, 121°58'20"W, 396 m, MBARI ROV station OPI #1, 20/VII/1992, coll G. VAN DYKHUIZEN) [proposed paratype of *O. "packardi"*]; **SBMNH 142124** (female, 18.5 mm ML, off Moss Landing, Soquel Canyon, 36°49'53"N, 121°58'29"W, 332.9 m, MBARI ROV, 27/IV/1992, coll B. ROBISON) [proposed paratype of *O. "packardi"*]; **SBMNH 142125** (sex?, 13.2 mm ML, off Moss Landing, Soquel Canyon, 36°49'46.05"N, 121°58'13.04"W, 335 m, MBARI ROV, 15/IX/1992, coll G. VAN DYKHUIZEN); **SBMNH 142126** (sex?, 15.5 mm ML, off Moss Landing, Soquel Canyon, 36°49'46.05"N, 121°58'13.04"W, 328 m, MBARI ROV, 15/IX/1992, coll G. VAN DYKHUIZEN); **SBMNH 142127** (sex? (juvenile), 6 mm ML, off Moss Landing, Soquel Canyon, 36°49'57.76"N, 121°58'17.81"W, 330 m, MBARI ROV dive 408, 4/VI/1992, coll G. VAN DYKHUIZEN); **SBMNH 142128** (sex? (juvenile), 12 mm ML, off Moss Landing, Soquel Canyon, 36°49'55.11"N, 121°58'22.9"W, 364 m, MBARI ROV station OPI #3, 20/VII/1992, coll G. VAN DYKHUIZEN); **SBMNH 142129** (sex? (juvenile), 8.2 mm ML, off Moss Landing, Soquel Canyon, 36°50'2.5"N, 121°58'15.97"W, 334 m, MBARI ROV station OPI #4, 20/VII/1992, coll G. VAN DYKHUIZEN); **SBMNH 142130** (2 spawned eggs; Monterey Bay Aquarium, laid on walls of aquarium, 6/V/1992, removed and preserved in August 1992; spawned by a mature female collected of Moss Landing by MBARI ROV on 19/II/1992, female died 8/V/1992 after spawning 5 eggs and was not retained (eggs illustrated by ZIEGLER et al. (2021)); **USNM 893774** (sex?, Monterey Bay, California, summer 1996, coll F. ANDERSON [sequenced by PIERTNEY et al. (2003) as *O.* "sp. 4"]) [proposed paratype of *O. "packardi"*]; **USNM 813106** (2 sex?, 10 mi off Santa Cruz (on bearing 42°True), 402–432 m, M/V N.B. "Scofield",

NBS locality 175, station 51-B.14, 19/II/1951) [proposed paratype of *O. "packardi"*]; **CASIZ 001931** (1 male, Monterey Bay, 36°46.8'N, 121°57.0'W, 462–480 m, Steinhart Aquarium Midwater Maintenance Program, SAMMP 20A-44, 12/III/1975, coll M. E. ANDERSON) [proposed paratype of *O. "packardi"*].

Revised diagnosis. An *Opisthoteuthis* with a small adult size (ML averaging 35 mm, maximum < 60 mm), low sucker counts (averaging 35 per arm, < 44 max), lacking web nodules, with orange pigmentation and with areolar spots minimal or absent; males with PESF and DESF on all arms, and with DESF comprising ~10–14 suckers with diameters < PESF maximum sucker diameter; internally with a unilobed digestive gland, intestine 1.2–1.7× oesophagus length (longer in females), AG1 dominating AGC, and with 6 lamellae per gill.

Description.

Body small (ML males 15–34.5–48 mm; females 21–35.4–60 mm), flabby, semi-gelatinous.

Mantle broader in males than females (MWI males 104.8, females 78.1); in females posterior mantle higher domed, more bell-shaped in profile than males.

Head much wider than mantle (HWI males 188.4, females 139.8) (Figs 2, 3).

Eyes very large, diameter typically greater than half ML (EDI males 68.4, females 55.5).

Fins relatively long (shorter in fresh condition; compare Fig. 2 (preserved state) to Fig. 3 (fresh condition)), distally rounded in fresh condition, becoming more acutely pointed distally in preserved material; fins longer in males than females (FLI males 78.1, females 51.4); length about twice width (FWI males 51.4, females 60.9).

Fin support cartilage U-shaped; depth dimorphic, deeper U-shaped in females (Fig. 5), shallower bow-shaped in males (Fig. 7), shell saddle with a posterior groove (see cross sections, Figs 6, 8); shell 'shoulders' well developed, fin musculature attached laterally and distally in groove, shell lateral wings terminating as spikes.

Pallial aperture narrow, tight around funnel (PAI males 39.2, females 37.2).

Pallial adductor muscle vestigial, reduced to thin, strap-like strip of tissue attached posteriad on inside mantle wall (visible Figs 14, 17).

Funnel long (FuLI males 71.4, females 52.9); free more than half its length (FFuLI males 68.0, females 66.4); funnel organ not described.

Arms short, 1.5–2.5 × ML, longer in males than females (ALI, arm 3, males 245.6 (average), females 179.2 (average)); thick, conical; lengths sub-equal, formula typically 3 = 4 > 1 > 2.

Normal suckers small (SDI 3.4–4.9–6.0); sucker shape urceolate, wider at base than aperture, embedded in flesh of arm, aperture flush with skin surface.

Enlarged suckers present in males in 2 fields on all arms (see Fig. 4), a proximal enlarged sucker field (PESF) and distal enlarged sucker field (DESF); enlarged suckers taller and wider based than normal suckers; suckers in proximal field larger at aperture than in distal field (SDI proximal field averaging 11.1, SDI distal field averaging 7.4); present on all arms; suckers number 33–35–39 on each arm; sucker distribution on males: 3 small suckers proximal to mouth + 3–5 enlarged suckers in proximal field (4th–6th or 8th) + 5–10 small suckers mid arm + ~10–14 enlarged suckers in the DESF (~ 15th–18th to 25th–29th) + 10–14 small suckers on arm tips; females ~3 small suckers nearer the mouth with suckers similarly sized mid arm before diminishing in size towards arm tips.

Cirri long (~1.0× mid-arm sucker diameter, or ~0.5× PESF sucker diameter), commencing between suckers 1 and 2 as minute buds (see Fig. 4).

Web simple, thick, gelatinous, deep (WDI 54.9–70.4–82.0); extends to near arm tips on dorsal edge of arms; web formula variable.

Digestive system dissected from male and female specimens (see Figs 9–11):

Buccal bulb with anterior salivary glands small, posterior glands absent,

Radula absent,

Oesophagus short, crop region slightly inflated, anterior diverticulum absent,

Stomach small, bipartite; caecum small, sac-like; intestine with shallow bend in males (Fig. 9) and deep, reflexed bend in females (Fig. 11), relative intestine length in male 1.2× oesophagus length, in female 1.7× oesophagus length; ink sac and anal flaps absent; digestive gland unilobular.

Upper beak (Fig. 12) with rostrum short, bluntly pointed, margin straight; hood elevated about ½ crest length,

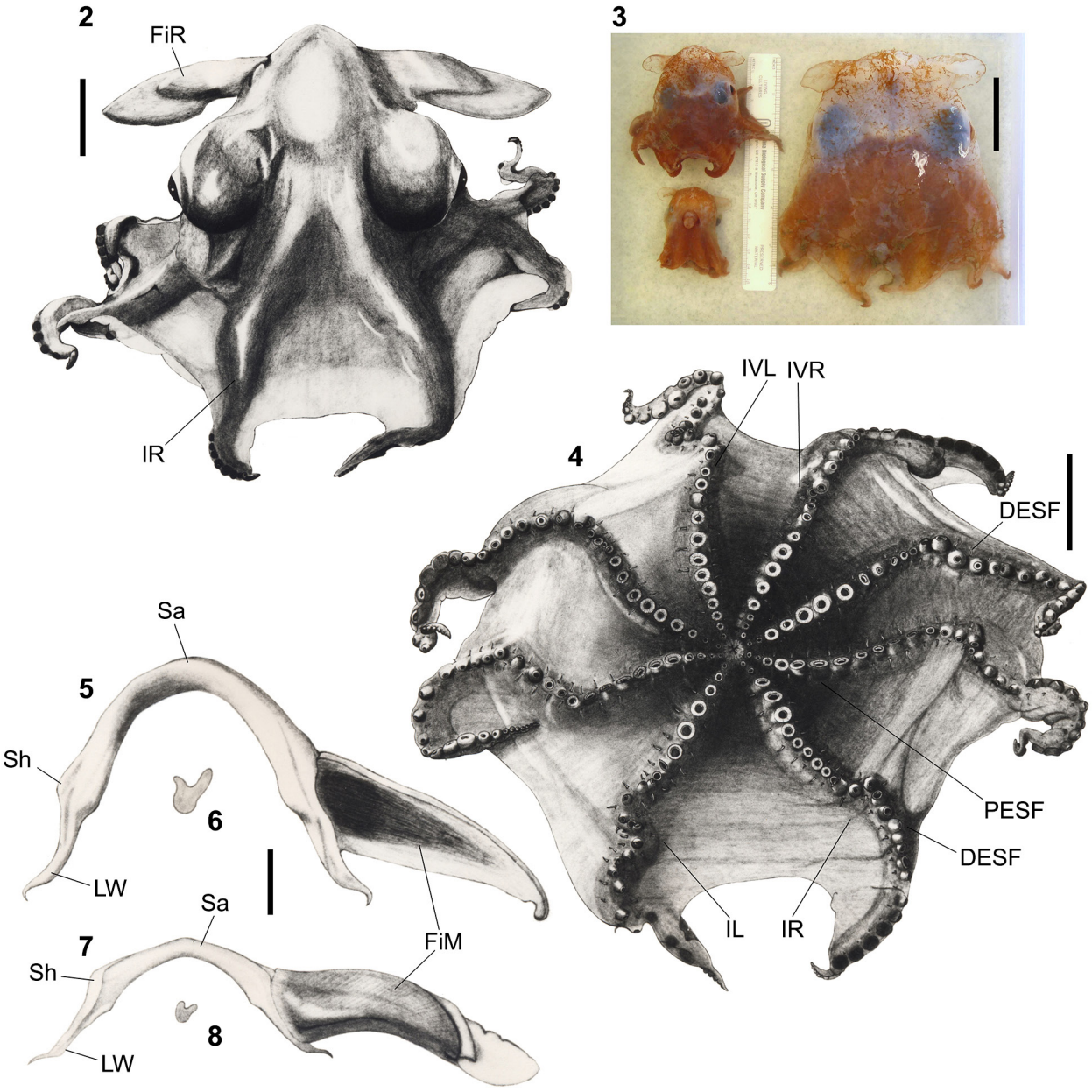
Lower beak (Fig. 13) with rostrum short, acutely pointed, margin curved; hood elevated, less than ½ crest length; wings tapered and rounded posteriorly, not indented.

Gills of 'half-orange' form and with 6 primary lamellae per gill (HOCHBERG noted this as 4 outer demibranch + 2 on inner demibranch), lamellae thick and fleshy (see Figs 14, 17).

Male reproductive tract (Figs 14–16) with testis small with thin membrane enclosing fluid-filled gonadal chamber; single water canal present, exits near junction of testis and vas deferens; spermatophoric gland with 3 distinct sections; Needham's

sac (spermatophoric sac) large and with visible spermatophores; accessory gland complex dominated by more proximal AG1, exceeding the combined dimensions of AG2 and AG3 (the latter two closely joined); terminal organ relatively long (TOLI 13.3–32.2), exceeding overall dimensions of combined AG2 and AG3 from which it projects, inflated proximally, without diverticulum;

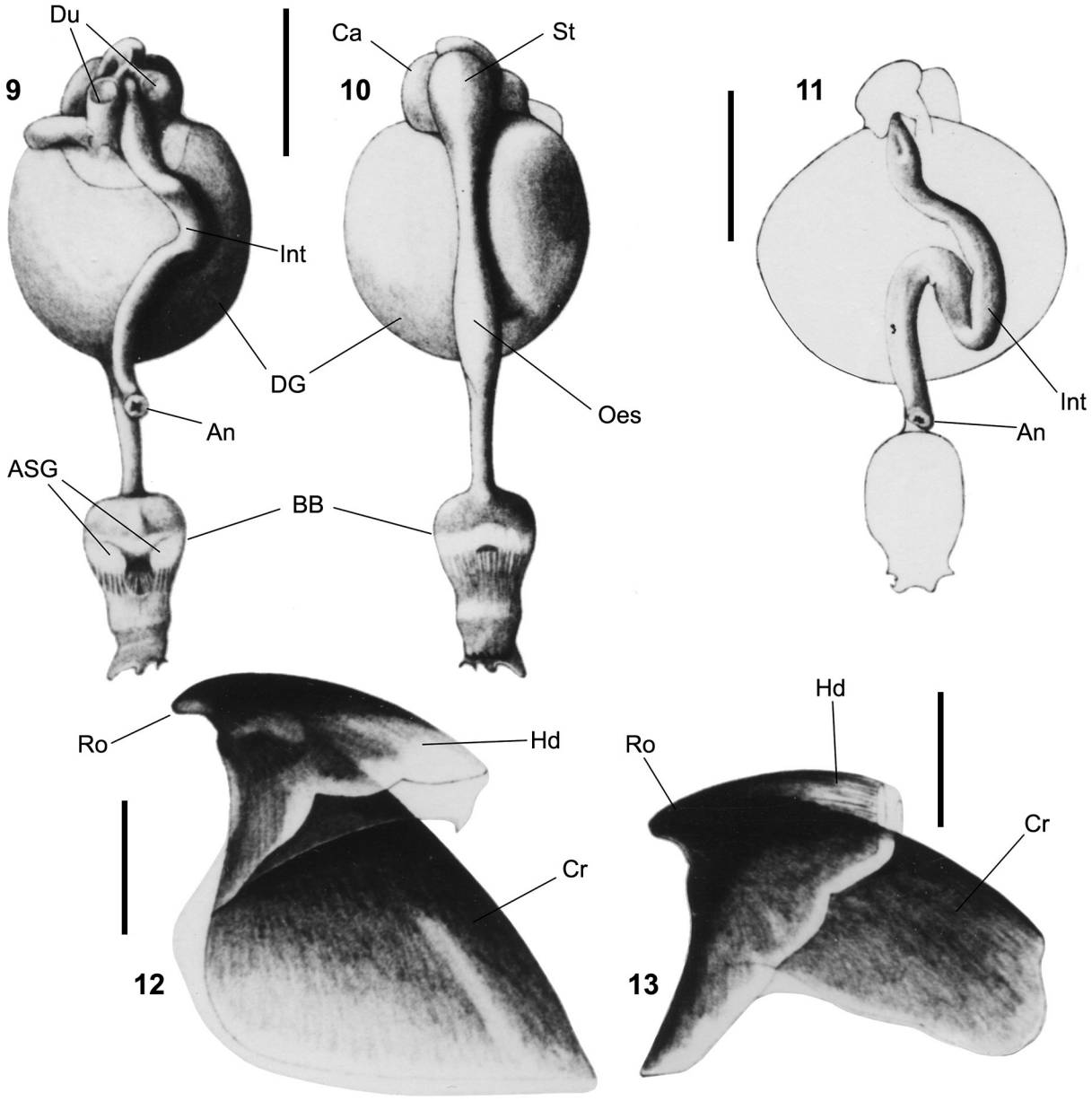
Female reproductive tract (Figs 17, 18) with ovary large; proximal oviduct long, wide, thin and semi-transparent, often packed with mature eggs; oviducal gland very large, bipartite with dis-



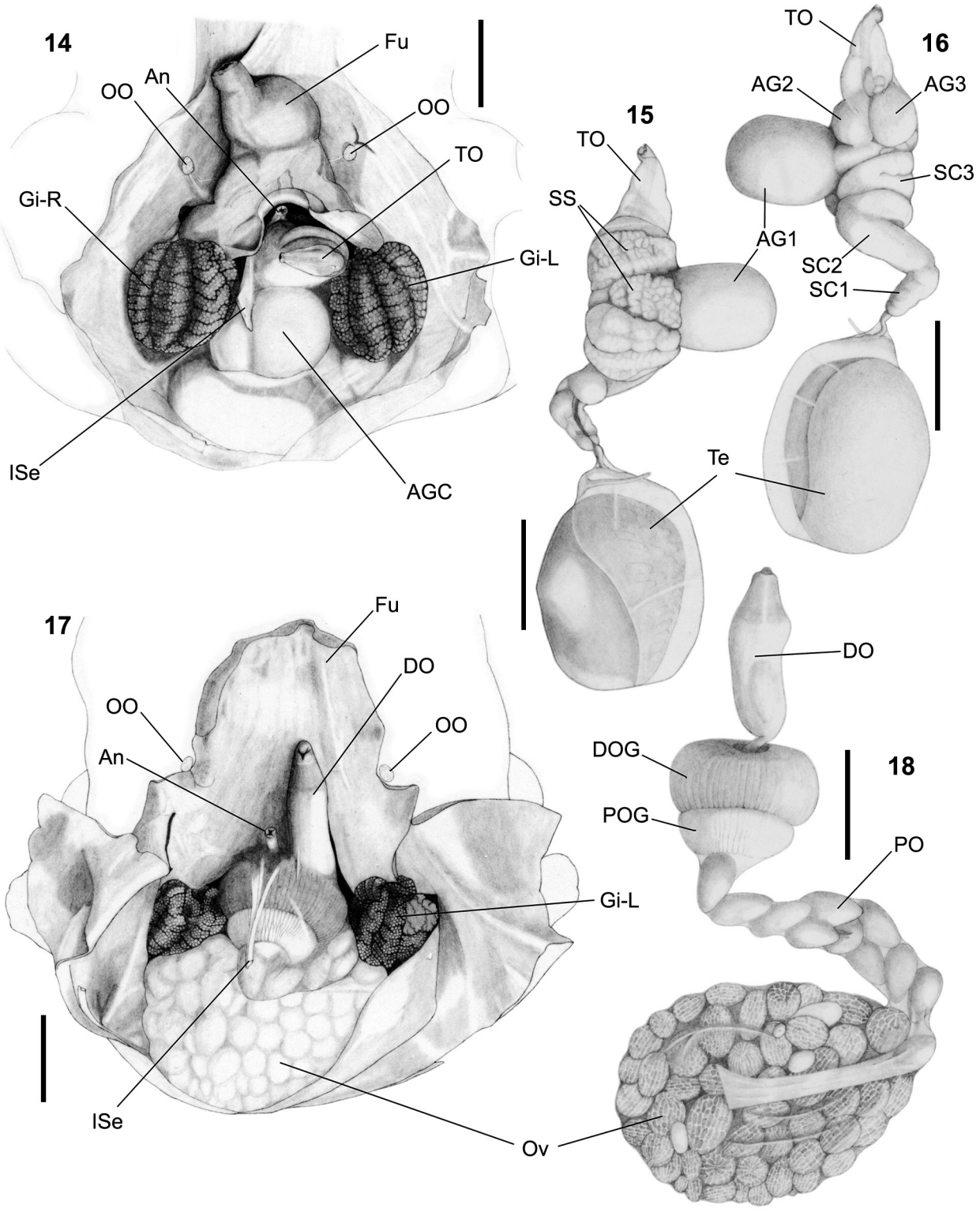
Figs 2–8. *Opisthoteuthis bruuni* from off California (HOCHBERG unpublished manuscript name *O. "hazardi"*), body and shell details: 2 – dorsal aspect of mature male (holotype, SBMNH 45973B, 42 mm ML, preserved); 3 – fresh condition specimens (possibly SBMNH 464912, larger specimen a mature male); 4 – oral aspect of enlarged suckers of mature male (holotype, SBMNH 45973B); 5, 6 – internal shell of mature female (paratype, SBMNH 45968C), dorsal aspect (5), and cross section across saddle (6); 7, 8 – internal shell of mature male (holotype, SBMNH 45973B), dorsal aspect (7) and cross section across saddle (8). Abbreviations: I or IV L/R – arms I or IV left/right, DESF – distal enlarged sucker field, FiR – fin (right), FiM – fin muscle, LW – lateral wing (of shell), PESF – proximal enlarged sucker field, Sa – saddle (of shell), Sh – shoulder (of shell). Scale bars: 10 mm (5–8); 20 mm (2, 4); 50 mm (3). Original illustrations by the late F. G. (ERIC) HOCHBERG (provided by SBMNH)

tinct striated chambers, proximal oviducal gland light coloured and distal oviducal gland dark; distal oviduct relatively long, muscular, about ½ length of proximal duct (nearly double length of the oviducal gland), region around genital pore dark coloured; distal oviduct often extends out through the funnel.

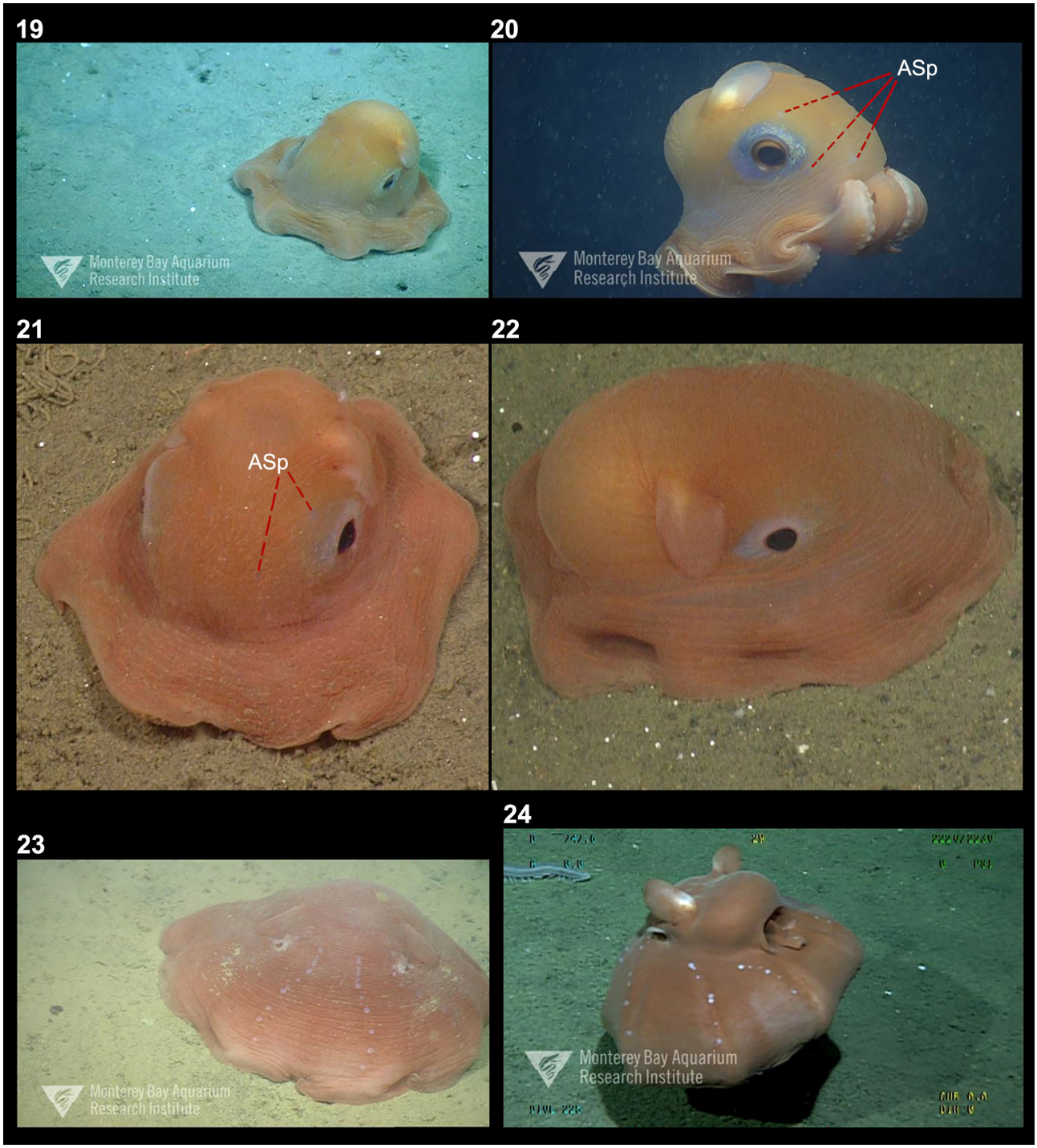
Ovarian eggs variable in size; typically 135–275 eggs present over 3 mm in chorion length (in n = 6 specimens); mature ovarian eggs medium size (chorion length 6–7 mm; width 3–4 mm); follicular folds lattice-like with numerous cross connections; mature eggs in proximal oviduct covered with smooth, white chorion; mature eggs in oviducal gland and distal oviduct encased in secondary egg capsule (casing dimensions not described or illustrated); the spawned egg documented by ZIEGLER et al. (2021: specimen G, fig. 3a–b) was likely from this species, and had a beige coloured, smooth, egg casing meas-



Figs 9–13. *Opisthoteuthis bruuni* from off California (HOCHBERG unpublished manuscript name *O. "hazardi"*), digestive tract and beaks: 9, 10 – digestive tract from mature male (holotype, SBMNH 45973B, 42 mm ML), with ventral (9) and dorsal (10) aspects depicted; 11 – ventral aspect of digestive tract from a mature female (paratype, SBMNH 45966A) depicting a slightly different intestine arrangement; 12, 13 – beaks from a mature male (holotype, SBMNH 45973B), lateral profiles of upper beak (12) and lower beak (13). Abbreviations: ASG – anterior salivary glands, An – anus, BB – buccal bulb, Ca – caecum, Cr – crest, Du – hepatic duct, Hd – hood, Int – intestine, Oes – oesophagus, Ro – rostrum, St – stomach. Scale bars: 10 mm (9–11); 1.0 mm (12, 13). Original illustrations by the late F. G. (ERIC) HOCHBERG (provided by SBMNH)



Figs 14–18. *Opisthoteuthis bruuni* from off California (HOCHBERG unpublished manuscript name *O. "hazardi"*), mantle cavity and reproductive system: 14 – mantle cavity of mature male, ventral aspect (holotype, SBMNH 45973B, 42 mm ML); 15, 16 – reproductive tract of mature male, dorsal and ventral aspects (paratype, SBMNH 45973A, 35 mm ML); 17 – mantle cavity of mature female, ventral aspect (paratype, SBMNH 45966A); 18 – reproductive tract from same mature female as previous figure. Abbreviations: AGC – accessory gland complex, AG1–3 – accessory glands 1–3, An – anus, DO – distal oviduct, DOG – distal oviducal gland, Fu – funnel, Gi-R/L – gill (right/left), ISe – interpallial septum, OO – olfactory organ, Ov – ovary sac, PO – proximal oviduct, POG – proximal oviducal gland, SC1–3 – spermatophoric complex parts 1 – 3, SS – spermatophoric sac (Needham's sac), Te – testis, TO – terminal organ. Scale bars: 10 mm. Original illustrations by the late F. G. (ERIC) HOCHBERG (provided by SBMNH)



Figs 19–24. Remotely operated vehicle (ROV) observations of opisthoteuthids off California. 19–22 – ROV observations of putative *Opisthoteuthis bruuni* from Monterey Bay, California: 19 – individual resting on seafloor (MBARI Dive 2301, 36.800N, 122.035W, 427.3 m depth, 29.I.2003), 20 – female individual swimming above seafloor and with areolar spots visible (MBARI Dive 1688, 36.796N, 121.883W, 365.1 m depth, 8.X.1999), 21 – anterior aspect of individual resting on seafloor, with areolar spots evident (MBARI Dive 3771, 36.796N, 121.995W, 441.5 m depth, 8.V.2014), 22 – lateral aspect of individual resting on seafloor (MBARI Dive 3769, 36.708N, 121.989W, 384.6 m depth, 31.III.2014); 23–24 – ROV observations of *Insigniteuthis albatrossi* (formerly *O. californiana*) from Monterey Bay, California: 23 – individual with highly flattened posture on seafloor with distinct rows of areolar spots (MBARI Dive 2358, 36.743N, 122.041W, 767.4 m depth, 9.V.2003), 24 – individual swimming above the seafloor (MBARI Dive 225, 36.972N, 122.651W, 746.7 m, 31.X.2000). Abbreviations: Lat – latitude, Long – longitude. Images credits: Monterey Bay Aquarium Research Institute (MBARI 2025a, 2025b), Deep Sea Guide (used with permission)

uring 10 × 4 mm, tightly enclosing a chorion measuring 6 × 3 mm.

Skin tight, smooth, often wrinkled in preserved state.

Colour in live condition yellow-orange uniformly over the body, head, and aboral arm faces, with pigmentation reduced around the eyes and the distal fin edges (see Figs 19–22), freshly collected specimens often have the skin variably abraded away from the net to reveal the un-pigmented underlying tissue (see various extent of skin abrasion Fig. 3); in preservation, with aboral surfaces of mantle, web, arms and fins, dark "burnt sienna" (darker orange); underlying gelatinous tissue pale violet; dorsal and ventral mantle often mottled with rust brown; arm tips blood red; eyes Payne's grey with pale flesh-colour ring around pupil surrounded by dark burn sienna ring; fins often a pale flesh-colour; pale areolar spots generally not observed on preserved specimens, though ROV footage of live animals does reveal a series of 1–3 rather indistinct areolar spots near each arm base, most visible for arm pair I & II where the proximal most spots occur on the head (see Figs 20–21); oral web blood red to burnt sienna; suckers and oral surfaces of arms light tan to pale flesh-colour.

Recognised distribution. Material covered by HOCHBERG (unpublished) as *O. "hazardi"* from the northeastern Pacific off California, from south of Point Conception [34°30'N] to the vicinity of San Diego [32°N]. Typical depth range 200–700 m; the largest numbers have been obtained from about 250 m. Material attributed to the manuscript name *O. "packardi"* (also assigned to *O. bruuni*, see Discussion) occurred a bit further north off Monterey Bay, California, depth range 285–480 m (see Fig. 1). *Opisthoteuthis bruuni* has previously been recorded from Peru and Chile (latitudes 5°S to 33°21'S), from 250–512 m depth (VOSS 1982, CARDOSO &

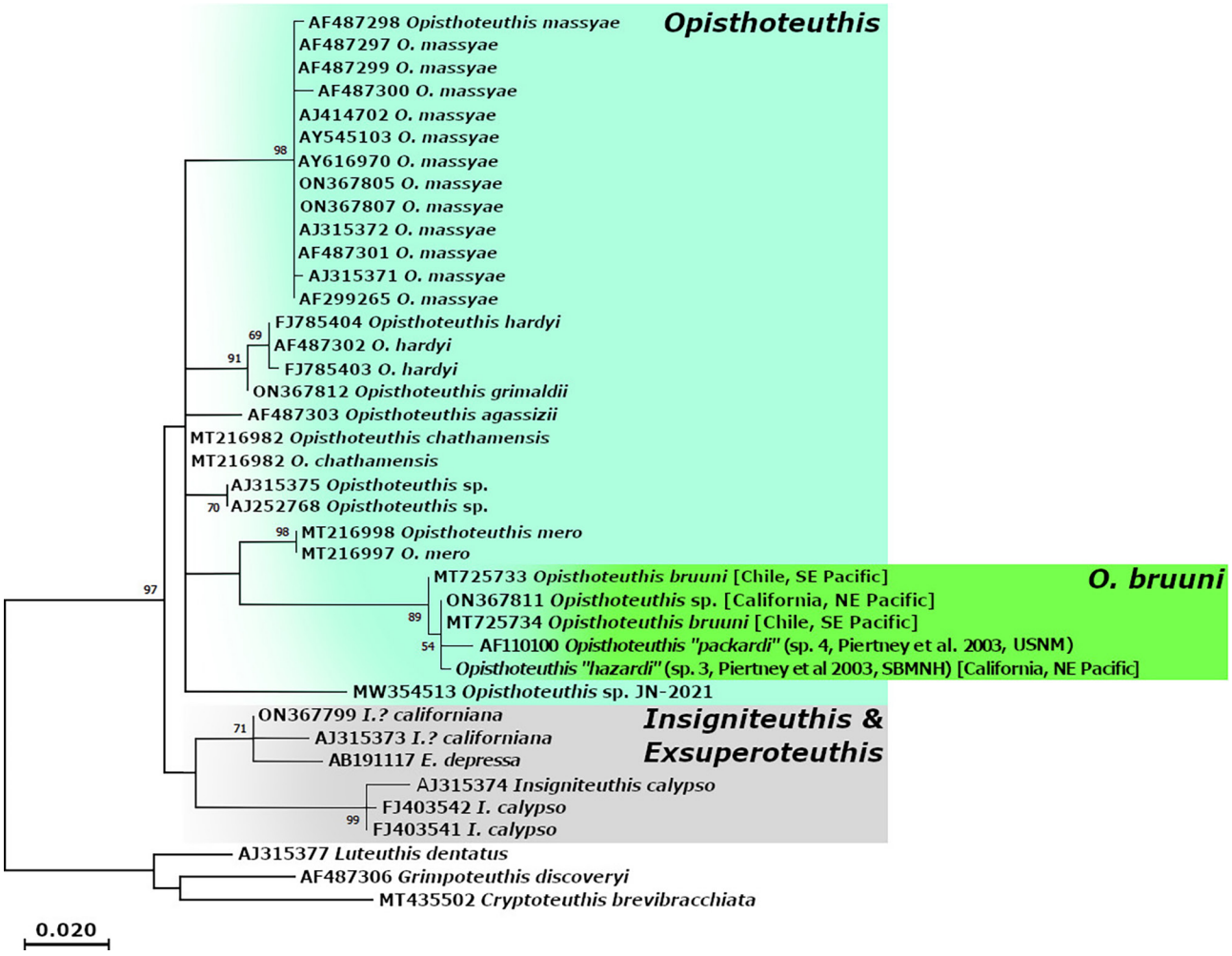


Fig. 25. Phylogenetic tree using ×39 16S sequences, depicting placement of sequences attributed to *O. "hazardi"* and *O. "packardi"* from the NE Pacific (California) relative to *O. bruuni* sequences from the SE Pacific (Chile). Other sequences attributed to opisthoteuthids are included, with three grimpoteuthid sequences used as an outgroup. Tree constructed with Maximum Likelihood (T92+G+I) model, tested with 1000 bootstrap replicates (clade support values indicated at nodes as percentages when > 50%). Branch lengths measured in number of substitutions per site. Original tree constructed in MEGA X

HOCHBERG 2012, PARDO-GANDARILLAS et al. 2021), the range being therefore extended north along the eastern Pacific coasts of the Americas to as far north as Point Conception (and slightly further into Monterey Bay if including HOCHBERG's *O. "packardi"*).

Results of molecular analyses. Phylogenetic tree construction was completed to assess the similarity of sequences attributed to *O. bruuni*, *O. "hazardi"*, and *O. "packardi"*, and the placement of these relative to other opisthoteuthids. Given the availability of sequences, the 16S gene was utilised. The sequences for *O. bruuni* (×2 sequences) from off Chile, and sequences from animals off California, *O. "hazardi"*, *O. "packardi"* and another *Opisthoteuthis* sp. sequence, were all extremely similar, and formed a well-supported clade (89% support with ML analysis) (Fig. 25), within this clade, one sequence of *O. bruuni* was slightly more separated from the other sequences, but not with any significance with the remaining 4 sequences (including the other sequence of *O. bruuni* from a Chilean specimen) being near identical (indicating these sequences all belong to *O. bruuni*). All other species of *Opisthoteuthis* formed well supported clades generally, though support values for higher classification within the Opisthoteuthidae failed to reach significance in this analysis (see VERHOEFF (2023) for a more robust analysis of all cirrate 16S sequences, as well as COI phylogenies which give more robust support values within this family).

Remarks. Very little is known concerning the biology of this species. A small animal was briefly maintained alive in a krysal and videotaped according to HOCHBERG (unpublished). The locomotion of this specimen was similar to that described for *Opisthoteuthis californiana* (see PEREYRA 1965). HOCHBERG also reported that he had observed an as yet undescribed dicyemid mesozoan in the renal coelom of *O. "hazardi"* (HOCHBERG 2011). The feeding behaviour of this species in captivity was described by HUNT (1999) (identified *Grimpoteuthis* sp. and later as *O. "packardi"*) using an individual captured by MBARI ROV on-board RV "Point Lobos" (captured 8 April 1994, Monterey Bay, 284 m) and maintained in captivity for 53 days.

DISCUSSION

The presence of a second species of Opisthoteuthidae in the waters off California, NE Pacific, other than *Opisthoteuthis californiana* (now *Insigniteuthis albatrossi*) has been known for several decades, but never published on, and this second taxon has been generally assumed to be a new species. While HOCHBERG (unpublished) believed the material described herein (as *O. "berryi"* and later as *O. "hazardi"*) represented a new species, further comparison of morphological and molecular data indicates the species is comparable to *O. bruuni* from off Peru and Chile, SE Pacific, indicating that this species extends northwards along the eastern Pacific coast to as far north as California. HOCHBERG was seemingly aware of the similarity of *O. bruuni* to his material, for in the 'FAO Catalogue' (HOCHBERG et al. 2014: p. 250) entry for *O. bruuni* it is remarked that "What appears to be a similar, or closely related, undescribed species, occurs in the northeastern Pacific off California".

The original description of *O. bruuni* (as *Grimpoteuthis bruuni*) by VOSS (1982) is consistent with *O. "hazardi"* in its unilobed digestive gland (see VOSS 1982: fig 2d), distinctly low arm sucker counts (up to 35 per arm per VOSS 1982, vs. 33–37 in *O. "hazardi"*), gill lamellae counts (6 per gill), upper beak form (compare VOSS 1982: fig 2a to Fig. 12), and male reproductive system (AG1 exceeding combined dimensions of AG2 and AG3) and female reproductive system with proportionally very elongate distal oviduct (compare VOSS 1982: figs 2e,f to Figs 15, 16, 18). The problem with VOSS' (1982) description is that it was based on a set of juvenile specimens, meaning that the enlarged sucker pattern of the males was not easily comparable to the adults of other species, seemingly contributing to HOCHBERG's allocation of the NE Pacific material to a new, but similar, species. As originally described (from juveniles) males of *O. bruuni* had a PESF of ~5 or 6 suckers (distal 3 per field most enlarged), but the DESF was seemingly at a very early stage of development, with all arms having ~3 or 4 slightly enlarged suckers near the webbing attachment points (these suckers being at most ½ size of PESF suckers) at ~17–20th sucker position, not entirely consistent at this developmental stage with either *Opisthoteuthis* or *Insigniteuthis* (as defined in VERHOEFF 2024). The recent re-description of *O. bruuni* was unfortunately limited in that no description was given of the enlarged suckers, or even the digestive gland lobation among other problems[2], but

[2] In the re-description of *O. bruuni* by PARDO-GANDARILLAS et al. (2021: fig. 3a), the authors described the intestine as narrow compared to the oesophagus but mistook the dorsal aorta (running parallel to the oesophagus) for the intestine, did not remark on the digestive gland lobation, and confused the gill lamellae terminology (the gills have 6 primary lamellae, with demibranches not really relevant for the highly compact and rounded gills of this family, yet they describe the gills as with 'four primary lamellae per side and six secondary lamellae per demibranch'). The authors also fixed these gelatinous and valuable specimens in 96% ethanol.

this work did examine more mature specimens with the maximum sucker counts slightly higher, though still rather low for the genus (up to 44 per arm), and confirm that both *O. bruuni* and *O. "hazardi"* have reduced/absent areolar spots and lack web nodules (further confirming the similarity in these populations). Chilean specimens illustrated by IBÁÑEZ et al. (2011: fig. 2) and PARDO-GANDARILLAS et al. (2021: figs 2E,F) clearly illustrate the DESF's of *O. bruuni* as comprising at least 6 or 7 enlarged suckers on arm pairs I, II, III & IV, consistent with *O. "hazardi"*, however, PARDO-GANDARILLAS et al. (2021: p. 161) erroneously describe the DESF as being only on "distal fields of arms III and IV", and report no sucker diameter measurements for the different fields.

Molecular analysis indicated that *O. "hazardi"* and a second *Opisthoteuthis* from off California that HOCHBERG (unpublished) was also describing (*Grimpoteuthis* or *Opisthoteuthis "packardi"*) are conspecific with *O. bruuni*. PIERTNEY et al. (2003) included sequences of *Opisthoteuthis* "sp. 3" and *Opisthoteuthis* "sp. 4" in their molecular analysis of cirrate 16S mitochondrial sequences, these two sequences being the most similar to each other and forming a distinct clade. The identification of *O.* "sp. 3" and *O.* "sp. 4" relative to HOCHBERG's manuscript names was not clarified, but can be determined since HOCHBERG submitted tissue samples for sequencing from both of his in-prep species *"O. hazardi"* and *O. "packardi"*. The sequence designated *Opisthoteuthis* "sp. 3" in PIERTNEY et al. (2003) (or *O.* "sp. 1" in HUDELOT 2000) was from the *O. "hazardi"* specimen **SBMNH 464912** (this was unclear in PIERTNEY et al. 2003, but early draft documents from HUDELOT & HOCHBERG (unpublished) indicate that this specimen "*Opisthoteuthis* sp. 1 (*berryi*)" was from Redondo, Canyon, NE Pacific, matching the collection location and date for **SBMNH 464912**). HOCHBERG's "*Gimpoteuthis packardi*" (HOCHBERG et al. 1996) was collected mostly around Monterey Bay, as well as off Los Angeles, California, and its description used a separate set of specimens than that used to describe *O. "hazardi"* (see material examined section), and one of these specimens (**USNM 893774**) was that sequenced as *Opisthoteuthis* "sp. 4" of PIERTNEY et al. (2003: supplementary data). Importantly, two 16S sequences of *O. bruuni* (from off Chile) are available for comparison to the sequences of *O. "hazardi"* and *O. "packardi"* plus another *Opisthoteuthis* sp. sequence from Monterey Bay. These sequences all form a well-supported clade distinct from all other *Opisthoteuthis*, with the two *O. bruuni* sequences intermixed with (and nearly identical to) the other sequences (rather than forming a clade separate to the specimens from the NE Pacific), strongly indicating that there is a single species involved with a distribution from off Chile to as far north as Monterey Bay. Some ambiguous base pair positions in one sequence due to poor sequencing quality (GenBank sequence AF110100.2) slightly exaggerated the branch length (as seen in results), but this did not change the overall structure of the tree.

According to HOCHBERG (unpublished) the material attributed to *Cirroteuthis macrope* Berry, 1911 by PHILLIPS (1934), *Stauroteuthis* sp. by BERRY (1912), *O. californiana* by PHILLIPS (1966), MCCOSKER & ANDERSON (1976) and ANDERSON (1978), *Grimpoteuthis* sp. by HUNT (1999) and *Grimpoteuthis* "sp. 2" by NORMAN (2000: p. 182) were all likely records of "*Grimpoteuthis packardi*". What few notes survive suggest that *G. "packardi"* was comparable to *O. "hazardi"*, being similarly small (ML ≤ 30 mm) and with a yellow-orange colour (ANDERSON 1978, HOCHBERG unpublished notes), and was also allocated to genus *Opisthoteuthis* by the time of its inclusion in PIERTNEY et al. (2003) as noted previously. Overall, even though HOCHBERG (unpublished) clearly believed that *O. "hazardi"* and *O. "packardi"* differed and were new species, there is not any clear morphological or genetic separation between them and *O. bruuni*, and therefore they are all regarded as synonymous herein.

Opisthoteuthis bruuni off California overlaps in distribution with the southern limit of *Opisthoteuthis californiana*, since recombined as *Insigniteuthis albatrossi* (regarding *O. californiana* as a synonym per VERHOEFF 2024, 2025). *Insigniteuthis albatrossi* is broadly distributed in the northern and northeastern Pacific, recorded from off Japan (central Honshu) at its westwards limit, into the Sea of Okhotsk, southern areas of Bering Sea, and to the east off Alaska, Oregon, Washington, and California, depth 124–1,340 m (TAKI 1963, PEREYRA 1965, AVDEEV 1986, NESIS 1987). The southeastern most limit of *I. albatrossi* (*californiana*) is uncertain, the species was recently recorded as far south as Mexico (latitude 24°32.60'N, ~700–1,600 m) (URBANO & HENDRICKX 2018), though these records were possibly *O. bruuni*, and URBANO & HENDRICKX (2018) did not illustrate their material. Regardless, the two species seem to be sympatric at least off California.

Distinguishing *O. bruuni* from *I. albatrossi* (syn. *O. californiana*) should be relatively simple, with the two species differing in a range of morphological features: unilobed digestive gland vs. bilobed in *I. albatrossi* (SASAKI 1929); much smaller size at maturity (vs. large size at maturity); lower sucker count (typically < 40 per arm vs. 60–70 on *I. albatrossi* (BERRY 1949)); presence of DESF on all arms (vs. arm pair I only); small size of these DESF suckers relative to the PESF suckers (vs. DESF suckers being much larger than PESF suckers on *I. albatrossi* (BERRY 1955, TAKI 1963)) and their relatively higher count per DESF; fewer gill lamellae (6 vs. 7 in *I. albatrossi*

(TAKI 1963)); areolar spots (few if any on *O. bruuni* vs. well-developed and distinct rows on each arm for *I. albatrossi* (compare Figs 19–22 to Figs 23–24)); pigmentation (yellow-orange on *O. bruuni* vs. darker red-brown on *I. albatrossi*); and smaller size of mature eggs in ovary and oviducts (6–7 mm long × 3–4 mm wide in *O. bruuni*, vs. 9–11 mm long × 5 mm wide (BERRY 1952, LAPTIKHOVSKY 1999)). Juvenile specimens of *I. albatrossi* may be confused with *O. bruuni* off California, but the difference in sucker counts should be evident even in juvenile specimens.

In VERHOEFF (2025) a key was presented for all species of Opisthoteuthidae, with the exception of *O. bruuni*, given that certain important features for the key were ambiguous. The clarification of these points herein enables comparison with other species in the family. The presence of DESF comprising a large number of suckers (~10) which are smaller in diameter than PESF suckers, places the species in genus *Opisthoteuthis* (as opposed to the recently split *Insigniteuthis* and *Exsuperoteuthis*), a conclusion which is seemingly consistent with molecular data, though species coverage is still an issue with cirrate phylogenies. Within *Opisthoteuthis*, the presence of a unilobed digestive gland is only comparable to a set of six species per VERHOEFF (2024) (*O. agassizi* Verrill, 1883, *O. philipii* Oommen, 1976, *O. robsoni* O'Shea, 1999, *O. pluto* Berry, 1918, *O. borealis* Collins, 2005 and *O. hardyi* Villanueva, Collins, Sánchez et Voss, 2002), and out of these taxa *O. bruuni* can be readily distinguished by its consistently low arm sucker count, averaging ~35 per arm, with a maximum recorded of 44, versus sucker counts upwards of 50 per arm and reaching nearly 100 in some taxa (in-fact out of all Opisthoteuthidae *O. bruuni* seems to have the lowest arm sucker counts on mature specimens) (VERHOEFF 2024, 2025). The key in VERHOEFF (2025: pp. 6–7) could be easily modified to accommodate *O. bruuni* by adding another couplet upon reaching step 10, to separate species with low arm sucker counts on mature specimens (≤ 44 per arm), i.e., *O. bruuni*, and species with high arm sucker counts on mature specimens (> 50–~100 per arm), the latter leading back to the six species covered in steps 10–14 of the original key (which would all need to be increased in number by one given the extra couplet).

While HOCHBERG's proposed *O. "hazardi"* and *O. "packardi"* are synonymous with the already described *O. bruuni*, it should be noted that HOCHBERG was also describing another species, *Opisthoteuthis "abyssicola"* 'nomen nudum' based on two specimens, a female intended holotype **SIO BI-70-37** (35 mm

Table 2. Surviving measurement for HOCHBERG's undescribed *Opisthoteuthis (=Grimpoteuthis?) "abyssicola"*. Some information is absent or ambiguous, sucker counts are missing, and web depth for sector 'E' (ventral sector) is not stated though can be inferred from the web formula (* denotes damage)

Specimen	SIO BI-70-37 Intended-holotype	SBMNH 45971 Intended-paratype
Sex	Female (mature / gravid)	Female (immature?)
TL	150 mm	117 mm
Total width (fin span)?	–	47.6 mm
ML	35 mm	27 mm
MW	27 mm	27 mm
HW	40 mm	50? mm
ED (L / R)	11 / 12 mm	17 / 17 mm
FuL	15 mm	19 mm
PA	12 mm	17 mm
FL	40 / 40 mm	21 / 21 mm
FW	~15 mm	~10 mm
AL I (L / R)	111 / 53* mm	81 / 82 mm
AL II (L / R)	112 / 46* mm	81 / 84 mm
AL III (L / R)	70* / 57* mm	83 / 81 mm
AL IV (L / R)	57* / 72* mm	81 / 81 mm
SD (Max)	2.0 mm	1.5 mm
WD sector A	40* mm	55 mm
WD sector B (L / R)	60 / 30* mm	47 / 54 mm
WD sector C (L / R)	63 / 34* mm	54 / 54 mm
WD sector D (L / R)	35 / 45 mm	23* / 46 mm
WD sector E	< 40 mm	< 46 mm
Web formula	B = C.D.A. = E	A = B = C.D.E.
Gill lamellae count	7 (per gill)	7 (per gill)
Egg count	29+ (mature eggs, ovarian + oviducal ducts?)	–
Max egg length	11 mm	–

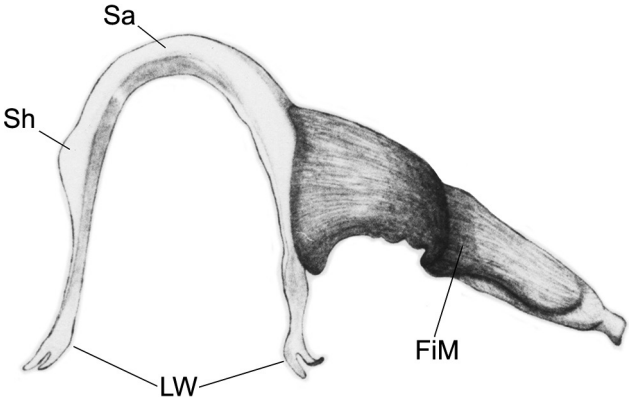


Fig. 26. Internal shell of HOCHBERG's (unpublished) *Opisthoteuthis (=Grimpoteuthis?) "abyssicola"* 'nomen nudum' (not to be confused with *Grimpoteuthis abyssicola* O'Shea, 1999), intended holotype specimen SIO BI-70-37 (female, 35 mm ML). The ventral face of the shell is depicted (posterior end at top), with the fin cartilage and musculature illustrated on one side of the shell

ML) from the abyssal plain off Baja California del Norte, 31°14.4'N, 120°09.6'W, 3,706–3,806 m (coll R. WISNER, S. LUKE & party, RV "Melville", stn. MV-70-III-6, 23/III/1970) and a female intended paratype **SBMNH 45971** from 27 nautical miles east of Isla San Marcos, Gulf of California, Mexico, 27°11'N, 111°31'W, 980–1,025 m (coll C. L. HUBBS & party, 16/I/1968). The surviving shell illustration for the species (see Fig. 26) bears greater resemblance to *Grimpoteuthis* in its strong U-shape with parallel lateral wings terminating in paired lobes, a relatively complete dataset also survives for the two specimens (though missing arm sucker counts) (see Table 2, included largely to ensure the preservation of this data and to make it available for others). The intended-paratype of *Opisthoteuthis "abyssicola"* was referenced by HOCHBERG (1980) many years earlier when he wrote regarding the Gulf of California that "A single specimen of the genus [*Opisthoteuthis*] has been recovered from a deep basin in the lower half of the gulf. Its exact status is presently being worked out, but in all probability it represents a new species". Dr KIR N. NESIS (1934–2003) also noted the presence this undescribed *Opisthoteuthis* from the Gulf of California (NESIS 1987: p. 288). Future work remains to be done to assess the true identification of this species, which may indeed turn out to be new.

ACKNOWLEDGEMENTS

I would like to extend my thanks to the staff of the Santa Barbara Museum of Natural History (SBMNH), Santa Barbara (USA), VANESSA DELNAVAZ (Associate Curator of Invertebrate Zoology) and PAUL VALENTICH-SCOTT (Curator Emeritus of Malacology) for generously providing the unpublished data and illustrations made by the late DR F. G. (ERIC) HOCHBERG, preventing this information form being otherwise lost. I also would like to thank two anonymous reviewers for comments and suggestions which improved the final manuscript.

REFERENCES

ANDERSON M. E. 1978. Notes on the cephalopods of Monterey Bay, California with new records for the area. The Veliger 21(2): 255–262.

AVDEEV G. V. 1986. New harpacticoid copepods associated with Pacific cephalopods. Crustaceana 51(1): 49–65.

BERRY S. S. 1911. Preliminary notices of some new Pacific cephalopods. Proceedings of the United States National Museum 40(1838): 589–592.

BERRY S. S. 1912. A review of the cephalopods of western North America. Bulletin of the Bureau of Fisheries 30(1910): 267–336.

BERRY S. S. 1918. Report on the Cephalopoda obtained by the F.I.S. "Endeavour" in the Great Australian Bight and other southern Australian localities. Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavour, 1909–1914 4(5): 201–298. http://www.biodiversitylibrary.org/part/119090

BERRY S. S. 1949. A new *Opisthoteuthis* from the eastern Pacific. Leaflets in Malacology 1(6): 23–26.

BERRY S. S. 1952. The flapjack devilfish, *Opisthoteuthis*, in California. California Fish & Game 38: 183–188.

BERRY S. S. 1955. The male flapjack devilfish. California Fish & Game 41(3): 219–224.

CARDOSO F., HOCHBERG F. G. 2012. Some deep-sea octopods found off Peru. Cephalopod International Advisory Council Symposium, Oct-Nov 2012 (Conference Abstract), Florianópolis, Santa Catarina, Brazil, p. 208.

COLLINS M. A. 2003. The genus *Grimpoteuthis* (Octopoda: Grimpoteuthidae) in the north-east Atlantic, with descriptions of three new species. Zoological Journal of the Linnean Society 139: 93–127. https://doi.org/10.1046/j.1096-3642.2003.00074.x

COLLINS M. A. 2005. *Opisthoteuthis borealis*: a new species of cirrate octopod from Greenland waters. Journal of the Marine Biological Association of the United Kingdom 85: 1475–1479

CUVIER G. 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts 2: 433–449.

GRIMPE G. 1916. *Chunioteuthis* – Eine neue Cephalopodengattung. Zoologischer Anzeiger 46(12): 349–359.

HOCHBERG F. G. 1990s–2011. A new species of *Opisthoteuthis* from off the coast of southern California (Cephalopoda: Cirrata). Unpublished Manuscript.

HOCHBERG F. G. 1976. Preliminary key to the benthic cephalopods of the eastern Pacific. Santa Barbara Museum of Natural History (unpublished), pp. 14–25. Available through the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) Toolbox: https://www.scamit.org/tools/toolbox-new/MOLLUSCA/Subphylum%20Conchifera/Class%20Cephalopoda/-OTHER%20USEFUL%20TOOLS/%2APreliminary%20Key%20to%20the%20Benthic%20Cephalopods%20of%20the%20eastern%20Pacific.pdf

HOCHBERG F. G. 1980. Class Cephalopoda. In: BRUSCA R. C. (ed.). Common intertidal invertebrates of the Gulf of California (2nd edition). The University of Arizona Press, Tuscon, Arizona, pp. 201–204.

HOCHBERG F. G., SHORT R. B. 1983. *Dicyemennea discocephala* sp. n. (Mesozoa: Dicyemidae) in a Finned Octopod from the Antarctic. The Journal of Parasitology 69(5): 963–966.

HOCHBERG F. G., VAN DYKHEUSEN G., HUNT J. 1996. *Grimpoteuthis packardi*, a new species of Cirroctopoda from off Monterey, California (Cephalopoda: Opisthoteuthidae). Unpublished Manuscript.

HOCHBERG F. G., NIXON M., TOLL R. B. 1992. Order Octopoda Leach, 1818. In: SWEENEY M. J., ROPER C. F. E., MANGOLD K. M., CLARKE M. R., V. BOLETZKY S. (eds). "Larval" and juvenile cephalopods: a manual for their identification. Smithsonian Contribution to Zoology 513: 213–280.

HOCHBERG F. G., NORMAN M. D., FINN J. K. 2014. Cirrate octopods. In: JEREB B., ROPER C. F. E., NORMAN M. D., FINN J. K. (eds). Cephalopods of the world, an annotated and illustrated catalogue of cephalopod species known to date, Volume 3. FAO Catalogue for Fisheries Purposes 4(3): 244–267.

HUDELOT C. 2000. La systematique des Octobrachia (Mollusca: Cephalopoda): Une approache moleculaire. PhD Thesis, Museum National d'Histoire Naturelle, Paris.

HUNT J. C. 1999. Laboratory observations of the feeding behavior of the cirrate octopod *Grimpoteuthis* sp.: one use of cirri. The Veliger 42(2): 152–156.

IBÁÑEZ C. M., PARDO-GANDARILLAS M. C., PÁRRAGA D. P., ZILLERUELO M., SELLANES J. 2011. Cephalopods collected in the continental slope off Central Chile. Amici Molluscarum 19: 37–40.

KUMAR S., STECHER G., LI M., KNYAZ C., TAMURA K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

LAPTIKHOVSKY V. V. 1999. Fecundity and reproductive strategy of three species of octopods from the Northwest Bering Sea. Russian Journal of Marine Biology 25(4): 342–346.

LEACH W. E. 1818. Cymothoadées, Cymothoadae. In: CUVIER F. (ed.). Dictionnaire des Sciences Naturelles, dans Lequel on Traite Methodiquement des Differens Etres de la Nature, Consideres Soit en Eux-memes, d'apres l'Etat Actuel de nos Connoissances, Soit Relativement a l'Utilite qu'en Peuvent Retirer la Medecine, l'Agriculture, le Commerce et les Artes 12, pp. 338–354. https://www.biodiversitylibrary.org/page/23002019

LEE R. S., BROPHY P. 1969. Additional bathymetric and locality data for some opisthobranchs and an octopus from Santa Barbara County, California. The Veliger 12(2): 220–221.

LILLY M., HORVATH B., LAMBERT G., VALENTICH-SCOTT P. 2024. In Memoriam, Dr Eric Hochberg. Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) Newsletter 41(5–6): 10–13.

MCCOSKER J. E., ANDERSON M. E. 1976. Aquarium maintenance of mesopelagic animals: a progress report. Bulletin of the Southern California Academy of Sciences 75: 211–219.

MBARI 2025a. Monterey Bay Aquarium Research Institute (MBARI). Deep-Sea Guide (DSG) page for *Opisthoteuthis* sp. A. Available online at: https://dsg.mbari.org/dsg/view/concept/Opisthoteuthis%20sp.%20A. Accessed (Consulted) 10 July 2025.

MBARI 2025b. Monterey Bay Aquarium Research Institute (MBARI). Deep-Sea Guide (DSG) page for *Opisthoteuthis cf. californiana*. Available online at: https://dsg.mbari.org/dsg/view/concept/Opisthoteuthis%20cf.%20californiana. Accessed (Consulted) 10 July 2025.

NESIS K. N. 1987. BURGESS L. A. (ed.). Cephalopods of the World: Squids, Cuttlefishes, Octopuses, and Allies (translated from 1982 Russian edition by LEVITOV B. S.). Tropical Fish Hobbyist Publications Inc. Ltd., USA.

NORMAN M. D. 2000. Cephalopods: a world guide. ConchBooks, Hockenheim, Germany.

OOMMEN V. P. 1976. A new species of the genus *Opisthoteuthis* Verrill, 1883 (Cephalopoda: Mollusca) from the southwest coast of India. Journal of the Marine Biological Association of India 18(2): 368–374.

O'SHEA S. 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). NIWA Biodiversity Memoir 112: 1–280.

PARDO-GANDARILLAS M. C., DIAZ-SANTANA-ITURRIOS M., FENWICK M., VILLANUEVA R., IBAÑEZ C. M. 2021. Redescription of the flapjack octopod, *Opisthoteuthis bruuni* (Cephalopoda: Opisthoteuthidae) from the southeastern Pacific Ocean and evolutionary relationships of cirrate octopods. Malacologia 63: 155–169.

PEREYRA W. T. 1965. New records and observations on the Flapjack Devilfish, *Opisthoteuthis californiana* Berry. Pacific Science 19: 427–441.

PHILLIPS J. B. 1934. Octopi of California. California Fish & Game 20: 20–29.

PHILLIPS J. B. 1966. Additional records of flapjack devilfish from California waters. California Fish & Game 52(2): 124.

PIERTNEY S. B., HUEDELOT C., HOCHBERG F. G., COLLINS M. A. 2003. Phylogenetic relationships among cirrate octopods (Mollusca: Cephalopoda) resolved using mitochondrial 16S ribosomal DNA sequences. Molecular Phylogenetics and Evolution 27: 348–353. https://doi.org/10.1016/S1055-7903(02)00420-7

ROBSON G. C. 1930. Cephalopoda, I. Octopoda. Discovery Reports 2: 371–402. http://biodiversitylibrary.org/page/15905216

ROBSON G. C. 1932. A monograph of the recent Cephalopoda based on the collections in the British Museum (Natural History). Part II. The Octopoda. British Museum (Natural History), London. https://biodiversitylibrary.org/page/48234249

SASAKI M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. Journal of the Faculty of Agriculture, Hokkaido Imperial University 20(Supplement): 1–357.

TAKI I. 1963. On four newly known species of Octopoda from Japan. Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University 5(1): 57–93.

URBANO B., HENDRICKX M. E. 2018. Offshore cephalopods (Mollusca: Cephalopoda) collected off the west coast of Mexico during the TALUD cruises. Molluscan Research 39(1): 13–28.

VEGA PETKOVIC M. A. 2007. Description of the female of *Grimpoteuthis bruuni* Voss, 1982. Gayana 71(2): 207.

VERHOEFF T. J. 2023. The molecular phylogeny of cirrate octopods (Cephalopoda: Octopoda: Cirrata) using COI and 16S sequences. Folia Malacologica 31(4): 175–196. https://doi.org/10.12657/folmal.031.026

VERHOEFF T. J. 2024. Flapjack octopods of Australia (Cephalopoda: Cirrata: Opisthoteuthidae). Part I. Southern Australia. Australian Journal of Taxonomy 68: 1–44. https://doi.org/10.54102/ajt.wij3l

VERHOEFF T. J. 2025. Flapjack octopods of Australia (Cephalopoda: Cirrata: Opisthoteuthidae). Part II. Northwestern Australia and adjacent waters. Australian Journal of Taxonomy 92: 1–28. https://doi.org/10.54102/ajt.c46g9

VERRILL A. E. 1883. Supplementary report on the "Blake" cephalopods. Bulletin of the Museum of Comparative Zoology 11(5): 105–115. https://biodiversitylibrary.org/page/30397620

VERRILL A. E. 1896. The Opisthoteuthidae, a remarkable new family of deep sea Cephalopoda, with remarks on some points in molluscan morphology. American Journal of Science ser. 4, 2(7): 74–80. https://www.biodiversitylibrary.org/page/40353964

VILLANUEVA R., COLLINS M. A., SÁNCHEZ P., VOSS N. A. 2002. Systematics, distribution and biology of the cirrate octopods of the genus *Opisthoteuthis* (Mollusca, Cephalopoda) in the Atlantic Ocean, with description of two new species. Bulletin of Marine Science 71(2): 933–985.

VOSS G. L. 1982. *Grimpoteuthis bruuni*, a new species of finned octopod (Octopoda: Cirrata) from the southeastern Pacific. Bulletin of Marine Science 32(2): 426–433.

ZIEGLER A., MILLER A., NAGELMANN N. 2021. Novel insights into early life stages of finned octopods (Octopoda: Cirrata). Swiss Journal of Palaeontology 140: 24. https://doi.org/10.1186/s13358-021-00240-0

Received: September 23rd, 2025
Revised: November 21st, 2025
Accepted: November 26th, 2025
Published on-line: February 11th, 2026

APPENDIX

HUDELOT (2000) sequenced 16S from a SBMNH specimen designated as *Opisthoteuthis* sp. 1 (tissue provided by Hochberg). Unpublished notes for a HUDELOT & HOCHBERG paper note this specimen as "*Opisthoteuthis* sp. 1 (*berryi*) NE Pacific Ocean: off southern California (Redondo Canyon)", with the sequence being that from HUDELOT (2000).

In PIERTNEY et al. (2003) supplementary data, this sequence became "*Opisthoteuthis* sp. 3 (Hochberg, in prep.)", and was stated as being accessioned on GenBank as AJ252769, however this sequence is a *Stauroteuthis syrtensis* sequence, not an *Opisthoteuthis*.

The location of Redondo Canyon (off South Santa Monica Bay), matches to **SBMNH 464912**, which was collected 17 Nov 1993, a date consistent with HOCHBERG loaning the tissue sample for HUDELOT's study.

The sequence as printed in HUDELOT (2000) is reproduced below.

> Opisthoteuthis sp3 [Hudelot Opisthoteuthis sp1] SBMNH Redondo Canyon, California

GTCTCTTTGTTTTTTACATATAAGGAGTCGGGCCTGCTCAGTGATATAAATATTTTAACAGCTGCAGTGTAATAACTG
TACTAAGGTAGCATAATAATTTGCCTTATAAATTAAGGCTAGAATGAATGGTTTGACGAAAGTTGATCTGTCTCTTAT
TTATTTATTAGAAATTAATTTTTATAGTGAAAAGCTTTAATTAATTAAAGGGACGAGAAGACCCTATTGAACTTTTATT
AGATATATATAAAATTAATTTGAGATTATATAGGAATAATTTTGATTGGGGTGATCGTGGAATAAATAAAATAATTAAT
AACTTCCTTAATTGTAAATTAAAATTGATGAATTAATTAACCAATATTTTCTTTCATGAATAAGTTACCATAGGGATAA
CAGCGTAATTTTTTTAGAGAGTTCTTATTAATAAAAAAGATTGCGACCTCGATGTTGGATTAAAATTACCTTAAGGTG
AAGAAGCTTTAATAGGTGAATCTGTTCGATTTTTAAAATTTTAC