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Northeast Pacific benthic shelled sea slugs

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Abstract

A compendium of the northeast Pacific benthic shelled sea slugs formerly classified in the paraphyletic group "Opisthobranchia" is provided. These include organisms with internal and/or reduced shells. Shell-less groups such as Nudibranchia or closely related benthic shelled clades such as the Pyramidelloidea and the Siphonarioidea are excluded. The Sacoglossa is not represented by any shelled forms in the northeast Pacific and therefore is also excluded. Descriptions include diagnostic characteristics, species abundance information, geographic and bathymetric ranges, and ecological data (if available). Short remarks for most species and higher taxa provide additional information published elsewhere and/or address outstanding taxonomic or nomenclatural issues. Illustrations of the shells and — in some cases — the live animals are provided. Species are arranged based on current classification schemes and a full list of primary synonyms, location of type material (if known), and type localities of all synonyms are provided for each species. Three new species are described in this paper: *Microglyphis michelleae* new species, *Microglyphis sabrinae* new species and *Bogasonia jennyae* new species. *Oscaniella purpurea* Bergh, 1897 is here designated the type species of *Oscaniella* Bergh, 1897.

Key words: "Opisthobranchia," identification guide, diagnostic data, taxonomy, systematics

Introduction

Shelled sea slugs, formerly considered members of the "Opisthobranchia," constitute a biological diverse and ecologically important paraphyletic assemblage of species, characterized by having different degrees of shell reduction and/or internalization. "Opisthobranchs" are primarily benthic, but are found in all marine environments, from the intertidal to abyssal depths, and include pelagic and neustonic forms (Gosliner *et al.* 2015). Most species occur in the Indo-Pacific tropics, but there is a remarkable diversity in the northeast Pacific, particularly of nudibranchs (Behrens & Hermosillo 2005).

Although the "Opisthobranchia" was traditionally considered one of the main groups of gastropods (a subclass of Gastropoda), during the last decade a number of phylogenetic analyses (morphological and molecular) have challenged its monophyly. The most recent phylogenomic study (Zapata *et al*. 2014) divided the traditional "Opisthobranchia" into three main groups: 1) Euopistobranchia, which includes umbraculids, anaspideans (sea hares), runcinids, pteropods and most cephalaspideans, 2) Nudipleura, which includes nudibranchs and pleurobranchids, and 3) Sacoglossa, which was moved into Panpulmonata, along with pulmonate gastropods. However, another phylogenomic analysis (Kocot *et al*. 2013) found Nudipleura to be paraphyletic. Other groups traditionally included in the "Opisthobranchia" such as Acteonidae, Ringiculidae, Aplustridae, Bullinidae are of uncertain placement. Zapata *et al.* (2014) placed Aplustridae as sister to Euopisthobranchia and Panpulmonata whereas Oskars *et al*. (2015) suggested Acteonidae and Aplustridae are sister to Nudipleura. Other papers have supported the monophyly of "opisthobranchs," for example, Medina *et al.* (2011) based on mitochondrial genomic data found that "opisthobranchs" are monophyletic when *Siphonaria* is included. They also recovered Acteonidae and Aplustridae as sister to Nudipleura (Actopleura), and a clade named Placoesophaga, which is largely equivalent to Euopisthobranchia. Because of the conflicting evidence on the hypothetical monophyly of the "Opisthobranchia" (Medina *et al.* 2011; Kocot *et*

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al. 2013; Zapata *et al*. 2014; Oskars *et al*. 2015), the name is placed in quotes to indicate it is likely paraphyletic.

In this paper, an overview of the diversity of "opisthobranchs" from the northeast Pacific is provided, including diagnoses, illustrations of shells and living animals, as well as ecological and distributional data to facilitate species identifications. Species are arranged based on current classification schemes (Bouchet & Rocroi 2017). Although the "Opisthobranchia" was not a primary focus of James H. McLean's research, he planned to include a chapter on shelled "opisthobranchs" in his monograph, excluding all shell-less forms, chiefly nudibranchs. Due to the long taxonomic history of "opisthobranchs" as a main gastropod group, and to honor J.H. McLean's original intention, all the shelled benthic "opisthobranch" groups he planned to include in this book are treated herein. Therefore, closely related benthic shelled clades such as the Pyramidelloidea and the Siphonarioidea are not treated in this paper. Also, because no shelled sacoglossans occur within the temperate or cold northeast Pacific, this important clade is not covered herein.

Methods

Most of the specimens here examined are dried shells and preserved specimens deposited at the Malacology Collection of the Natural History Museum of Los Angeles County (LACM) and the Cal Poly Pomona Invertebrate Collection (CPIC). The specimens were collected by various individuals and research expeditions over several decades. Photographs of live animals were obtained from colleagues or the LACM photographic archives. Preserved specimens were photographed in the laboratory with Nikon D70 digital camera or a JEOL JSM-6010 scanning electron microscope (SEM). Type specimens, additional material examined, or information on the location of type material was obtained from museums.

Abbreviations

BPBM: Bernice Pauahi Bishop Museum, Honolulu, USA.
CASIZ: California Academy of Sciences, Invertebrate Zoology Collection, San Francisco, USA.
CAS(F): California Academy of Sciences, Fossil Collection, San Francisco, USA.
LACM: Natural History Museum of Los Angeles County (Malacology Collection), Los Angeles, USA.
LACM(IP): Natural History Museum of Los Angeles County (Invertebrate Paleontology Collection), Los Angeles, USA.
LMA: Löbbecke Museum + Aquazoo, Düsseldorf, Germany.
MCZ: Museum of Comparative Zoology (Harvard University), Cambridge, USA.
MM: Manchester Museum, University of Manchester, UK.
MHNH: Muséum national d'Histoire naturelle, Paris, France.
MZUSP: Museu de Zoologia, Universidade de São Paulo, Brazil.
NHMD: Natural History Museum of Denmark, Copenhagen, Denmark.
NHMO: Naturhistorisk Museum, Universitetet i Oslo, Norway.
NHMUK: Natural History Museum of the United Kingdom, London, UK.
NPCNZ: National Paleontological Collection (GNS Science), Lower Hutt, New Zealand.
OMNH: Osaka Museum of Natural History, Osaka, Japan.
RAMM: Royal Albert Memorial Museum and Art Gallery, Exeter, UK.
RBCM: Royal British Columbia Museum, Victoria, Canada.
RM: Redpath Museum (McGill University), Montreal, Canada.
RSM: Royal Scottish Museum (National Museums of Scotland), Edinburgh, UK.
SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, USA.
SDNHM: San Diego Natural History Museum, San Diego, USA.
SMNH: Swedish Museum of Natural History, Stockholm, Sweden.
UCMP: University of California Berkeley Museum of Paleontology, Berkeley, USA.
UMUT: University Museum (University of Tokyo), Tokyo, Japan.
USNM: National Museum of Natural History (Smithsonian Institution), Washington, D.C., USA.

Systematics

Acteonida Minichev, 1967

Description. Shell external, solid, oval, transversely sulcate; surface with punctuated spiral grooves; spire elevated, variable in shape; aperture longitudinal; columella thickened; operculum present.

Remarks. The classification of Acteonida is controversial and fluid (see Mikkelsen 1996, Malaquias *et al*. 2009, Zapata *et al*. 2014, Oskars *et al*. 2015, Kano *et al.* 2016). The most recent phylogenetic analysis questioned the monophyly of acteonids and ringiculds and suggested a sister relationship of Ringiculidae to Nudibranchia and Pleurobranchida (Kano *et al.* 2016). Only Acteonidae and Aplustridae are represented in the northeast Pacific.

Acteonidae d'Orbigny, 1843 (1842–1843)

(Figure 1)

Description. Same as for Acteonida.

Remarks. Genera distinguished based on radular morphology (Rudman 1971, Valdés 2008).
Acteonids are found subtidally to the deep sea; all species studied to date feed on polychaete worms. This group is well represented in the fossil record. Only three species are found in the northeast Pacific. Diversity is unremarkable.

Acteon Montfort, 1810

(Figure 1C–D)

Acteon Montfort, 1810: 315. Type species (OD): *Voluta tornatilis* Linnaeus, 1758. Northeast Atlantic.

Tornatella Lamarck, 1816: pl. 452. Type species (SD: Herrmannsen 1852 [1846–1852]: 580): *Voluta tornatilis* Linnaeus, 1758. Northeast Atlantic.

Speo Risso, 1826: 235. Type species (M): *Voluta bifasciata* Gmelin, 1791 [= *Acteon tornatilis* (Linnaeus, 1758)]. Northeast Atlantic.

Description. Shell 12 mm, external, solid, oval, transversely sulcate; surface with punctuated spiral grooves; spire elevated, variable in shape; aperture longitudinal, anteriorly rounded; inner lip thickened; columella with one fold; operculum present. Animal can retract fully into shell; cephalic shield large, divided into two posteriorly projecting lobes by deep medial slit; radula with numerous denticulate, small teeth.

Acteon traskii Stearns, 1897

(Figure 1C–D)

Actaeon traskii Stearns, 1897: 14. Syntype USNM 130320. San Diego, California, Holocene.

Description. Shell to 18 mm, solid, elongate, with convex sides; body whorl large, 3/4–4/5 of shell length; spire conical, elongate, with 3–5 whorls; suture channeled; umbilicus absent; aperture long, ~3/4 of body whorl length, wide anteriorly, narrowing abruptly about half-length; columellar margin thickened, slightly oblique, with small, simple fold posteriorly, anteriorly merging into external lip; sculpture with oval, fused punctured spiral grooves; color cream to reddish, with white band on posterior end of whorl.

Distribution. Santa Barbara, California to Colombia; 3–100 m, rarely to 305 m (D. Cadien, pers. comm.). Uncommon.

Remarks. Live animal is unknown. Radula and anatomy were described by Ev. Marcus (1972) and Valdés & Camacho-García (2004). The species was originally described from fossil material.

FIGURE 1. Acteonidae. **A–B.** ***Rictaxis punctocaelatus*** (Carpenter, 1864), (A), 16 mm (LACM 55145), Laguna Beach, California (photo: Sabrina Medrano), (B) live animal, southern California (photo: Kevin Lee). **C–D.** ***Acteon traskii*** Stearns, 1897, Magdalena Bay, Baja California (photos: Sabrina Medrano), (A) 16 mm (LACM 178902), (B) 15 mm (LACM 157903); **E.** ***Rictaxis painei*** (Dall, 1903), 21 mm (LACM 119036), Santa Monica Bay, California (photo: Sabrina Medrano).

***Rictaxis* Dall, 1871**
(Figure 1A–B)

Rictaxis Dall, 1871: 236. Type species (OD): *Tornatella punctocaelata* Carpenter, 1864.

Description. Shell 19–22 mm, external, solid, oval, transversely sulcate; surface with punctuated spiral grooves; spire elevated, variable in shape; aperture longitudinal; columella thickened, obliquely truncate at base; operculum absent. Animal can retract fully into shell; cephalic shield divided into left, right halves, each with an anterior, posterior lobe; radula with several denticulate teeth; outer teeth elongate

Remarks. The placement of *Rictaxis* in Acteonidae is dubious. Göbbeler & Klussmann-Kolb (2010) based on molecular data found *Rictaxis* to be sister to Aplustridae, rendering Acteonidae paraphyletic if *Rictaxis* is included. *Rictaxis* shares with other Aplustridae the absence of an operculum but shares with Acteonidae several other anatomical and conchological features (see Göbbeler & Klussmann-Kolb 2010). Therefore, *Rictaxis* is herein provisionally placed in Acteonidae until additional research is conducted.

***Rictaxis punctocaelatus* (Carpenter, 1864)**
(Figure 1A–B)

Tornatella punctocaelata Carpenter, 1864: 646. Lectotype (Palmer 1958: 239) USNM 14914. San Diego, California.
Acteon punctocaelatus var. *coronadensis* Stearns, 1899: 299. Syntype USNM 148266. San Diego, California.
Acteon punctocoelata vancouverensis I. S. Oldroyd, 1927: 25, pl. 1, fig. 19, 20. Syntypes CASIZ 060979, CASIZ 060980. Departure Bay, Vancouver Island, British Columbia, 3 fm.

Description. Shell to 19 mm, solid, elongate, with convex sides; body whorl very large occupying most of shell length; spire short, conical, with 1–2 whorls; suture slightly channeled; umbilicus absent; aperture long, ~3/4 of body whorl length, wider anteriorly, narrowing abruptly about half-length; columellar margin thickened, slightly oblique, with small, simple fold posteriorly, anteriorly obliquely truncate, abruptly differentiated from external lip; sculpture with oval punctuations fused into spiral grooves; color white under fine periostracum, with two broad spiral brown to grey bands on body whorl. Live animal translucent white with opaque white spots; cephalic shield vertically divided by a shallow groove into left, right halves, each with an anterior, posterior lobe; foot wide extending laterally beyond, posteriorly up to end of shell. Anatomy comprehensively described by Göbbeler & Klussmann-Kolb (2010).

Distribution. Prince of Wales Island, Alaska to Magdalena Bay, Baja California, Mexico; 0–230 m, rarely to 305 m (D. Cadien, pers. comm.). Seasonally common.

Remarks. This species occurs on mud and sand bottoms in bays, typically at low tide and shallow sublittoral zones, less commonly at greater depths. Ev. Marcus (1972) found unidentified polychaetes in the gut of dissected specimens.

***Rictaxis painei* (Dall, 1903)**
(Figure 1E)

Actaeon (*Rictaxis*) *painei* Dall, 1903: 172. Holotype USNM 109301. Santa Catalina Island, California, 91 m.
Actaeon (*Rictaxis*) *painei* var. *grandior* Grant & Gale, 1931: 444, pl. 24, f. 12. Holotype SDNHM 208. Holser Canyon, Los Angeles County, late Pliocene.

Description. Shell to 22 mm, fragile, elongate, with convex sides; body whorl very large occupying most of shell length; spire elongate, conical, with 4 whorls; suture slightly channeled; umbilicus absent; aperture long, ~1/2 of body whorl length, wider anteriorly, narrowing abruptly about half-length; columellar margin thickened, lacking folds, anteriorly obliquely truncate, abruptly differentiated from external lip; sculpture with large oval punctuations forming spiral grooves; color white. Live animal unknown.

Distribution. Santa Catalina Island, Palos Verdes Peninsula, and Santa Monica Bay, Los Angeles County, California; 27–110 m, rarely to 327 m (D. Cadien, pers. comm.). Recent and Middle Pliocene. Rare.

Remarks. Probably not a *Rictaxis*, anatomy needs to be examined for a generic placement.

Aplustridae Gray, 1847
(Figure 2A)

Description. Shell oval, globose, extraordinarily thin, fragile, with sunken spire; operculum absent; color white or beige. Live animal cannot retract completely into shell.

Remarks. This family has been known as Hydatinidae, but the family name was fixed as Aplustridae by Bouchet & Rocroi (2005). Aplustrids are specialized feeders, eating cirratulinid polychaete worms. Tropical species have bands or stripes on the shell and vividly colored bodies. The family is represented in the northeast Pacific by a single new species of *Parvaplustrum* noticed but not named by Gosliner (1996).

FIGURE 2. Aplustridae and Ringiculidae (images: Ángel Valdés). **A.** ***Parvapustrum cadieni*** Valdés, Gosliner & Warén, 2017, Holotype, 2.1 mm (LACM 3329), off Tanner Bank, California **B.** ***Microglyphis breviculus*** (Dall, 1902), 3.5 mm (LACM 87-356.4), Sitka Sound, Alaska. **C.** ***Microglyphis michelleae*** n. sp., Holotype, 2.5 mm (LACM 3332), Point Arguello, California. **D.** ***Microglyphis sabrinae*** n. sp., Holotype, 2.9 mm (LACM 3330), Aleutian Trench, Alaska.

Parvaplustrum **Powell, 1951**
(Figure 2A)

Parvaplustrum Powell, 1951: 180. Type species (OD): *Parvaplustrum tenerum* Powell, 1951. Falkland Islands.

Description. Shell ovate, globose, without operculum; sculpture of extremely fine, dense spiral striations. Live animal with two extensible appendages on each side of headshield; radula with single petaliform lateral tooth in each row, gizzard lacking plates.

Remarks. One species is illustrated from the northeast Pacific. A second possible species, identified as *Meloscaphander* sp. A by Cadien (1995), is not illustrated here due to lack of well-preserved shells. It has a more globose shell than *P. cadieni*, and is very similar to *P. japonicum*. *Parvaplustrum cadieni* is typically found in shallower waters, 30–605, from Goleta, Santa Barbara County to San Diego, California

Parvaplustrum cadieni **Valdés, Gosliner & Warén, 2017**
(Figure 2A)

Parvaplustrum cadieni Valdés, Gosliner & Warén, 2017: 97–99. Holotype LACM 3329; off Tanner Bank, California (32°40.97'N, 119°14.04'W), 390 m.

Description. Shell to 2 mm, thin, pyriform, body whorl slender to very rotund; spire involute, posterior margin of outer forming raised lip; aperture wide, narrowing slightly mid-length; sculpture absent, rarely with very fine spiral lines of punctuations; color transparent to translucent white. Live animal unknown, preserved specimens with differentiate posterior appendage on each side of headshield; posterior end of body forming well-defined tail; gill plume unipinnate, located above head; penis elongate, simple; radula with single row of petaliform lateral teeth on each side.

Distribution. Oregon, possibly from Puget Sound, Washington (D. Cadien pers. comm.) to Todos los Santos Bay, Baja California, Mexico; 3–809 m. Occasionally very common.

Remarks. Found in chemosynthetic deep-water environments including whale falls and cold seeps as well as organic-rich shelf sediments and deeper portions of bays.

Ringiculida Minichev & Starobogatov, 1979

Description. Shell external, oval; surface with punctuated spiral grooves; spire short, with several whorls; aperture narrow obstructed by folds on columella, sometimes on outer lip; outer lip thickened or not, with or without folds; operculum absent

Remarks. Ringiculids were recovered as sister to Nudipleura by Kano *et al.* (2016), who introduced the new name Ringipleura for this clade. Only *Microglyphis* is represented in the northeast Pacific.

Ringiculidae Philippi, 1853
(Figure 2B–C)

Description. Same as for Ringiculida.

Remarks. Several genera of Ringiculidae have been described but only one, *Microglyphis*, is represented in the northeast Pacific with three species. Typically small animals; inhabit fine sand environments from the intertidal to 5,000 m. They are probably generalists feeding on small benthic organisms.

***Microglyphis* Dall, 1902**
(Figure 2B–C)

Microglyphis Dall, 1902: 512. Type species (OD): *Actaeon curtulus* Dall, 1890. Southern Argentina.

Description. Shell external, white, small, short; sculpture of faint spiral grooves; spire elevated, with several whorls; columella thickened, with 1–2 conspicuous folds; outer lip smooth, not thickened.

Remarks. *Microglyphis* is similar to *Ringicula* but lacks thickly callused aperture.

***Microglyphis brevicula* (Dall, 1902)**
(Figure 2B)

Actaeon (*Microglyphis*) *breviculus* Dall, 1902: 512. Holotype USNM 109042. Santa Rosa Island, California.
Actaeon (*Microglyphis*) *estuarinus* Dall, 1908: 238. Holotype USNM 110598. Estero Bay, San Luis Obispo County, California.
Actaeon (*Microglyphis*) *schencki* Berry, 1941: 3, pl. 2, fig. 6. Holotype SBMNH 34512. San Pedro, Lower Pleistocene.

Description. Shell to 5.5 mm, external; body whorl large, about 4/5 of shell length; spire elevate, with three whorls; columella thickened with notched basal fold; surface with faint punctuated spiral grooves. Live animal unknown.

Distribution. Gulf of Alaska to San Diego, California (D. Cadien pers. comm.). 44–2432 m. Common.

Remarks. Woodring *et al.* (1946) suggested *M. schencki* was probably a synonym of *M. breviculus*. *Microglyphis estuarinus* is also synonymized here because supposed differences in spiral sculpture cannot be detected in material in the LACM collection (J. McLean manuscript note).

***Microglyphis michelleae* n. sp.**
(Figure 2C)

Type. Holotype LACM 3332 (LACM 91-131), 4,100 m, 226 km W of Point Arguello, Santa Barbara County, leg. Ken Smith.

Description. Shell to 2.5 mm, external; body whorl large occupying most of shell length; aperture about 9/10 of shell length, narrowing progressively towards apex, posterior end truncated; spire short, with two whorls; columella thickened with conspicuous basal fold; surface with faint punctuated spiral grooves. Live animal unknown.

Distribution. Point Arguello, Santa Barbara County, California. 4100 m. Rare.

Etymology. Named after Michelle Schwengel for her contributions to the illustration of this volume.

Remarks. Much wider than *M. brevicula*, also has a larger body whorl and aperture. Columellar fold is very conspicuous and simple.

***Microglyphis sabrinae* n. sp.**
(Figure 2D)

Type. Holotype LACM 3330, TVGKG sta. 49, 4809 m, Aleutian Trench, Alaska (54°18.056'N, 157°12.107'W), 3.9 mm, leg. Heiko Sahling.

Description. Shell to 2.9 mm, external; body whorl large occupying most of shell length; aperture about 9/10 of shell length, narrowing progressively towards apex, posterior end narrow; spire short, with two whorls; columella thickened with basal fold; surface with faint punctuated spiral grooves. Live animal unknown.

Distribution. Aleutian Trench; 4,809 m. Rare.

Etymology. Named after Sabrina Medrano for her help photographing specimens and gathering data for this paper.

Remarks. Columellar projection much weaker and anterior end of shell more rounded than that of *M. michelleae* new species.

Pleurobranchida Minichev & Starobogatov, 1975

Description. Shell internal or absent, flat, semi-rectangular or oval, spire flat; protoconch visible. Body rounded, convex; head hidden under anterior edge of mantle; two enrolled rhinophores, no oral tentacles; velum reduced, between base of rhinophores, mouth; shell internal or absent; mantle cavity absent; gill bipinnate, on right side of body, between mantle, foot.

Remarks. Pleurobranchida is sister to Nudibranchia (forming Nudipleura) (Wägele & Willan 2000, Zapata *et al.* 2014). Unlike nudibranchs, most pleurobranchids have internal shells in the adult state and therefore this group is treated here.

Pleurobranchidae J. E. Gray, 1827
(Figures 3–4)

Description. Same as for Pleurobranchida.

Remarks. Pleurobranchidae was reappraised by Willan (1987), who established the current classification of genera. This family is represented in the northeast Pacific by several species but shell-less groups such as *Pleurobranchea* are not treated here. Diversity is remarkable.

***Berthella* Blainville, 1824**
(Figures 3A–B, 4A, 4C–D)

Berthella Blainville, 1824: 262. Type species (M): *Bulla plumula* Montagu, 1803. Europe.
Bouvieria Vayssière, 1896: 114, 116. Type species (SD, Odhner 1926: 22) *Pleurobranchus aurantiacus* Risso, 1818. Europe.
Cleanthus Leach *in* J. E. Gray, 1847: 163. Type species (OD): *Bulla plumula* Montagu, 1803. Europe.
Gymnotoplax Pilsbry, 1896 [1895–1896]: 210. Type species (SD, Ev. Marcus 1977b: 418): *Pleurobranchus americanus* Verrill, 1885. Caribbean.

Description. Shell plate-like, semi-rectangular, large, covering entire viscera; spire flat, with protoconch visible on posterior end; sculpture of strong growth lines crisscrossed by faint transverse lines. Live animal oval; mantle smooth or with low tubercles; velum small, triangular; rhinophores enrolled, emerging between velum, mantle; radular teeth short, hook-shaped.

Remarks. Represented in the fossil record. Species graze on plakinid sponges. The taxonomy of the northeast Pacific species of *Berthella* was reviewed by Gosliner & Bertsch (1988).

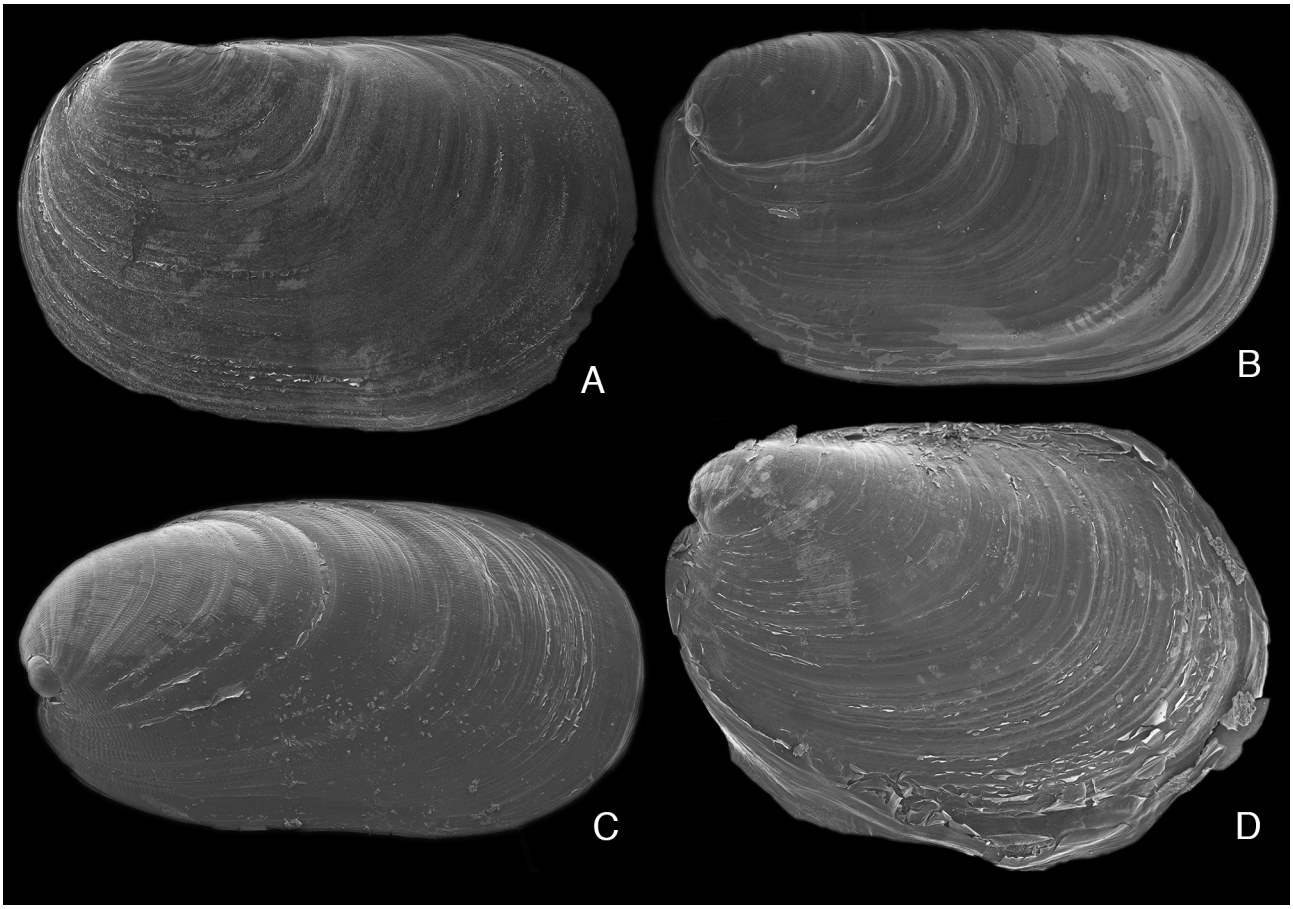

FIGURE 3. Pleurobranchidae. Images: Ángel Valdés. **A.** ***Berthella californica*** (Dall, 1900), 14 mm (CPIC 1409), Cape Arago, Oregon. **B.** ***Berthella strongi*** MacFarland, 1966, 4.1 mm (CPIC 1408), La Jolla, California. **C.** ***Berthellina ilisima*** Ev. & Er. Marcus, 1967, 2.8 mm (LACM 153334), Jicarón Island, Panama. **D.** ***Pleurobranchus digueti*** Rochebrune, 1895, 6.1 mm (LACM 178960), Ceralvo Island, Baja California.

Berthella californica **(Dall, 1900)**
(Figures 3A, 4C–D)

Pleurobranchus californicus Dall, 1900b: 92. Syntypes CASIZ 064302, USNM 107893. San Pedro, Los Angeles County, California.

Pleurobranchus chacei Burch, 1944: 17–18. Syntype CASIZ 65576. Crescent City, Humboldt County, California.

Pleurobranchus californicus denticulatus MacFarland, 1966: 84–89, pl. 5, figs 1–5, pl. 13, figs 25–34, pl. 16, fig. 12. Syntypes CASIZ 021629, CASIZ 021630, CASIZ 021664, USNM 575223. Point Pinos, Monterey Bay, California.

Description. Shell to 40 mm, usually no longer than 20 mm, semi-rectangular to oval, slightly narrower at apex; spire flat forming elevate apex with visible protoconch; periostracum thick; sculpture of conspicuous growth lines. Live animal to 85 mm, usually no longer than 50 mm; body translucent white to brownish background (in southern California) with numerous opaque white spots on mantle, oral veil, foot; edge of mantle, foot with opaque white line; dorsum covered with low tubercles.

Distribution. Point Craven, Alaska to the Galapagos Islands; also reported from Russia and Japan; intertidal and subtidal. Uncommon.

Remarks. There is molecular and morphological evidence that *B. californica* is a species complex of two allopatric species, with a geographic boundary near Point Conception. The systematics of this species complex will be addressed in a future paper.

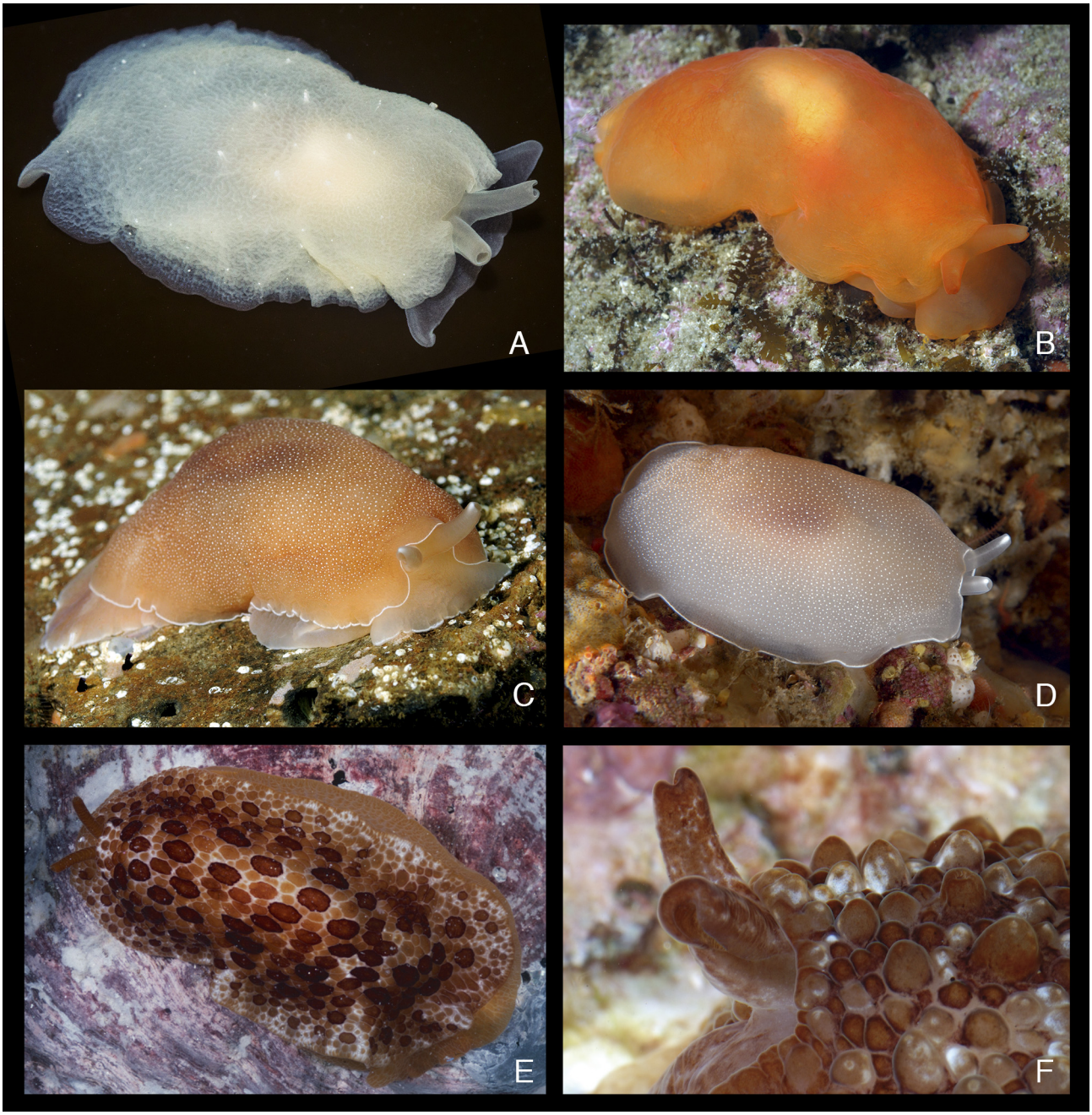

FIGURE 4. Pleurobranchidae. **A.** ***Berthella strongi*** MacFarland, 1966, Morro Bay, California (photo: Marlin Harms). **B.** ***Berthellina ilisima*** Ev. Marcus & Er. Marcus, 1967, California (photo: Kevin Lee). **C–D.** ***Berthella californica*** (Dall, 1900), color variation, California (photos: Kevin Lee), (A) brown specimen, (D) white specimen. **E–F.** ***Pleurobranchus digueti*** Rochebrune, 1895, (E) La Jolla, California (photo: David Behrens), (F) detail of the head, Baja California (photo: Ángel Valdés).

Berthella strongi **(MacFarland, 1966)**
(Figures 3B, 4A)

Pleurobranchus strongi MacFarland, 1966: 89–93, pl. 6, figs 3–7, pl. 15, figs 1–15, pl. 16, figs 13–14. Holotype CASIZ 25743. White Point, San Pedro, Los Angeles County, California.

Description. Shell to 10 mm, oval, with nearly parallel sides; spire flat forming an elevate apex with visible protoconch; periostracum thick; sculpture of growth lines and conspicuous, irregular, longitudinal grooves.

Live animal to 25 mm, translucent white with few opaque white spots on mantle, oral veil, foot; edge of mantle, foot lacking an opaque white line; dorsum covered with low tubercles.

Distribution. Moss Beach, San Mateo County, California to Rosarito Point, Baja California, Mexico; a record from Nanaimo, Vancouver Island, British Columbia appears to be an El Niño related anomaly; intertidal. Uncommon.

Berthellina Gardiner, 1936

(Figures 3C, 4B)

Berthellina Gardiner, 1936: 198. Type species (OD): *Berthellina engeli* Gardiner, 1936. Europe.

Description. Shell plate-like, elongate, narrower at apex, large, situated anteriorly on viscera; spire flat, with protoconch visible on posterior end; sculpture of strong growth lines crisscrossed by faint transverse lines. Live animal globose, typically orange or red; mantle smooth; velum small, triangular; rhinophores enrolled, emerging between velum, mantle; radular teeth comb-shaped, elongate.

Remarks. Species of *Berthellina* feed on Demospongiae of the genera *Sigmadocia* and *Oscarella*.

Berthellina ilisima Ev. & Er. Marcus, 1967

(Figures 3C, 4B)

Berthellina engeli ilisima Ev. Marcus & Er. Marcus, 1967: 160–163, fig. 18. Holotype USNM 678401; Puerto Peñasco, Sonora, Mexico.

Description. Shell to 10 mm, oval, with narrower anterior, posterior ends; spire flat forming an elevate apex with visible protoconch; periostracum thin; sculpture of growth lines, conspicuous, irregular, longitudinal grooves. Live animal to 100 mm; uniformly orange to red, sometimes with few white spots; dorsum smooth.

Distribution. Santa Barbara, California to the Galapagos Islands; reports from California occur during El Niño events; intertidal to subtidal. Rare in California, relatively common in the Panamic Province.

Remarks. The animals are active at night, feed on sponges.

Pleurobranchus Cuvier, 1804

(Figures 3D, 4E–F)

Pleurobranchus Cuvier, 1804: 267–275. Type species (M): *Pleurobranchus peronii* Cuvier, 1804. Indo-Pacific.

Oscaniella Bergh, 1897: 94–95. Type species (here designated): *Oscaniella purpurea* Bergh, 1897 [= *Pleurobranchus peronii* Cuvier, 1804]. Indo-Pacific.

Oscanius Leach *in* J. E. Gray, 1847: 163. Type species (OD): *Lamellaria membranacea* Montagu, 1816. Europe.

Pseudolibania de Stefani *in* de Stefani & Pantanelli, 1879: 12. Type species (OD): *Daudebardia tarentina* de Stefani & Pantanelli, 1879 [=*Pleurobranchus testudinarius* Cantraine, 1835]. Mediterranean, South Atlantic.

Susania J. E. Gray, 1857: 201–202. Type species (SD, White 1946: 52) *Pleurobranchus testudinarius* Cantraine, 1835. Mediterranean, South Atlantic.

Description. Shell plate-like, semi-rectangular to oval, small, situated anteriorly on viscera; spire flat, with protoconch visible on posterior end; sculpture of growth transverse lines. Live animal oval; mantle covered with tubercles; velum small, triangular; rhinophores enrolled, emerging between velum, mantle.

Remarks. Only one species in the northeast Pacific. Nocturnally active, feeding on tunicates. For a revision of the genus see Goodheart *et al*. (2015).

Pleurobranchus digueti Rochebrune, 1895

(Figures 3D, 4E–F)

Pleurobranchus digueti Rochebrune, 1895: 240. Syntypes MNHN, BPBM 258974; Mogote, La Paz Bay, Mexico.

Description. Shell to 10 mm, semi-rectangular to oval, sometimes narrower at apex; spire flat forming elevate apex with visible protoconch; periostracum thick; sculpture of conspicuous growth lines. Live animal to 106

mm; body oval covered with large, tentacular tubercles, with pointed apices, surrounded by smaller, polygonal tubercles; posterior end of foot projecting from mantle; rhinophores with horizontal striations; gill rachis tuberculate at base of pinnae; color light brown, with opaque white pigment on some tubercles; radular teeth smooth, hook-shaped.

Distribution. Santa Barbara, California to Ecuador; intertidal and subtidal. Uncommon.

Remarks. Previously considered a population of the Caribbean *Pleurobranchus areolatus* Mörch, 1863 (Ev. Marcus 1984), the Eastern Pacific species *Pleurobranchus digueti* was resurrected by Goodheart *et al*. (2015) based on molecular and morphological evidence. For anatomical descriptions see Goodheart *et al*. (2015). The species lives under rocks during the day and is nocturnally active.

Umbraculida Odhner, 1939

Description. Shell patelliform (limpet-like), external, well calcified; sculpture faint; periostracum brown, extending over shell margin; apex central to subcentral; shell covers entire animal. Body elongate; head with two enrolled rhinophores, two oral tentacles; velum between base of rhinophores, mouth; mantle cavity absent; gill bipinnate, on right side of body, between mantle, foot.

Remarks. Umbraculida was included with Pleurobranchida in the Notaspidea (Willan 1987) but it is now considered a group of Euopisthobranchia, which also includes Aplysiida, Runcinoidea, Pteropoda and Cephalaspidea (Jörger *et al.* 2010). There are only a handful of species worldwide. Two families were recognized by Willan (1987), Tylodinidae and Umbraculidae; only the first is represented in the northeast Pacific with two species.

Tylodinidae J. E. Gray, 1847
(Figure 5)

Description. Same as for Umbraculida.

Remarks. The animals live and feed on sponges, on which they are well camouflaged. Diversity is unremarkable.

***Anidolyta* Willan, 1987**
(Figure 5E–F)

Anidolyta Willan, 1987: 232. Type species (OD): *Tylodina duebeni* Lovén, 1846. North Atlantic.

Description. Shell external, patelliform; apex subcentral; periostracum rough, lamellate; muscle scar complete; animal not larger than shell.

***Anidolyta spongotheras* (Bertsch, 1980)**
(Figures 5E–F)

Roya spongotheras Bertsch, 1980: 233, figs 1–3. Holotype LACM 1916. Jervis Inlet, Vancouver Island, British Columbia, 25–100 m.

Description. Shell to 20 mm, patelliform, flat, whitish; periostracum rough, lamellate, extending over shell margin; apex subcentral; sculpture irregular, of undulating radial ribs; muscle scar oval. Live animal yellow green.

Distribution. Queen Charlotte Islands to Jervis Inlet, Vancouver Island, British Columbia; 25–350 m. Rare.

Remarks. The species feeds on sponges.

***Tylodina* Rafinesque, 1814**
(Figures 5A–D)

Tylodina Rafinesque, 1814: 162. Type species (M): *Tylodina punctulata* Rafinesque, 1814 [= *Tylodina perversa* (Gmelin, 1791)]. Mediterranean.

Joannisia Monterosato, 1884: 149. Type species (OD): *Tylodina citrina* Joannis, 1833 [= *Tylodina perversa* (Gmelin, 1791)]. Mediterranean.

Tylodinella Mazzarelli, 1897: 596–600. Type species (M): *Tylodinella trinchesii* Mazzarelli, 1897 [= *Tylodina perversa* (Gmelin, 1791)]. Mediterranean.

Description. Shell external, patelliform; apex subcentral; periostracum adherent, smooth; muscle scar incomplete; animal not larger than shell.

Remarks. The species feed on sponges on which they are very cryptic.

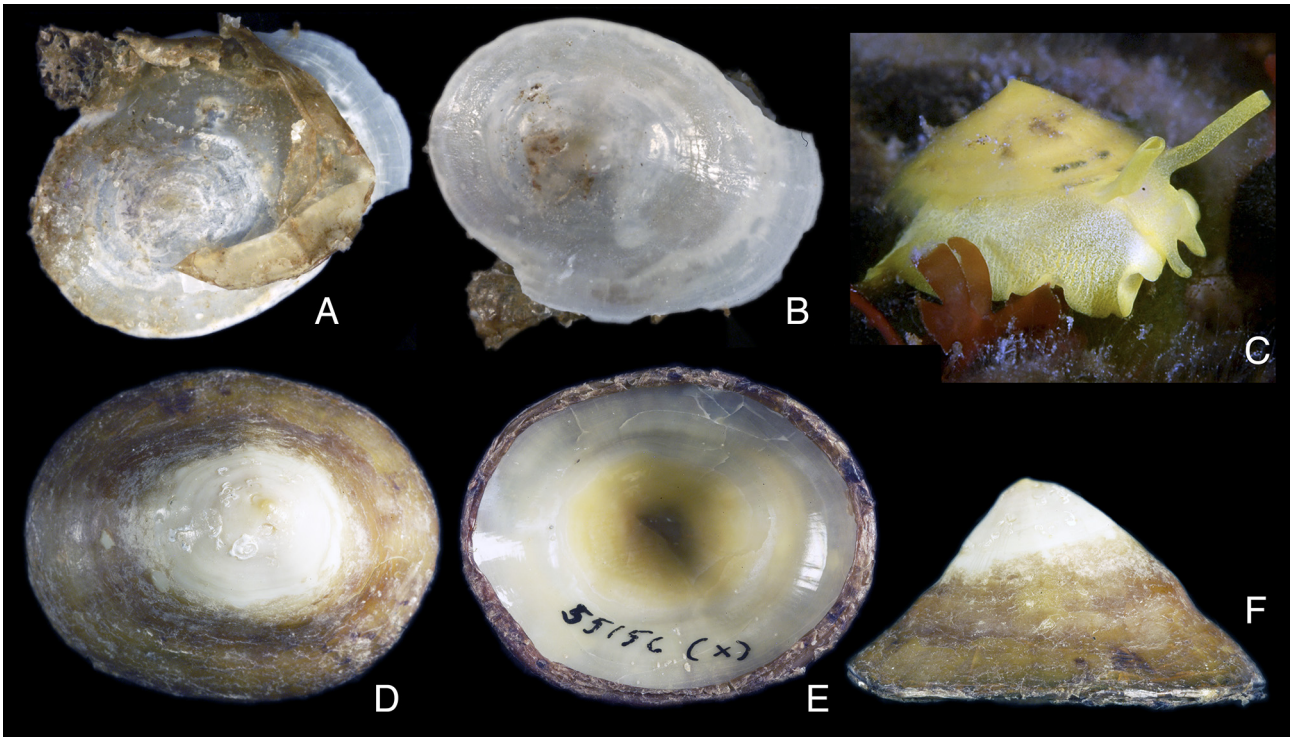

FIGURE 5. Tylodinidae. **A–B.** ***Anidolyta spongotheras*** (Bertsch, 1980), 7 mm (LACM 1916, holotype) Jervis Inlet, British Columbia (photos: Sabrina Medrano), (A) dorsal view, (B) ventral view. **C.** ***Tylodina fungina*** Gabb, 1865, live animal, California (photo: Kevin Lee). **D–F.** ***Tylodina fungina*** Gabb, 1865, 32 mm (LACM 55156), Laguna Beach, California (photos: Jenny McCarthy), (D) dorsal view, (E) ventral view, (F) lateral view.

Tylodina fungina **Gabb, 1865**
(Figures 5A–D)

Tylodina fungina Gabb, 1865: 188. Holotype UCMP 125553. Santa Barbara Island, California.

Description. Shell to 35 mm, patelliform, thin, elevate, yellow; periostracum thick, brown, extending over shell margin; apex subcentral; sculpture irregular, of undulating radial ribs; interior glossy, muscle scar horseshoe-shaped, opening at side of shell. Live animal bright yellow, matching yellow, orange sponges.

Distribution. Morro Bay, San Luis Obispo County, California to Banderas Bay, Jalisco, Mexico; low intertidal and subtidal. Uncommon.

Aplysiida Minichev & Starobogatov, 1975 (=Anaspidea, Aplysiomorpha)

Description. Shell fragile, internal, plate-like, or external, cylindrical to slightly bulloid. Live animal with pair of parapodia extending laterally, typically with pair of flattened oral tentacles, pair of dorsal grooved rhinophores; mantle cavity enclosed, with plicate gill and often ink glands.

Remarks. This monophyletic group includes sea hares and relatives. Aplysiids may have external or internal shells, or no shell at all. The parapodia are typically large, and in some cases can be used for

swimming, but in some groups are reduced and fused together. Sea hares are typically found in shallow waters in association with macroalgae or sea grasses. *Aplysia* is the most diverse genus with just over 30 species. Five species are represented in the northeast Pacific. Diversity is remarkable.

Akeridae Mazarelli, 1891
(Figure 6A–B)

Description. Shell external, fragile, translucent, cylindrical to slightly bulloid; spire flattened to elevated, protoconch partially embedded; aperture equal to length of spire or slightly shorter; periostracum thin forming flange at keel. Live animal unable to retract fully into shell, but can stretch over twice its length; body with posterior pallial tentacle; parapodia extending laterally, meeting mid-dorsally over shell.

Remarks. This family contains only one genus, *Akera* with a small number of species of worldwide distribution. Diversity is unremarkable.

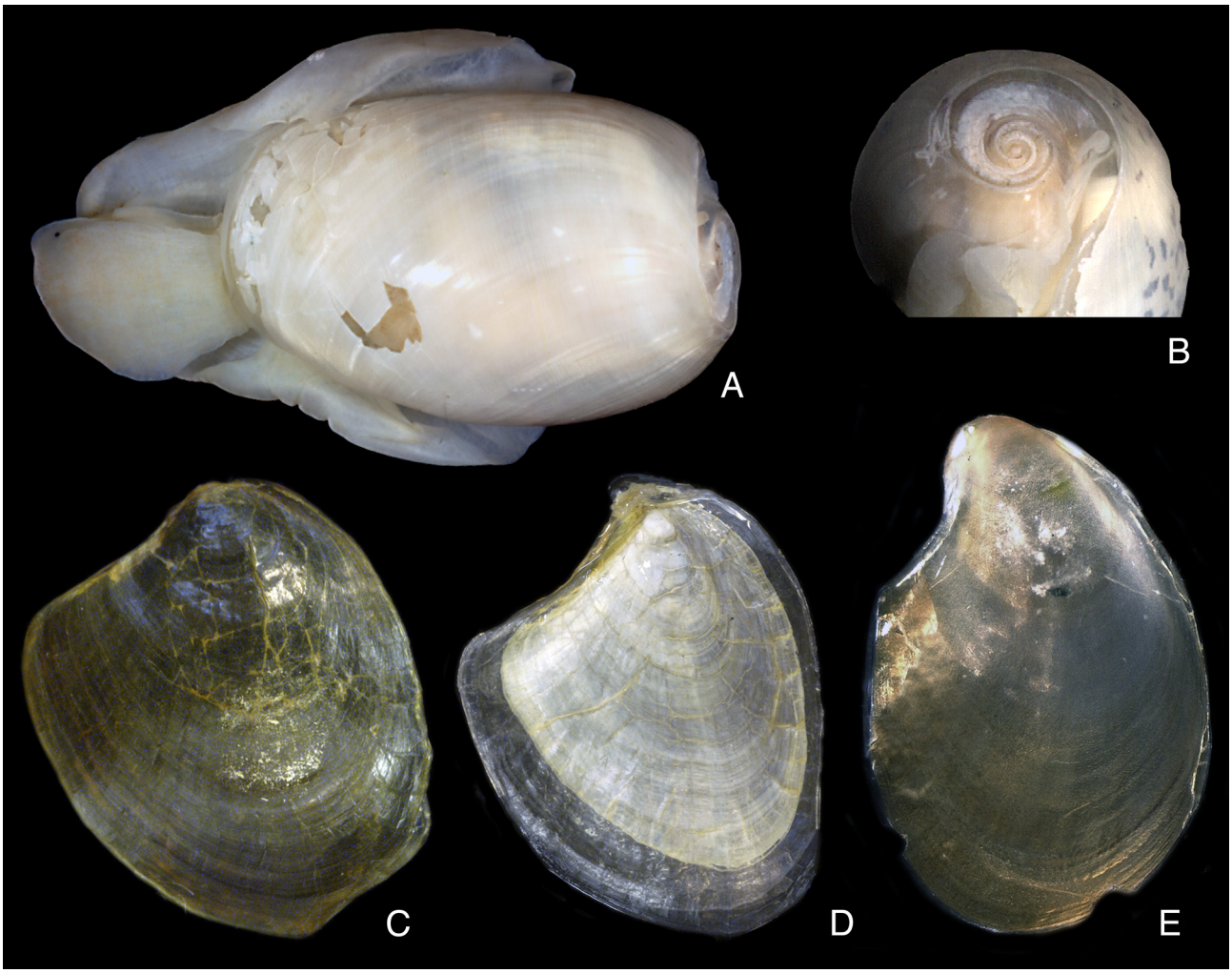

FIGURE 6. Akeridae and Aplysiidae. **A–B.** ***Akera julieae*** Valdés & Barwick, 2005, 10 mm (LACM 3033, holotype), Santa Catalina Island, California (photos: Kelvin Barwick), (A) dorsal view, (B) apical view. **C.** ***Aplysia vaccaria*** Winkler, 1955, 19 mm (LACM 1937-110.5) Dana Point, California (photo: Ángel Valdés). **D.** ***Aplysia californica*** (Cooper, 1863), 30 mm (LACM 178961) Puerto Refugio, Baja California (photo: Ángel Valdés). **E.** ***Aplysia* cf. *parvula*** Mörch, 1863, 4 mm (CPIC 01844) Belches Point, Baja California (photo: Ángel Valdés).

***Akera* Müller, 1776**
(Figure 6A–B)

Akera Müller, 1776: 242. Type species (M): *Akera bullata* Müller, 1776. Europe.

Description. Same as for Akeridae.

Remarks. Only one species represented in the northeast Pacific.

Akera julieae Valdés & Barwick, 2005

(Figure 6A–B)

Akera julieae Valdés & Barwick, 2005: 44, figs 1–4. Holotype LACM 3033. Off SW end Catalina Island, California, 41 m.

Description. Shell to 7 mm, bullomorph, fragile, well-calcified; whorls with peripheral keels, pattern of strong wrinkles, separated by deep, channeled suture; whorls attached to preceding one just below periphery; apical region flattened; aperture broad below, narrow above, extending into deep sinus along suture of upper lip; columella with thin callus; sculpture of numerous low, thin spiral ribs and axial growth lines; periostracum thin, brownish; protoconch smooth, ~200 µm. Live animal unknown.

Distribution. Santa Catalina Island, California, possibly to Costa Rica; 40 m. Rare.

Aplysiidae Lamarck, 1809

(Figures 6C–E, 7–8)

Description. Shell plate-like, internal; body smooth, typically large, with pair of oral tentacles, pair of dorsal rhinophores; parapodia large or reduced, free or fused.

Remarks. Members of Aplysiidae are herbivorous and feed on a variety of red, green or brown algae. Their color is diet-derived from algal pigments. They accumulate toxins from their diet for defense. Only the genera *Aplysia* and *Phyllaplysia* are represented in the northeast Pacific.

Aplysia Linnaeus, 1767

(Figures 6C–E, 7)

Aplysia Linnaeus, 1767: 1082. Type species (ICZN 1954: Opinion 200): *Aplysia depilans* Gmelin, 1791. Europe.
Neaplysia Cooper, 1863: 57. Type species (M): *Aplysia* (*Neaplysia*) *californica* Cooper, 1863. East Pacific.
Tullia Pruvot-Fol, 1933: 41–42. Type species (SD, Engel & Eales 1957: 85): *Aplysia juliana* Quoy & Gaimard, 1832 (1832–1833). Circumtropical.
Pruvotaplysia Engel & Hummelink, 1936: 15. Type species (OD): *Aplysia parvula* Mörch, 1863. Caribbean.
Varria Eales, 1960: 271–272. Type species (OD): *Aplysia dactylomela* Rang, 1828. Atlantic Ocean.

Description. Shell reduced, internal, plate-like, typically uncalcified; body oval, tall, large, with elongate head; rhinophores inrolled, elongate, dorsal; oral tentacles large, flat, with ruffled anterior edges; parapodia broad, mainly separate from each other.

Remarks. Species of *Aplysia* are voracious herbivores feeding on various macroalgae. Two common temperate species, *Aplysia californica* and *A. vaccaria* are found mainly intertidally and subtidally, respectively. *Aplysia* cf. *parvula* occurs occasionally in the area covered by this book during El Niño events.

Aplysia californica (Cooper, 1863)

(Figures 6D, 7A–D)

Pleurophyllidia californica Cooper, 1863: 57–58, fig. 14. Type material unknown; San Pedro, Los Angeles County, California.
Aplysia nettiae Winkler, 1959: 8–10, pl. 5. Holotype LACM 2013; Mouth of Topanga Canyon, Los Angeles County, California.

Description. Shell to 75 mm, typically to half that size, plate-like, convex; right side with deep posterior sinus; mainly membranous, partially calcified; color translucent brown, calcified portions white. Live animal to 750 mm, typically to half that size; body soft, flaccid; color highly variable, from greyish-green to dark brown or red (juveniles), some specimens with dark patches, whitish spots, and/or network of fine brown lines; head narrow, elongate; parapodia well-developed, thick, fused posteriorly, separate anteriorly.

Distribution. Yaquina Bay, Lincoln County, Oregon to Guaymas, Sonora, Mexico; records from Central America and Japan need verification; adults mainly intertidal, juveniles to 18 m. Common.

Remarks. This species is a generalist herbivore that feeds on a variety of macroalgae including *Laurencia*

pacifica, *Plocamium pacificum*, *Ceramium* spp. and *Ulva* spp.; the color of the animal depends on its diet. It congregates in large groups to reproduce, attracted by pheromones released by individuals laying eggs. It releases purple ink when disturbed. It is a model organism in neuroscience and commercially farmed for research purposes.

FIGURE 7. Aplysiidae. **A–D.** ***Aplysia californica*** (Cooper, 1863), California, (A) red juvenile (photo: Kevin Lee), (B) spotted juvenile (photo: Kevin Lee), (C) light spotted adult (photo: Kevin Lee), (D) dark spotted adult (photo: Ángel Valdés). **E.** ***Aplysia* cf. *parvula*** Mörch, 1863, Belches Point, Baja California (photo: Craig Hoover). **F.** ***Aplysia vaccaria*** Winkler, 1955, California (photo: Craig Hoover).

***Aplysia vaccaria* Winkler, 1955**
(Figures 6C, 7F)

Aplysia vaccaria Winkler, 1955: 5–7, pls. 2–3. Holotype LACM 2010; Point Fermin, San Pedro, Los Angeles County, California.

Description. Shell to 200 mm, typically to half that size, plate-like, convex, thick, brown; right side with shallow sinus; no distinct calcified region. Live animal to 1,000 mm, typically to half that size; body leathery, rigid; color uniform dark brown to black, sometimes with fine grey or white markings; head wide, short to elongate; oral tentacles flat, broad, sometimes outlined in red; parapodia narrow, thick, fused posteriorly, well separate anteriorly.

Distribution. Monterey Bay to the Gulf of California; typically subtidal. Common.

Remarks. It feeds primarily on the brown algae *Egregia* and does not produce purple ink.

***Aplysia* cf. *parvula* Guilding *in* Mörch, 1863**
(Figures 6E, 7E)

Aplysia parvula Guilding *in* Mörch, 1863: 22–23. Syntype NHMD 288589. St. Thomas and St. Vincent, US Virgin Islands.

Description. Shell to 15 mm, plate-like, elongate, convex, fragile, yellowish-grey; completely calcified. Live animal to 60 mm; body rounded with elongate, narrow head; parapodia large, fused posteriorly; color variable, typically reddish brown with opaque white dots; parapodia edged in black.

Distribution. San Clemente Island, California to the Galapagos Islands; intertidal to 20 m. Common. Records from California are related to El Niño events.

Remarks. *Aplysia parvula* was originally described from the Caribbean Sea. Subsequently it has been reported from tropical locations around the world and it is currently considered a pantropical species (Bebbington 1977). Unpublished molecular evidence suggests *A. parvula* is a species complex. The correct name for the Eastern Pacific populations remains to be determined. Several synonyms are listed in the literature but not included here since their actual identity remains unknown.

***Phyllaplysia* P. Fischer, 1872**
(Figure 8)

Phyllaplysia P. Fischer, 1872: 296. Type species (SD, Dall 1900: 91): *Phyllaplysia lafonti* P. Fischer, 1872. Mediterranean.

Description. Shell reduced, internal, plate-like, fragile, calcified; body oval, flattened, typically small, with undifferentiated head; rhinophores inrolled, short, dorsal; oral tentacles flat, elongate; parapodia greatly reduced, fused anteriorly, posteriorly.

Remarks. Species of *Phyllaplysia* occur mainly on sea grasses and less commonly macroalgae, feeding on epiphytic growth, mainly diatoms; they are typically very cryptic on their habitat. Only one species is represented in the northeast Pacific.

***Phyllaplysia taylori* Dall, 1900**
(Figure 8)

Phyllaplysia taylori Dall, 1900a: 91–92. Holotype USNM 107892. Near Nanaimo, Vancouver Island, British Columbia.
Phyllaplysia zostericola McCauley, 1960: 549–576, figs 1–6. Holotype CASIZ 020204. Mitchel Bay, San Juan County, Washington.

Description. Shell to 10 mm, flat, plate-like, calcified; nucleus near mid-length, eccentric; color translucent whitish. Live animal to 80 mm, typically to half that size; body elongate, narrow; color usually bright green, occasionally yellow-orange, with pattern of white longitudinal lines, outlined with black, transverse thin black lines, solid or broken in to rows of black dots; transverse lines more conspicuous in some specimens; parapodia reduced to small right flap between inhalant, exhalant openings.

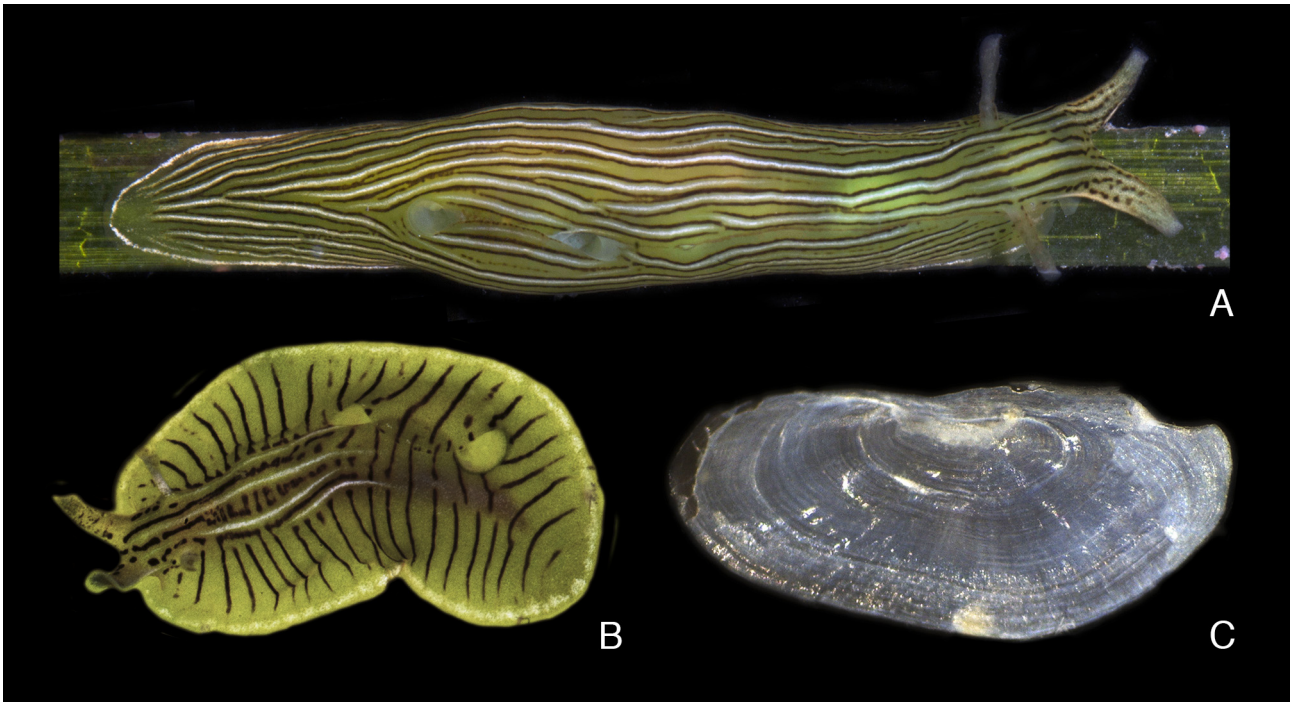

FIGURE 8. Aplysiidae, ***Phyllaplysia taylori*** Dall, 1900 (photos: Ángel Valdés). **A.** Long Beach, California (CPIC 00060). **B.** San Francisco Bay, California (CPIC 00412). **D.** 5 mm (CPIC 00060), Long Beach, California.

Distribution. Vancouver Island, British Columbia, to San Diego, California; 0–5 m. Locally common.

Remarks. Highly camouflaged on the sea grass *Zostera marina*, it increases crypsis by orienting its body lengthwise along the leaves; it feeds by grazing the film of organisms, mainly diatoms, off blades of *Zostera*, leaving a characteristic feeding scar on the leaves.

Cephalaspidea P. Fischer, 1883

Description. Shell external, internal, typically calcified, variable in shape. Head flattened, forming burrowing cephalic shield, with pair of antero-lateral Hancock's organs; mantle cavity typically enclosed, containing plicate gill; parapodia typically present; digestive system often with grinding gizzard, radula present or absent.

Remarks. Cephalaspidea in its original meaning (a group of opisthobranchs with a cephalic shield) was found to be paraphyletic (Mikkelsen 1996, Malaquias *et al*. 2009), but the name was redefined and maintained. The most recent classification scheme of Oskars *et al*. (2015) is followed here. Cephalaspideans are found worldwide from the intertidal to the deep sea, although they are most diverse in the shallow tropical Indo-Pacific. Most species inhabit soft bottoms of sand or mud, but several occur in close association with sea grass and algae and others in coral rubble and sponges. A single genus is known to inhabit exposed rocky shores. Species of Cephalaspidea feed preferentially upon diatoms, filamentous algae, foraminiferans, small bivalves, gastropods and polychaetes.

Diaphanidae Odhner, 1914 (1857)
(Figure 9)

Description. Shell variable, external, thin, operculate. Live animal can retract fully into shell; foot usually forked posteriorly; parapodia absent; radula usually with single lateral tooth; jaws, gizzard plates absent; penis armed.

Remarks. Diaphanidae is used here in the restricted sense of Oskars *et al*. (2015). Chaban (1996) reviewed the family in the northwest Pacific and Arctic oceans. Diaphanid snails are small (typically <5 mm),

found from the intertidal zone to abyssal depths (4,500 m) across all ocean basins from the Artic to the Antarctic (Ohnheiser & Malaquias 2014). Species live on soft substrates, algae, bryozoans, and hydroids, but their diet is unknown (Schiøtte 1998). Four species are known from the northeast Pacific; diversity is unremarkable.

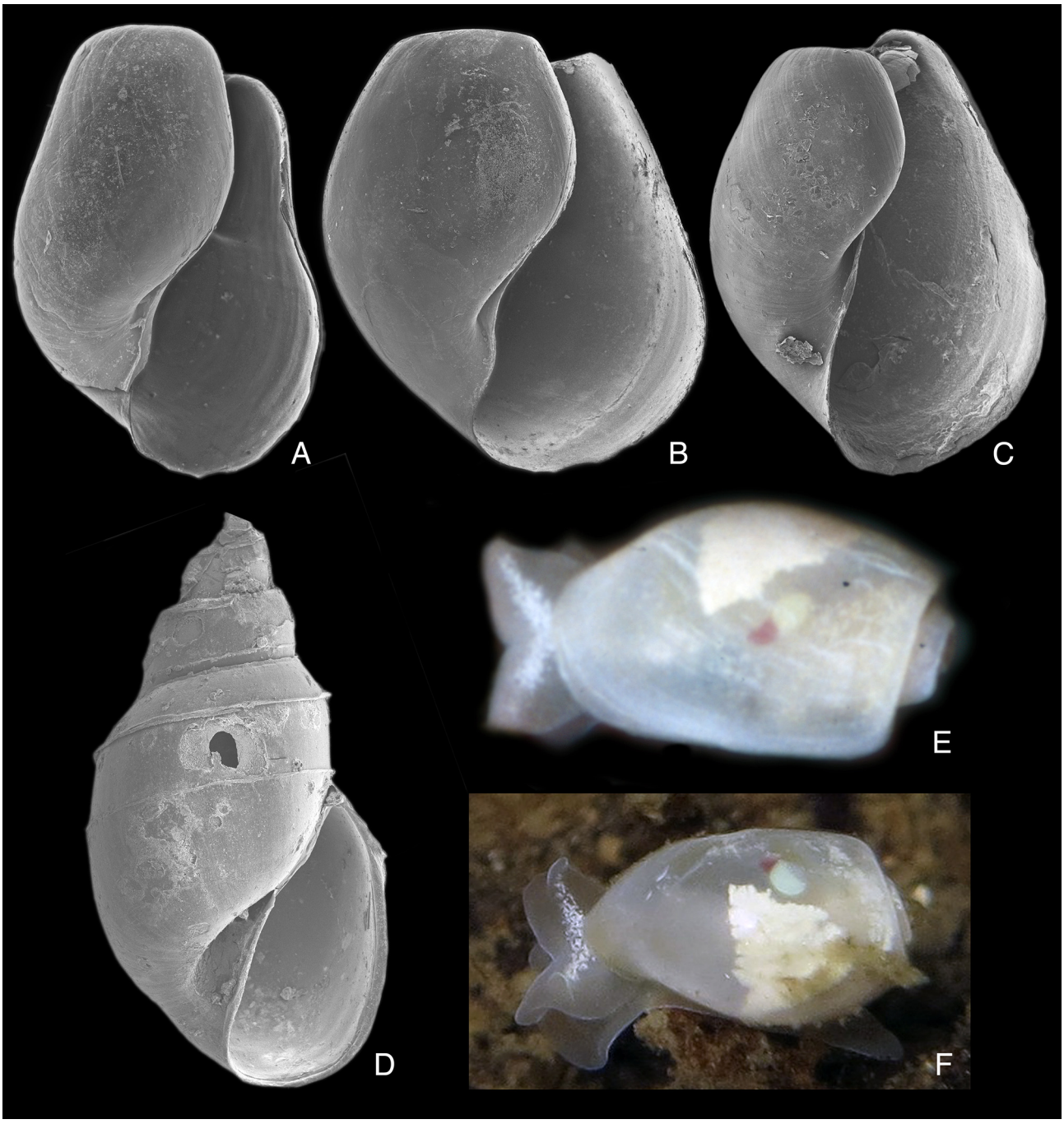

FIGURE 9. Diaphanidae. **A.** ***Diaphana californica*** Dall, 1919, 2.2 mm (LACM 67-60.37), San Martín Island, Baja California (image: Ángel Valdés). **B.** ***Diaphana minuta*** Brown, 1827, 2.9 mm (LACM 1990-190.5), Kodiak Island, Alaska (image: Ángel Valdés). **C.** ***Diaphana pacifica*** Schiøtte, 1998, 2.1 mm (LACM 2875), Santa Catalina Island, California (image: Ángel Valdés). **D.** ***Bogasonia jennyae*** n. sp., Holotype, 3.6 mm (LACM 3331), from Kuiu Island, Alaska (image: Ángel Valdés). **E–F.** ***Diaphana californica*** Dall, 1919, live animal, Washington (photo: Terry Gosliner) (E), live animal, Washington (photo: Karin Fletcher) (F).

Diaphana Brown, 1827
(Figure 9A–C, F)

Diaphana Brown, 1827: pl. 38, fig. 7. Type species (SD, Pilsbry 1895: 280 [1895–1896]): *Diaphana minuta* Brown, 1827. Great Britain.

Amphisphyra Lovén, 1846: 10–11. Type species (SD, Woodward 1870: 328): *Diaphana pellucida* Brown, 1827 (=*Diaphana minuta* Brown, 1827). Great Britain.

Physema H. & A. Adams, 1858 (1854–1858): 21. Type species (M): *Physema hiemalis* (Couthouy, 1839). North Atlantic.

Utriculopsis M. Sars, 1870: 65–67. Type species *Bulla vitrea* M. Sars, 1866 [= *Diaphana hiemalis* (Couthouy, 1839)]. North Atlantic.

Austrodiapahana Pilsbry, 1895 (1895–1896): 287. Type species (M): *Diaphana brazieri* Angas, 1877. West Pacific.

Description. Shell globose, external, thin, umbilicate; operculum present. Cephalic shield with triangular flaps; rhinophores simple; radula with bilobed rachidian teeth; lateral teeth arched with fine denticulation.

Remarks. Schiøtte (1998) and Ohnheiser & Malaquias (2014) reviewed the taxonomic status and diversity of *Diaphana*.

Diaphana californica Dall, 1919
(Figure 9A, F)

Diaphana californica Dall, 1919: 299. Lectotype (Schiøtte 1998) USNM 130561. Long Beach, Los Angeles County, California.

Description. Shell to 4.3 mm, pentagonal with bend on columella; umbilicus open; sculpture of thin growth lines; color uniformly translucent white to light brown. Live animal translucent white, with opaque white dots on cephalic shield; cephalic shield divided anteriorly; prostate with two unequal branches, about two whorls on thick branch, thickened at end.

Distribution. Kayostla Beach, Jefferson County, Washington, to the Coronados Islands, Baja California, Mexico; 0–353 m. Uncommon.

Remarks. This species is typically found in bays on algae, sand and in kelp holdfasts, but also offshore in deeper waters

Diaphana minuta Brown, 1827
(Figure 9B)

Diaphana minuta Brown, 1827: pl. 38, figs 7–8. Neotype RSM 1985033 (Schiøtte 1998). Loch Torridon, Scotland.

Diaphana brunnea Dall, 1919: 299. Holotype USNM 208718. Kodiak Island, Alaska.

Description. Shell to 5.8 mm, pentagonal with rounded shoulders. Live animal unknown; foot forked posteriorly; prostate with two branches, about three whorls on thick branch, not thickened at end.

Distribution. Arctic, North Atlantic and North Pacific to Japan and British Columbia, possibly to Cedros Island, Baja California, Mexico; 0–327 m. Uncommon.

Remarks. Chaban (1996) synonymized *Diaphana brunnea* with *D. minuta*. Schiøtte (1998) listed many more synonyms for *D. minuta* from Europe. Schiøtte (1998) suggested *D. minuta* and *D. californica* might interbreed because intermediate specimens occur in the area of overlap. Confusion with *D. californica* makes the range of *D. minuta* in the northeast Pacific uncertain

Diaphana pacifica Schiøtte, 1998
(Figure 9C)

Diaphana pacifica Schiøtte, 1998: 128, fig. 26. Holotype LACM 2875. Off Santa Catalina Island, California, 82 m.

Description. Shell to 2.5 mm, elongate, pentagonal; spire involute with rapidly enlarging whorls; upper lip with shallow notch at suture. Live animal unknown.

Distribution. Santa Catalina Island, California; 82 m. Rare

***Bogasonia* Warén, 1989**
(Figure 9D)

Bogasonia Warén, 1989: 20. Type species (OD): *Bogasonia volutoides* Warén, 1989. Iceland.

Description. Shell, external, fragile; spire elevate with several whorls; shell surface keeled. Live animal unknown, radula with unicuspid rachidian tooth; lateral teeth plate-like if present.

Remarks. The phylogenetic position of *Bogasonia* is unclear (Jensen 1996, Schiøtte 1998, Oskars *et al.* 2015). *Bogasonia* is here provisionally maintained in Diaphanidae

***Bogasonia jennyae* n. sp.**
(Figure 9D)

Type. Holotype LACM 3331 (LACM 87-393), 346 m, West of Point Croley, Southeast side of Kuiu Island, Sitka County, Alaska (56º06.00'N, 134º48.53'W), leg. Rae Baxter, R/V *Nore Dick*, 6 September 1987. Paratype LACM 3648 (LACM 86-306), 112 m, Agattu, Aleutian Islands, Alaska,1 specimen, leg. Rae Baxter.

Description. Shell to 3.8 mm, external, elongate, umbilicate; body whorl large, about 3/4 of shell length; spire elevate, with three whorls; columella slightly thickened; surface smooth except for two conspicuous spiral keels. Live animal unknown.

Distribution. Agattu to Kuiu Island, Alaska; 112–346 m. Rare.

Etymology. Named after Jenny McCarthy for her help photographing specimens and gathering specimen data for this chapter.

Remarks. The new species is similar to *Bogasonia gorjachevi* Chaban, 1998, from the Sea of Japan, but more elongate and umbilicate. It differs from *Bogasonia volutoides* Warén, 1989, from Iceland, by having a well-formed umbilicus, a shorter spire and a more round anterior end of the shell.

Cylichnidae H. & A. Adams, 1854 (1854–1858)
(Figures 10–12)

Description. Shell external, solid, variable in shape, typically elongate, involute, with apex concealed or umbilicated. Animal fully retractable into shell; radula with broad bilobed denticulate rachidian tooth, several curved lateral teeth, with denticulation along inner edge; jaws present, gizzard plates corneous, not calcified; male reproductive system with undivided tubular structure.

Remarks. The definition of Cylichnidae has changed substantially over time (see Malaquias *et al*. 2009, Oskars *et al*. 2015). In the current classification scheme, only *Cylichna* is found in the northeast Pacific.

***Cylichna* Lovén, 1846**
(Figures 10–11)

Cylichna Lovén, 1846: 10. Type species (SD, Herrmannsen 1846 [1846–1852]: 42): *Bulla cylindracea* Pennant, 1777. Northeast Atlantic.

?*Cylichnoides* Minichev, 1977: 432. Type species (OD): *Cylichna occulta* (Mighels in Mighels & C. B. Adams, 1842). Panboreal.

Description. Shell external, oval to subcylindrical; only one whorl visible, forming nearly entire shell, apex concealed or umbilicated; sculpture of spiral incisions; aperture as long as shell, narrow posteriorly, wider anteriorly. Live animal with large cephalic shield; parapodia reduced; radula with series of hamate, denticulate lateral teeth; rachidian teeth present; gizzard with three oval, corneous, not calcified, smooth plates; jaws present.

Remarks. For a complete synonymy see Valdés (2008). Minichev (1977) described the subgenus *Cylichnoides* for species of *Cylichna* with oval teleoconchs, lacking heterostrophic larval shells, and with differentiated penial sacs. Several authors maintained *Cylichnoides* as a valid genus for several boreal species such as *Cylichna occulta* (Mighels & C.B. Adams, 1842), *C. scalpta* (Reeve, 1855) and *C. densistriata* (Leche, 1878) (Martynov *et al*. 2006, Chaban & Martynov 2006, Gulbin & Chaban 2009, Nekhaev 2014).

Species of *Cylichna* are typically found on soft bottoms, from intertidal areas to abyssal depths. Four species occur in the northeast Pacific, excluding strictly Panamic and Arctic species. Diversity is remarkable.

***Cylichna alba* (Brown, 1827)**
(Figure 10A–C)

Volvaria alba Brown, 1827: 3, pl. 38, figs 43–44. Type material unknown, not found at MM. Greenock, U.K.

Description. Shell to 9 mm, solid, variable in shape, oval to subcylindrical, with nearly parallel sides; apex flat, anomphalous, with aperture lip rising from center; aperture as long as shell, wider anteriorly, narrowing abruptly at ~1/4 of length; columellar margin conspicuously thickened; umbilicus absent; sculpture absent; color white; columella opaque white. Live animal white; cephalic shield wider posteriorly, notched, with two large lobes.

Distribution. North Atlantic and Arctic Ocean; northeast Pacific from the Aleutian Islands and Bering Sea, Alaska to Boundary Bay, British Columbia; 20–350 m. Rare.

Remarks. Additional synonyms from north Atlantic localities were listed by Lemche (1948). This list includes *Cylichna nucleola* (Reeve, 1855), which was recognized as a valid species by Dall (1921) but is here regarded as a synonym of *Cylichna corticata* (Beck *in* Møller, 1842). Northeast Pacific shells of *C. alba* differ from North Atlantic shells here examined suggesting this species may need further splitting

***Cylichna corticata* (Beck *in* Møller, 1842)**
(Figures 10I–L, 11A)

Bulla corticata Beck *in* Møller, 1842: 79. Syntypes ZMUC GAS-23. West Greenland.
Bulla nucleola Reeve, 1855: 393, pl. 32, fig. 2. Syntype NHMUK 1890.1.23.6. Arctic Seas. H.M.S. *Assistance*.

Description. Shell to 14 mm, solid, cylindrical, variable in width, with nearly parallel sides; apex flat, anomphalous, with aperture lip rising slightly from center; aperture as long as shell, wider anteriorly, narrowing abruptly at ~1/5 of length; columellar margin slightly thickened; umbilicus absent; sculpture of spiral lines; color white, covered with thick reddish-brown or yellowish periostracum; columella opaque white. Live animal white; cephalic shield wider posteriorly with two indistinct lobes.

Distribution. North Atlantic and Arctic Ocean; North Pacific from the Bearing Sea to the Gulf of Alaska; intertidal to 455 m. Common.

Remarks. *Cylichna corticata* has been considered as a variety of *C. alba* (Brown, 1827) (see Lemche 1948), but according to Nekhaev (2014) it differs from the typical form by its larger size, the presence of a reddish or yellowish periostracum and thin but clearly visible spiral striation on the shell surface. Chaban (2004) also noted differences in the number of marginal teeth between these two species. In the Arctic Ocean *C. corticata* is a coastal species whereas *C. alba* usually does not occur in shallow waters (Nekhaev 2014).

***Cylichna attonsa* Carpenter, 1865**
(Figures 10D–E, 11B)

Cylichna (?*cylindracea* var.) *attonsa* Carpenter, 1865: 647. Holotype USNM 4495. Puget Sound, Washington.

Description. Shell to 16 mm, solid, cylindrical, very elongate, with nearly parallel sides; apical umbilicus partially or completely covered; aperture lip rising from center of apex; aperture as long as shell, wider anteriorly, narrowing gradually at ~1/5 of length; columellar margin thickened, with conspicuous callus; sometimes medially grooved; umbilicus small, sometimes covered by columellar callus; sculpture of irregular spiral lines more conspicuous, dark reddish brown near anterior, posterior ends of shell; color dirty white, covered with pale brown or yellowish periostracum, with reddish brown areas near anterior, posterior ends of shell; columella opaque white. Live animal white; cephalic shield wider posteriorly with lateral expansions.

Distribution. Kodiak Island, Alaska to the San Benito Islands, Baja California, Mexico; 20–150 m. Uncommon.

Remarks. Easily identifiable by its elongate shell and reddish-brown spiral lines

FIGURE 10. Cylichnidae (photos: Jenny McCarthy). **A–B.** ***Cylichna alba*** (Brown, 1827), 9 mm (LACM 72-256.20) Beaufort Sea, Alaska, (A) ventral view, (B) apical view. **C.** ***Cylichna alba*** (Brown, 1827), 4 mm (LACM 78-122.3) Prince William Sound, Alaska. **D–E.** ***Cylichna attonsa*** Carpenter, 1864, 12 mm (LACM 1964-75.5), Cape Foulweather, Oregon, (D) ventral view, (E) apical view. **F–G,** ***Cylichna diegensis*** (Dall, 1919), 9 mm (LACM 41-228.5), Seal Beach, California, (F) ventral view, (G) apical view. **H.** ***Cylichna diegensis*** (Dall, 1919), 8 mm (LACM 178904), Santa Catalina Island, California. **I–J.** ***Cylichna corticata*** (Beck *in* Møller, 1842), 13.5 mm (LACM 90-309.12), Chukchi Sea, Alaska, (I) ventral view, (J) apical view. **K–L.** ***Cylichna corticata*** (Beck *in* Møller, 1842), 13 mm (LACM 71-362.9), Beaufort Sea, Alaska, (K) ventral view, (L) apical view.

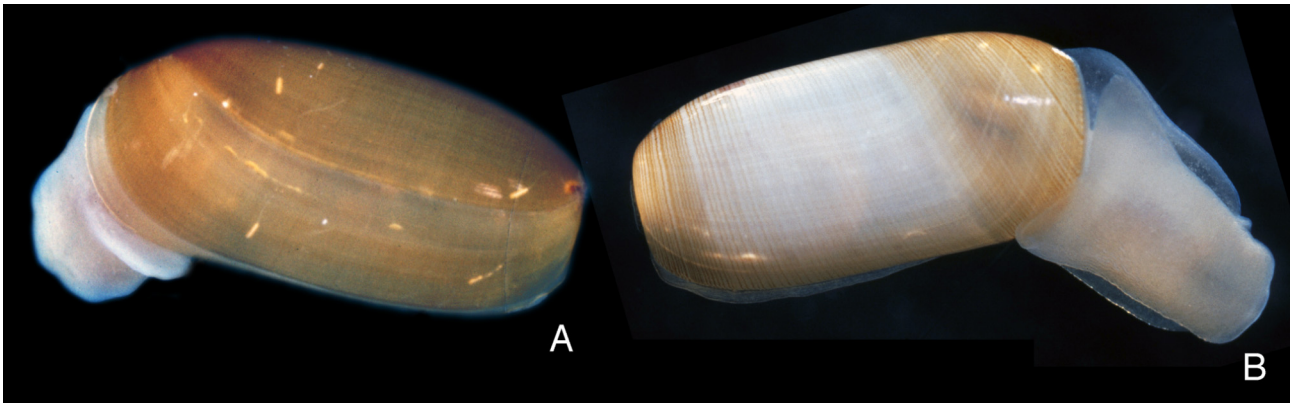

FIGURE 11. Cylichnidae. **A.** ***Cylichna corticata*** (Beck in Møller, 1842), British Columbia (photo: Ron Long). **B.** ***Cylichna attonsa*** Carpenter, 1864, California (photo: Gary McDonald).

Cylichna diegensis (Dall, 1919)

(Figures 10F–H)

Cylichnella (*Bullinella*) *diegensis* Dall, 1919: 300. Holotype USNM 209071. San Diego, California.

Description. Shell to 10 mm, solid, cylindrical, variable in length, with nearly parallel sides; apex umbilicate, with aperture lip rising from center; aperture as long as shell, wider anteriorly, narrowing abruptly at ~1/6 of length; columellar margin slightly thickened; umbilicus absent; sculpture of dark reddish brown spiral lines on anterior, posterior ends; color white, covered with thick reddish or yellowish periostracum; columella opaque white. Live animal unknown.

Distribution. Queen Charlotte Islands, British Columbia to Todos los Santos Bay, Baja California, Mexico; 37–353 m. Common in the southern portion of the range, where density can exceed 40/m^2 (D. Cadien, pers. comm.).

Remarks. *Cylichna diegensis* is clearly distinguishable from other northeast Pacific species by having brown spiral lines on the anterior and posterior ends of the shell and the apical area depressed and umbilicate.

Haminoeidae Pilsbry, 1895 (1895–1896)

(Figures 12–13)

Description. Shell typically thin, fragile, translucent; shell shape variable, from bulloid to cylindrical or elongate, with involute spire; spiral grooves either at anterior or posterior ends, covering entire shell, or absent. Live animals typically dull in color, but there are some colorful species; muscular buccal bulb with chitinous jaws; radula with variable rachidian tooth, hook-shaped lateral teeth; gizzard with three plates having pointed rods.

Remarks. Species in this family are found worldwide in both tropical and temperate waters. Most species feed on diatoms by shredding them with their gizzard plates, some feed on macroalgae. Four species are found in the northeast Pacific, one of them non-native.

Haminoea Turton & Kingston, 1830

(Figures 12A–H, 13)

Haminoea Turton & Kingston, 1830: 8. Type species (SD, J. E. Gray 1847: 161): *Bulla hydatis* Linnaeus, 1758. Northeast Atlantic and Mediterranean.

Description. Shell globose, fragile, thin, hyaline, truncated posteriorly; periostracum thin; aperture wider anteriorly, typically longer than involute spire; lip thin, sharp; columellar callus with varying levels of thickness; sculpture formed by growth lines, thin spiral striae. Live animals typically translucent with brown, grey, white mottling, some colorful species.

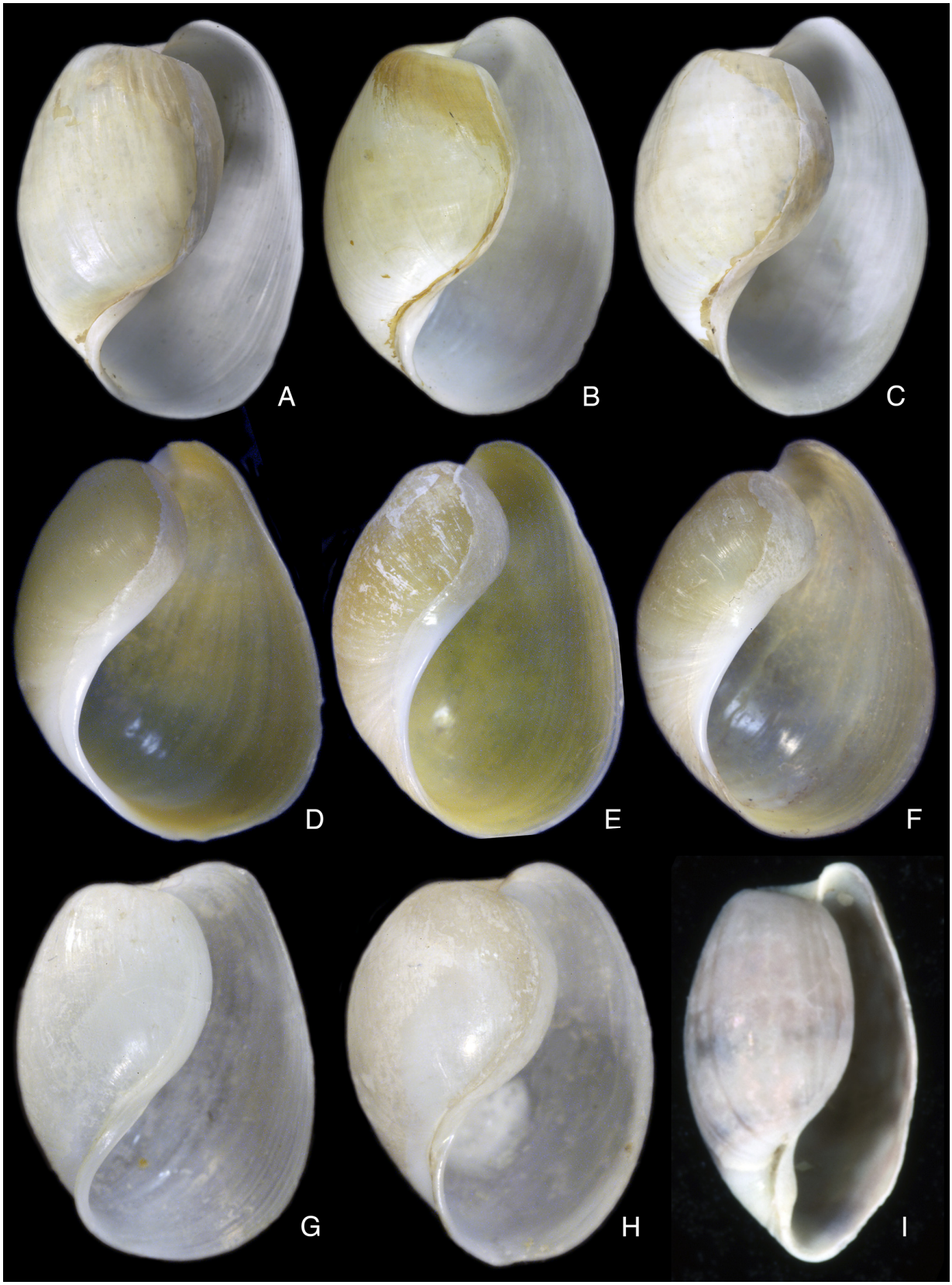

FIGURE 12. Haminoeidae (photos: Sabrina Medrano). **A–C.** ***Haminoea vesicula*** (Gould, 1855) (LACM 55147), San Pedro, California, (A) 22 mm, (B) 23 mm, (C) 23 mm. **D–F.** ***Haminoea virescens*** (Sowerby, 1833) (LACM 152916), Laguna Beach, California, (A) 13.5 mm, (B) 14 mm, (C) 15 mm. **G–H.** ***Haminoea japonica*** (Pilsbry, 1895) (LACM 178905), San Leandro, California, (A) 8 mm, (B) 9 mm. **I.** ***Aliculastrum exaratum*** (Carpenter, 1857) (LACM 179063), San Clemente Island, California, 2 mm.

***Haminoea vesicula* (Gould, 1855)**
(Figures 12A–C, 13C–D)

Bulla (*Haminea*) *vesicula* Gould, 1855: 26. Type material unknown; San Diego, California.
Haminoea olgae Dall,1919: 300. Holotype USNM 216812. Olga, San Juan County, Washington.
Haminoea angelensis Baker & Hanna, 1927: 129–130, pl. 4, fig. 1. Holotype CASIZ 32113. Los Ángeles Bay, Baja California, Mexico.

Description. Shell to 24 mm, fragile, globose, translucent white to beige or pale green; apical end relatively broad with aperture lip rising from center; aperture as long as shell, wider anteriorly, narrowing gradually at ~1/2 of length; columellar margin thickened, opaque white; sculpture of irregular growth lines. Live animal to 50 mm, elongate, translucent grey with opaque white mottling; viscera white with black, sometimes orange dots; cephalic shield lacking notch, with longitudinal central white stripe; eyes small, surrounded by pale grey area; short parapodia, covering anterior end of shell; posterior end of foot forming broad tail.

Distribution. Ketchikan, Alaska to Mazatlan, Sinaloa, Mexico; 0–10 m. Locally and seasonally common.

Remarks. This species is restricted to bays, where it probably feeds on *Ulva* and *Polysiphonia*. It is typically found on mud flats and floating structures.

***Haminoea virescens* (Sowerby, 1833)**
(Figures 12D–F, 13E)

Bulla virescens Sowerby, 1833 (1825–1834), pl. 39, fig. 2. Three possible syntypes (NHMUK 20150365). Pitcairn Islands [sic.] (see remarks).
Haminea cymbiformis Carpenter, 1857: 174. Holotype NHMUK 1857.6.4.793. Mazatlan.
Haminoea strongi Baker & Hanna, 1927: 130, pl. 4, fig. 2. Holotype CASIZ 032114. San Esteban Island, Baja California, Mexico.
Haminoea virescens var. *rosacea* Spicer, 1933: 53–54. Holotype unknown, paratypes (6) SDNHM 44067. San Diego, California.

Description. Shell to 24 mm, fragile, pyriform, yellowish to pale brown, semi-translucent; apical end narrow with aperture lip rising from center; aperture as long as shell, wider anteriorly, narrowing gradually at ~2/3 of length; columellar margin thickened, white; sculpture of irregular growth lines. Live animal to 45 mm, wide, short, brownish-green with opaque white mottling; viscera dark grey with large brown dots; cephalic shield lacking notch, with longitudinal central white stripe; eyes large, surrounded by broad pale grey area; short parapodia, covering anterior end of shell; posterior end of foot forming broad tail.

Distribution. Prince William Sound, Alaska to Mazatlán, Sinaloa, Mexico. Intertidal In rocky areas at low tide on the open coast, as well as in bays and lagoons. Occasionally common.

Remarks. The type locality of *H. virescens* was not indicated in the original description (Sowerby 1833 [1825–1834]). Reeve (1868) subsequently mentioned that this species was originally collected by Cuming in the Pitcairn Islands, as the label of the syntypes (NHMUK 20150365) indicates. However, Pilsbry (1933) commented that Cuming's localities were notoriously unreliable, and Tomlin (1934) examined the type series as well as additional specimens from California finding them identical. Therefore, it is likely that the label of the syntypes is incorrect and that the type series of *H. virescens* was originally collected in the northeast Pacific.

***Haminoea japonica* Pilsbry, 1895 [introduced species]**
(Figures 12G–H, 13A–B)

Haminea binotata var. *japonica* Pilsbry, 1895b: 185–186. Type material unknown. "Nemoto, Bishiu," Japan.
Haminoea callidegenita Gibson & Chia, 1989: 915, figs 1–2, 5, 8a. Holotype RBCM 988-00026-001. Spencer's Spit, Lopez Island, San Juan County, Washington.

Description. Shell to 20 mm, fragile, globose, variable in shape from oval to quadrangular; apical end relatively broad; color translucent white. Live animal to 40 mm, elongate, pale to dark greenish-grey with opaque white mottling, dark patches; viscera grey with black, conspicuous orange-red dots; cephalic shield

divided by deep notch; eyes small, surrounded by pale grey area; short parapodia, covering anterior end of shell; posterior end of foot forming broad tail.

Distribution. Native to Japan and Korea, broadly established in Europe and the Pacific coast of North America from British Columbia to San Francisco Bay, California, through oyster trade.

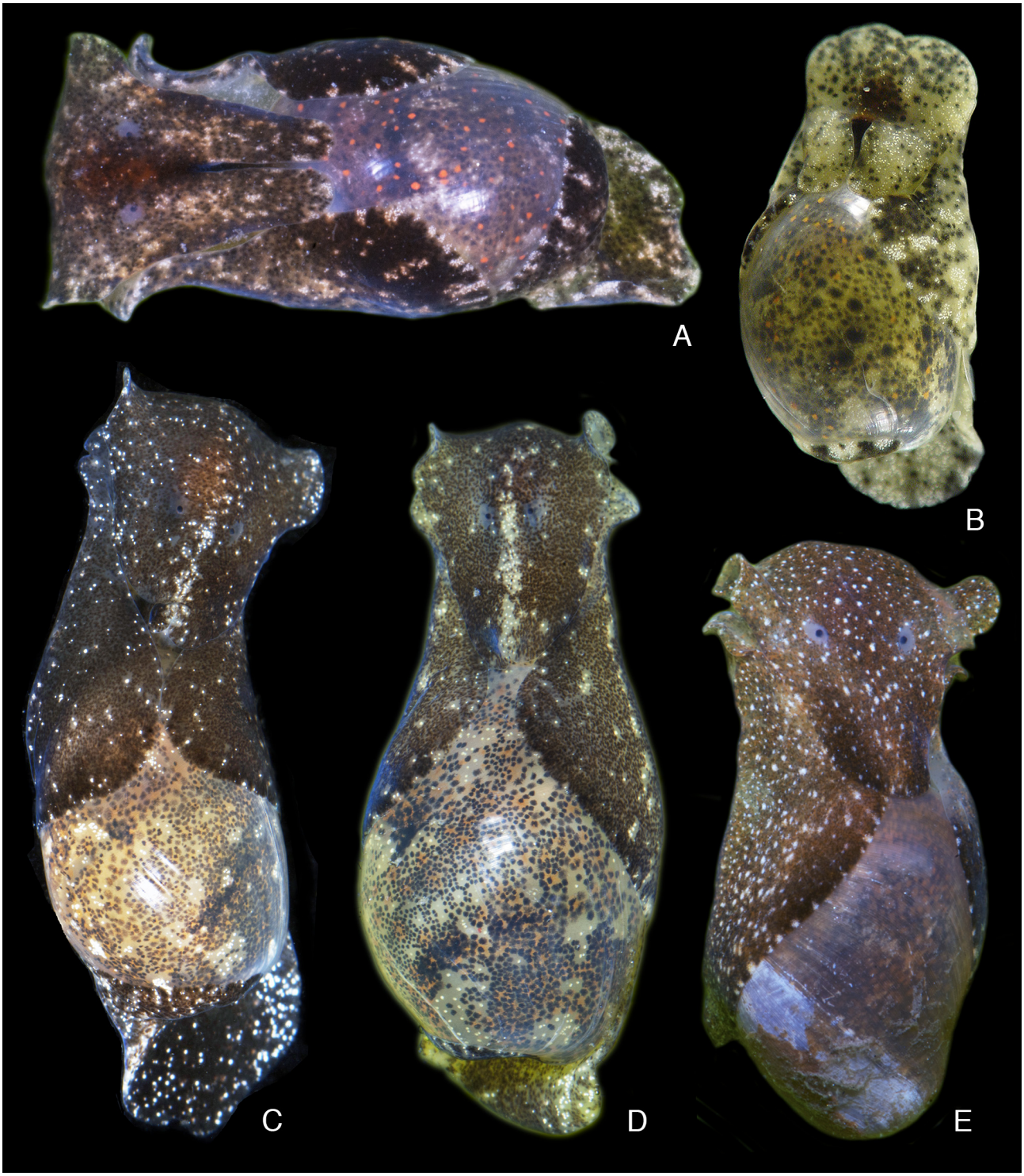

FIGURE 13. Haminoeidae. **A–B.** ***Haminoea japonica*** (Pilsbry, 1895), San Leandro, California (A) adult (photo: Ángel Valdés), (B) juvenile (photo: Leslie Harris). **C–D.** ***Haminoea vesicula*** (Gould, 1855), Long Beach, California (photos: Ángel Valdés). **E.** ***Haminoea virescens*** (Sowerby, 1833), Long Beach, California (photo: Ángel Valdés).

Remarks. The species is difficult to distinguish from *H. vesicula* based on shell characters or external morphology, except for the presence of a deep notch in the cephalic shield. For anatomical descriptions see Gosliner & Behrens (2006), for population genetics, vector, dispersal pathway and range see Hanson *et al*. (2013a, b).

***Aliculastrum* Pilsbry, 1896**
(Figure 12I)

Alicula Ehrenberg, 1831 [1828–1831]: page unnumbered [not Eichwald, 1830]. Type species (M): *Alicula cylindrica* Ehrenberg, 1831.
Aliculastrum Pilsbry, 1896 [1895–1896]: 237 [replacement name for *Alicula* Ehrenberg, 1831].

Description. Shell cylindrical, solid; columellar thickened; sculpture formed by spiral grooves on both ends of shell. Live animals typically translucent white with grey mottling; cephalic shield short, notched posteriorly.

Remarks. Too *et al*. (2014) proposed a new taxonomy for several genera of Haminoeidae and separated *Aliculastrum* from *Atys.* This is a mainly tropical genus, only one Panamic species treated here because the northernmost portion of the range includes southern California

***Aliculastrum exaratum* (Carpenter, 1857)**
(Figure 12I)

Bulla exarata Carpenter, 1857: 173. Holotype NHMUK 1857.6.4.791. Mazatlan, Sinaloa, Mexico.
Atys casta Carpenter, 1864: 314. Lectotype (Palmer 1958: 240) USNM 4014. San Lucas Cape, Baja California Sur, Mexico.
Atys chimera Baker & Hanna, 1927: 126, pl. 4, fig. 4. Holotype CASIZ 032115. Puerto Escondido, Baja California Sur, Mexico.
Cylichna veleronis Strong & Hertlein, 1939: 191. Holotype CASIZ 065663. Honda Bay, Panama.
Cylichna stephensae Strong & Hertlein, 1939: 190. Holotype CASIZ 065662. Honda Bay, Panama.
Atys liriope Hertlein & Strong, 1951: 71, pl. 8, fig. 2. Holotype CASIZ 06495. Arena Bank, Gulf of California, Mexico.

Description. Shell to 6 mm, solid, oval to elongate, uniformly whitish to pale gray; apical end rounded, depressed, not umbilicate; aperture lip conspicuously rising from left side forming short wing; aperture long, wide anteriorly, narrowing at ~1/3 of length; columellar margin slightly oblique, with thickened margin, lacking folds; umbilicus absent; sculpture of simple spiral grooves, more conspicuous and densely concentrated near anterior, posterior ends. Live animal unknown.

Distribution. Southern California to Panama, 0–90 m depth. Locally common.

Remarks. This species was considered a member of *Atys* Montfort, 1810 (Valdés & Camacho-García 2004) but it is here transferred to *Aliculastrum* Pilsbry, 1896, based on the revised taxonomy of Haminoeidae by Too *et al*. (2014).

Tornatinidae P. Fischer, 1883 (1880–1887)
(Figures 14–15)

Description. Shell external, high, white, thick cylindrical; typically smooth sometimes with fine axial lines; apex slightly projecting as moderate spire; protoconch conspicuously protruding on top of spire; bilobed denticulate rachidian teeth, large curved denticulated lateral teeth; gizzard plates calcified.

Remarks. Tornatinidae is considered distinct from Cylichnidae following Oskars *et al*. (2015: as Acteocinidae). Valdés (2008) summarized the history of the generic names; some uncertainties remain. There are six northeast Pacific species, most of them temperate; diversity is remarkable.

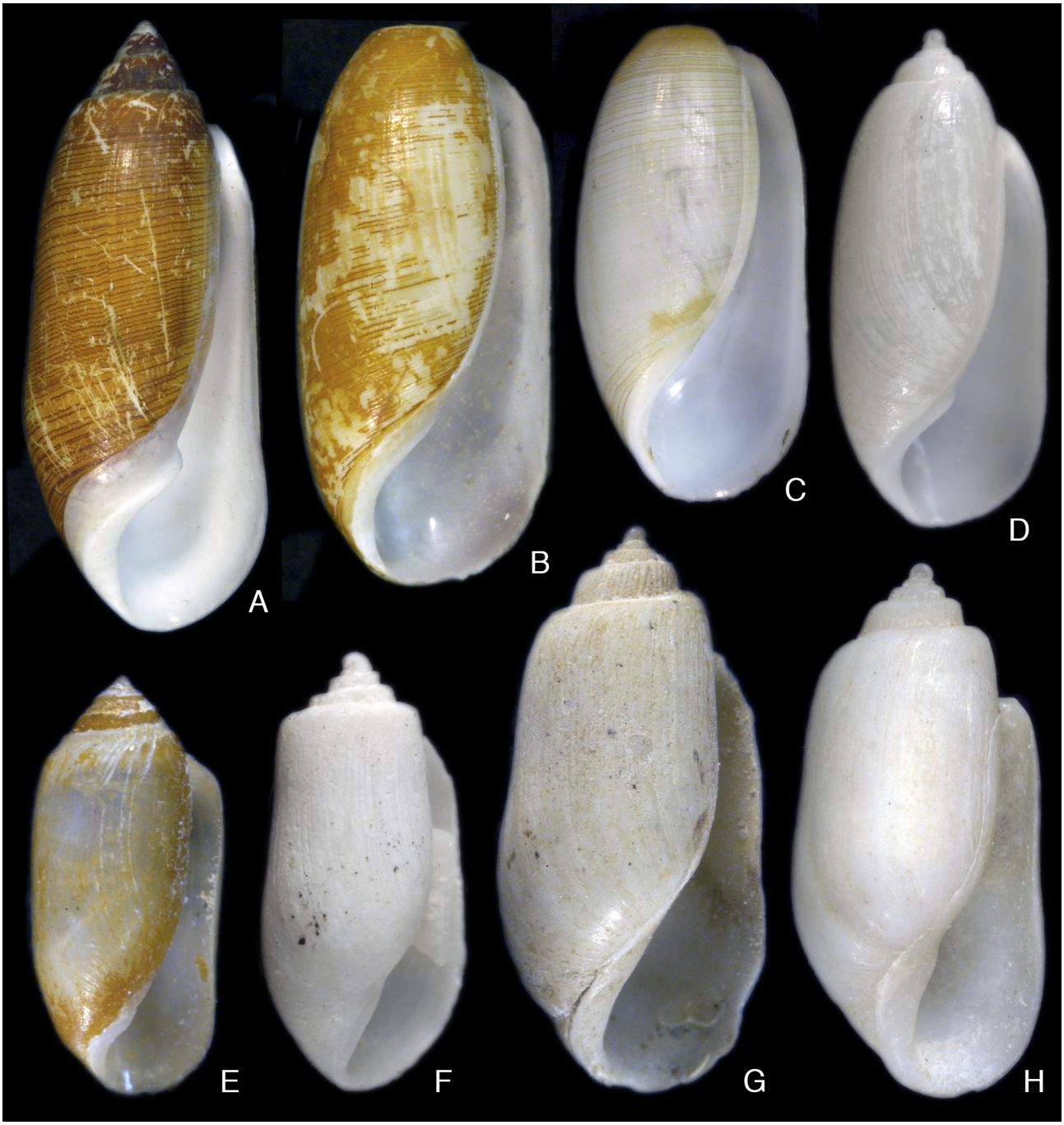

FIGURE 14. Tornatinidae. **A.** ***Acteocina culcitella*** (Gould, 1853), 20 mm (LACM 55148), Newport Beach, California (photo: Sabrina Medrano). **B.** ***Acteocina cerealis*** (Gould, 1853), 13.5 mm (LACM 60-23.37), Pacific Grove, California (photo: Sabrina Medrano). **C.** ***Acteocina cerealis*** (Gould, 1853), 12 mm (LACM 157833), Forrester Island, Alaska (photo: Sabrina Medrano). **D.** ***Acteocina infrequens*** (C. B. Adams, 1852), 5.5 mm (LACM 1971-151.55), Cedros Island, Baja California. **E.** ***Acteocina inculta*** (Gould, 1855), 4 mm (LACM 55151), San Pedro California (photo: Jenny McCarthy). **F.** ***Acteocina harpa*** (Dall, 1871), 5 mm (LACM 1933-150.13), San Miguel Island, California (photo: Jenny McCarthy). **G.** ***Acteocina harpa*** (Dall, 1871), 8 mm (LACM 157845), Forrester Island, Alaska (photo: Jenny McCarthy). **H.** ***Acteocina oldroydi*** Dall, 1925, 6.8 mm (LACM 178962), Graham Island, British Columbia.

Acteocina J. E. Gray, 1847
(Figures 14–15)

Acteocina J. E. Gray, 1847: 160. Type species (OD): *Acteon wetherelli* Lea, 1833 [= *Acteocina canaliculata* (Say, 1822)]. Pleistocene and Recent, western Atlantic and Caribbean.

Tornatina A. Adams, 1850: 554. Type species (SD, Cossmann 1895: 81) *Bulla voluta* Quoy & Gaimard, 1833 (1832–1833). Guam.

Utriculastra Thiele, 1925: 269. Type species (OD): *Volvaria canaliculata* Say, 1822. Caribbean.

?*Tornastra* Ev. Marcus, 1977a: 5. Type species (OD): *Bulla eximia* Baird, 1863 [= *Bulla cerealis* Gould, 1853]. Northeast Pacific.

Description. Shell external, solid, oval to elongate; aperture longitudinal, long, anteriorly rounded; spire typically short, conical, sometimes absent; columella thickened, often with anterior callus; operculum absent; protoconch flattened, attached to teleoconch by aperture. Live animal with large headshield, posterior end divided into two projecting lobes; radula with or without rachidian teeth, denticulate lateral tooth on each side of half-row; gizzard with three lobate plates.

Remarks. Two species treated here, *A. infrequens* and *A. inculta* (=*A. carinata*) are mainly Panamic but their ranges extend into the Californian region. The rest are temperate species endemic to the northeast Pacific. Animals are typically found in bays and estuaries on soft bottoms in association with green algae. Some species can be locally abundant.

Acteocina oldroydi Dall, 1925

(Figure 14H)

Acteocina oldroydi Dall, 1925: 25. Holotype USNM 333664. Departure Bay, British Columbia.

Description. Shell to 8.5 mm, white, solid, elongate, with nearly parallel sides; body whorl large occupying most of shell; spire short, with three whorls; shoulder rounded, slightly carinate; umbilicus absent; aperture shorter than body whorl, ~3/4 of shell length, narrow, wider anteriorly, narrowing sharply mid-length; columellar margin thickened, oblique, with an inconspicuous callus; surface smooth. Live animal unknown.

Distribution. Cook Inlet, Alaska to British Columbia; 22–24 m. Rare.

Remarks. *Acteocina oldroydi* was described based on an eroded specimen in which the sculpture and shell shoulders were not clearly visible. Examination of intact specimens revealed that in *A. oldroydi* the shoulder carination is not as sharply angulate and projecting as in *A. harpa* and, therefore, is here considered distinct.

Acteocina harpa (Dall, 1871)

(Figure 14F–G)

Tornatina harpa Dall, 1871: 136, pl. 15, fig. 11. Holotype USNM 56179. Monterey, California.

Description. Shell to 9 mm, white, solid, elongate, with nearly parallel sides; body whorl large occupying most of shell; spire short, with three whorls; shoulder angular, conspicuously carinate; umbilicus absent; aperture as long as body whorl, ~5/6 of shell length, narrow, wider anteriorly, narrowing sharply mid-length; columellar margin conspicuously thickened, oblique; sculpture with strong axial striations on upper half of whorl. Live animal unknown. Anatomy described by Gosliner (1996).

Distribution. Kenai, Alaska to Rocas Alijos, Mexico; 0–230 m. Common on sand gravel and mud.

Acteocina inculta (Gould, 1855)

(Figures 14E, 15C–D)

Bulla (*Tornatina*) *inculta* Gould, 1855: 26. Type material unknown. San Diego, California.

Tornatina carinata Carpenter, 1857: 171. Syntypes (5) NHMUK 1857.6.4.784. Mazatlan, Sinaloa, Mexico.

Acteocina smirna Dall, 1919: 296. Holotype USNM 271492. San Diego, California.

Description. Shell to 4.5 mm, white, solid, elongate, with nearly parallel sides; body whorl large occupying most of shell; spire short, with three whorls; shoulder rounded to angulate; umbilicus absent; aperture as long as body whorl, ~5/6 of shell length, narrow, wider anteriorly, narrowing gradually mid-length; columellar margin thickened, oblique, with an inconspicuous callus; sculpture with faint axial lines, some specimens with stronger axial indentations just below shoulder. Live animal white; cephalic shield deeply split posteriorly; parapodia small.

Distribution. Morro Bay, San Luis Obispo County, California to northern Peru; 0–30 m. Common on mudflats in bays and lagoons, also offshore

Remarks. The above synonymy is introduced here. This species varies from specimens with a rounded to angulate shoulder, some showing short axial indentations just below the shoulder, but not extending across the body whorl as in *A. harpa*. It had been assumed that *A. inculta* was the Californian species and *A. carinata* the Panamic species, but distribution is continuous throughout the range and distinctions cannot be made, although northern specimens are larger.

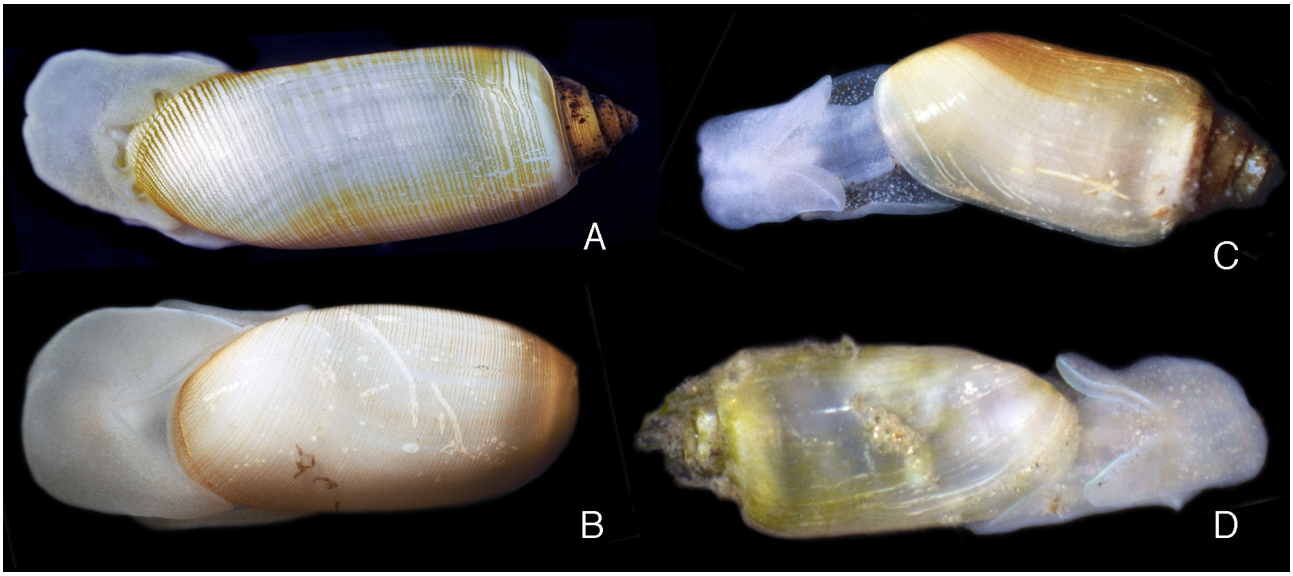

FIGURE 15. Tornatinidae. **A.** ***Acteocina culcitella*** (Gould, 1853), California (photo: Gary McDonald). **B.** ***Acteocina cerealis*** (Gould, 1853) Monterey, California (photo: Gary McDonald). **C–D.** ***Acteocina inculta*** (Gould, 1855), (C) Morro Bay, California (photo: Gary McDonald). (D) Anaheim Bay, California (photo: Ángel Valdés).

Acteocina culcitella **(Gould, 1853)**

(Figure 14A, 15A)

Bulla (*Akera*) *culcitella* Gould, 1853: 375, pl. 14, fig. 2. Type material unknown. Santa Barbara, California.

Tornatina tumida T. S. Oldroyd, 1921: 116, pl. 5, fig. 8. Type material unknown, not in CASIZ; San Pedro, California, Pleistocene.

Acteocina pedroensis T. S. Oldroyd, 1925: 23, pl. 2, fig. 9. Holotype USNM 352346. San Pedro, Los Angeles County, California, Pleistocene.

Utriculastra (*Tornastra*) *rolleri* Ev. Marcus, 1977a: 29, fig. 82–84. Holotype LACM 1774. San Diego, California.

Description. Shell to 22 mm, often to half that size; shell whitish, with brown periostracum showing numerous dark spiral lines corresponding to spiral striae of shell; shell solid, elongate, wider anteriorly; body whorl large occupying most of shell; spire relatively high, with three whorls, suture channeled; shoulder subangulate; umbilicus absent; aperture as long as body whorl, ~6/7 of shell length, narrow, wider anteriorly, narrowing sharply near anterior end; columellar margin thickened, oblique, with prominent callus. Live animal white; cephalic shield split posteriorly; parapodia small.

Distribution. Kodiak Island, Alaska to San Ignacio Lagoon, Baja California Sur, Mexico; 0–70 m. Sporadically common in bays and lagoons, on sand and mud.

Remarks. *Tornatina tumida* and *A. pedroensis*, both characterized by having a strong callus on the columella and a relatively high spire are synonymized with *A. culcitella*. The species is often included in *Tornastra*, further research is necessary to determine the validity of this genus. See Shonman & Nybakken (1978) for feeding behavior.

***Acteocina cerealis* (Gould, 1853)**
(Figures 14B–C, 15B)

Bulla (*Tornatina*) *cerealis* Gould, 1853: 378, pl. 14, fig. 9. Type material unknown. Santa Barbara, California.
Cylichna planata Carpenter, 1864: 647. Holotype UCMP 33501. Cenozoic, San Diego, California.
Tornatina eximia Baird, 1863: 67–68. Syntypes (5) NHMUK 1860.3.21.44/1–5; (4) NHMUK 1860.3.21.44/6–9. Esquimalt Harbour, Vancouver Island, British Columbia.
Acteocina culcitella intermedia Willett, 1928: 37. Holotype LACM 1015. Santa Catalina Island, California.

Description. Shell to 14 mm, whitish, with brown periostracum showing numerous dark spiral lines corresponding to spiral striae of shell; shell solid, elongate, with near parallel sides; body whorl occupying entire shell length; spire low, almost flat; shoulder rounded; umbilicus absent; aperture almost as long as body whorl, narrow, wider anteriorly, narrowing sharply near anterior end; columellar margin thickened, oblique, callus inconspicuous. Live animal white; cephalic shield shallowly split posteriorly; parapodia small; foot wide.

Distribution. Gulf of Alaska to central Baja California, Mexico; 20–250 m. Locally common.

Remarks. This species is recognized in the northeast Pacific literature as *A. cerealis* (see Behrens 1991) or *A. eximia* (see Gosliner 1996). Ev. Marcus (1977a) treated both *A. cerealis* and *A. eximia* as separate species, but for *A. cerealis* incorrectly illustrated a shell with a columellar fold like that of *A. culcitella*. Although Gould's type of *A. cerealis* has not been located, the original figure is well drawn and clearly represents an immature specimen of this species, showing the low spire, inflated body whorl, and weak callus on the columella. The species is often included in *Tornastra*. Typically offshore, but reported on intertidal flats in Bodega Harbor, Sonoma County, California.

***Acteocina infrequens* (C. B. Adams, 1852)**
(Figure 14D)

Bulla (*Tornatina*) *infrequens* C. B. Adams, 1852: 520. Lectotype (Turner 1956: 57) MCZ 186451. Panama.
Acteocina magdalenensis Dall, 1919: 296. Holotype USNM 218410. Magdalena Bay, Baja California, Mexico.
Acteocina angustior Baker & Hanna, 1927: 124, pl. 4, fig. 5. Holotype CASIZ 032116. Puerto Escondido, Baja California, Mexico.
Acteocina anomala Willett, 1945: 28 Holotype LACM(IP) 1082. Salton Sink, Imperial and Riverside counties, California, Mio-Pliocene or possibly Pleistocene extension of the Gulf of California.

Description. Shell to 9 mm, white, solid, elongate, with nearly parallel sides; body whorl large occupying most of shell; spire short, with two whorls; shoulder angulate; umbilicus absent; aperture shorter than body whorl, ~4/5 of shell length, narrow, wider anteriorly, narrowing gradually mid-length; columellar margin thickened, oblique, callus inconspicuous; sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Live animal unknown.

Distribution. Southern California to Santa Cruz Island, Galapagos Islands. Rare.

Remarks. Valdés & Camacho-García (2004) described the radula and gizzard plates. This species lacks rachidian teeth, thus if *Tornastra* is eventually found to be monophyletic, *A. infrequens* should be placed in *Tornastra*.

Bullidae Gray, 1827
(Figures 16–17)

Description. Shell ovoid, solid, mottled in drab colors; spire involute; aperture slightly longer than shell. Animal fully retractable into shell; cephalic shield produced antero-laterally, forming pair of siphon-like tentacles; gizzard contains uncalcified plates with longitudinal keels; radula with broad, denticulate rachidian teeth; inner, outer later teeth distinct; penis invaginable.

Remarks. This family contains only one genus, *Bulla* with a worldwide distribution and a small number of species, mainly found in tropical areas. Only one northeast Pacific species.

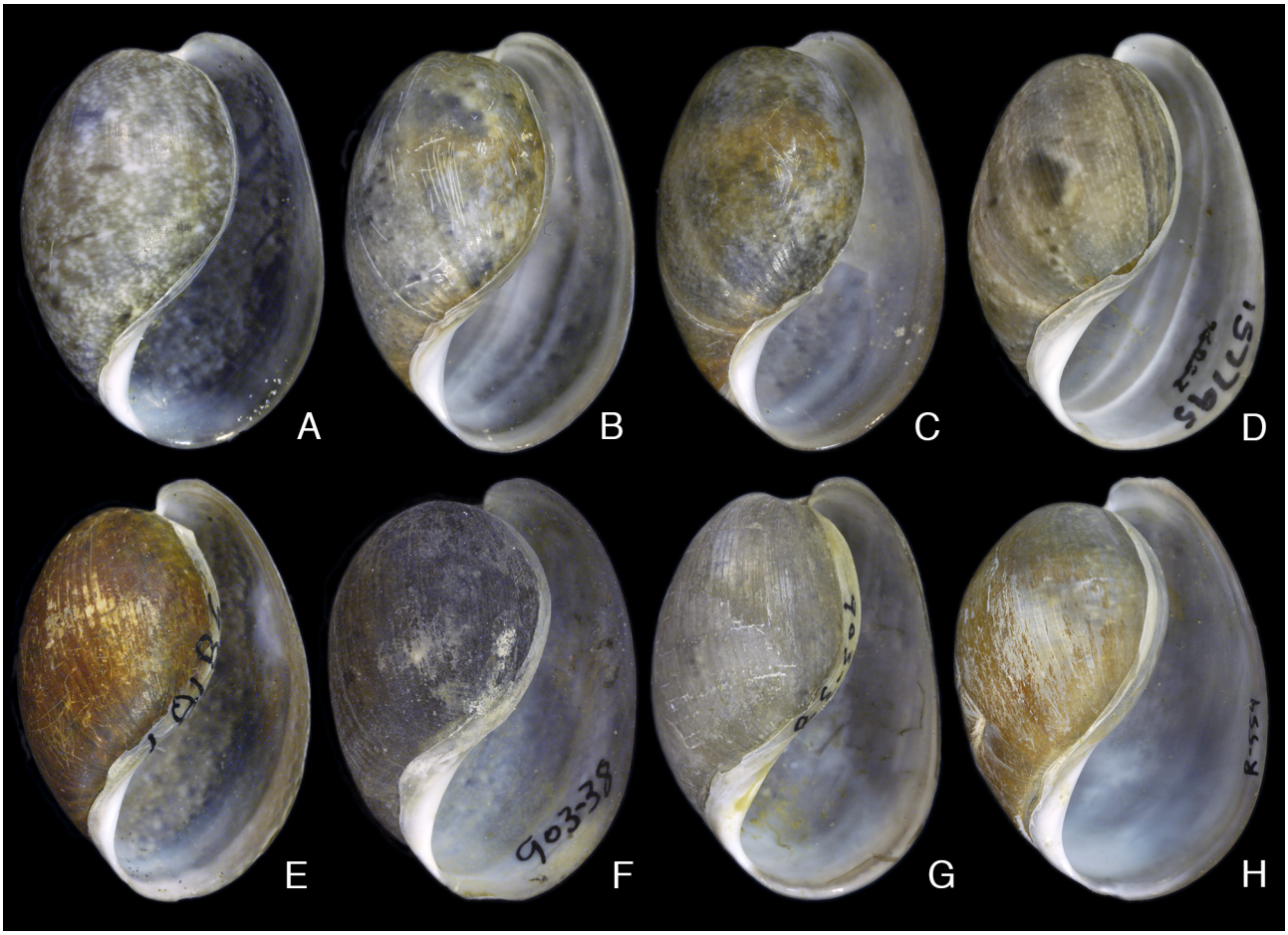

FIGURE 16. Bullidae (photos: Sabrina Medrano). **A–H.** ***Bulla gouldiana*** Pilsbry, 1895, shells, (A–C) (LACM 71-182.16), Puerto San Carlos, Baja California, (A) 22.5 mm, (B) 23 mm, (C) 23 mm, (D) 37 mm (LACM 157795), Ensenada, Baja California, (E) 23 mm (LACM 58187), San Pedro, California, (F) 36 mm (LACM 38-172.4), Anaheim Slough, California, (G) 40 mm (LACM 38-172.4), Anaheim Slough, California, (H) 42 mm (LACM 178906), Newport Bay, California.

Bulla **Linnaeus, 1758**
(Figures 16–17)

Bulla Linnaeus, 1758: 725. Type species (ICZN 1954: Opinion 196): *Bulla ampulla* Linnaeus, 1758. Indo-Pacific.

Description. Same as for Bullidae.

Remarks. *Bulla* was reviewed by Malaquias & Reid (2008) from which the diagnosis was extracted. Species of *Bulla* can be seasonally common on intertidal mudflats and tide-pools, down to 70 m depth. They are best known from their distinctive shells that are frequently washed ashore.

Bulla gouldiana **Pilsbry, 1895**
(Figures 16–17)

Bulla nebulosa Gould *in* A. Adams, 1850: 578, pl. 123, figs 79–80 [not Schröter, 1804]. Neotype NHMUK 20050360. Guaymas, Sonora, Mexico.

Bulla gouldiana Pilsbry, 1895 (1895–1896): 340 [replacement name for *Bulla nebulosa* Gould *in* A. Adams, 1850].

Bulla esteroensis Burch, 1945: 29, pl. 2, fig. 24. Holotype USNM 434054. Estero Todos Santos, Baja California, Mexico.

Description. Shell to 55 mm, ovoid, solid; aperture broadly rounded anteriorly, not flaring; color variable, pink-grey to brown, often with cloudy brown maculations bordered by white on side away from lip; columella

white, thickened. Live animal yellow or pinkish-brown, with numerous opaque white spots; anterior end of shell partially covered by two short parapodia; head with two elongate antero-lateral expansions, forming siphon-like tentacles.

Distribution. Morro Bay, San Luis Obispo County, California, to Mazatlán, Sinaloa, Mexico; 0–10 m. Common, in bays and lagoons at low tide, occasionally found in protected areas along more exposed coast.

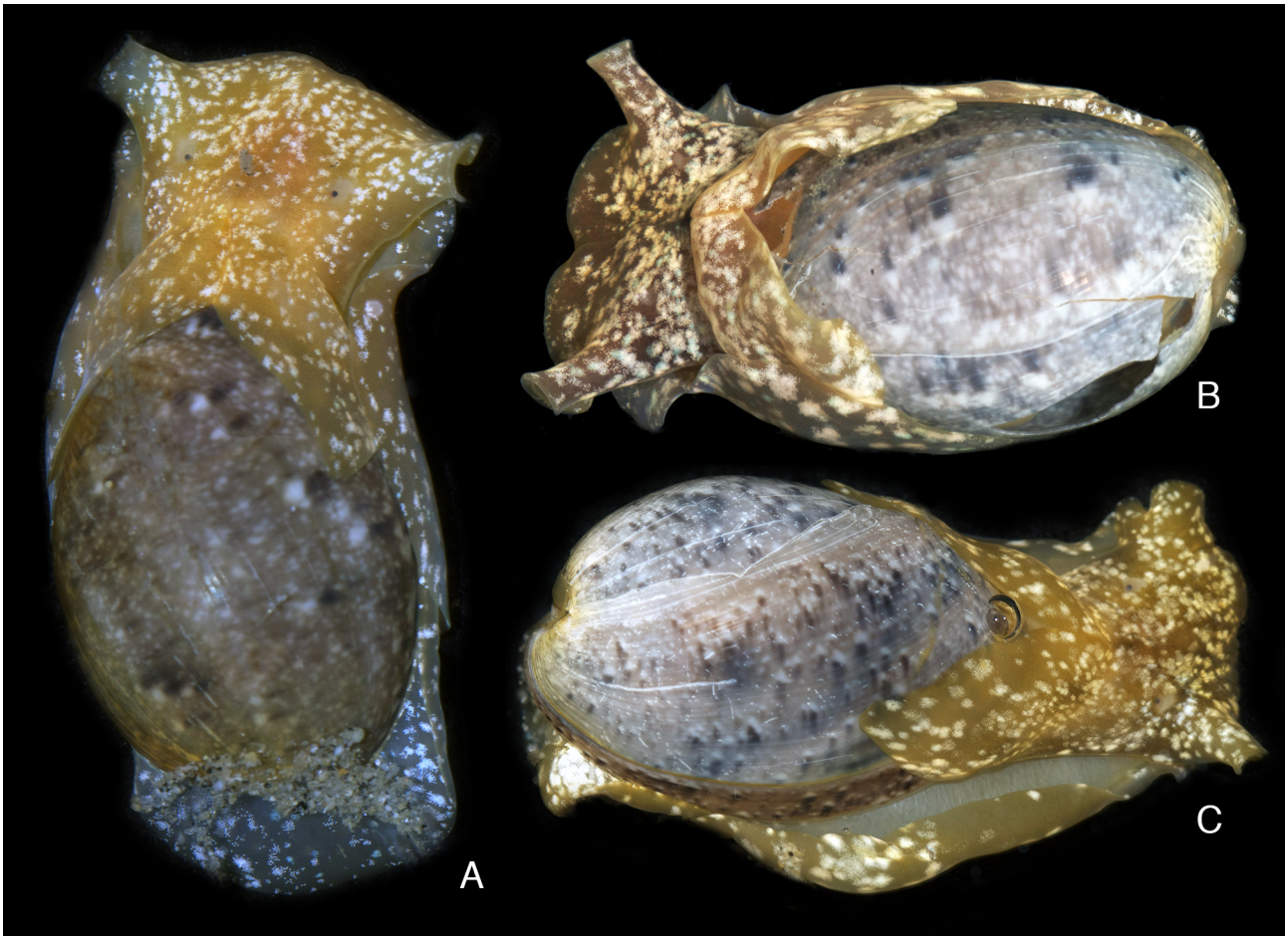

FIGURE 17. Bullidae. **A–C.** ***Bulla gouldiana*** Pilsbry, 1895 (photos: Ángel Valdés), live animals from Long Beach, California, (A) yellow specimen, (B) pinkish specimen, (C) juvenile.

Scaphandridae G. O. Sars, 1878
(Figure 18)

Description. Shell external, solid, typically pyriform, involute, with apex concealed or umbilicate. Animal not fully retractable into shell; radula with hamate lateral teeth; rachidian tooth present in some species; jaws absent, gizzard plates calcified.

Remarks. Previously considered a subfamily of Cylichnidae, molecular evidence (Malaquias *et al*. 2009, Oskars *et al*. 2015) places this group in its own family. Three northeast Pacific species, mainly deep-water. Diversity is unremarkable.

Cylichnium Dall, 1908
(Figure 18D)

Cylichnium Dall, 1908: 242. Type species (OD): *Utriculus domitus* Dall, 1889. Caribbean.
Volvulopsis Schepman, 1913: 463. Type species (OD): *Volvulopsis ancillarioides* Schepman, 1913. Indonesia.

Description. Shell external, solid, elongate, one whorl visible; aperture longitudinal, as long as shell,

anteriorly rounded; columella slightly thickened, often lacking folds; operculum absent. Live animals unknown; radula composed of simple, hamate lateral teeth, rachidian teeth absent; reproductive system monaulic, with complex female copulatory organ; penis unarmed.

Remarks. The taxonomic status of *Cylichnium* was reviewed by Valdés (2008) and the Eastern Pacific species by Valdés & McLean (2015).

FIGURE 18. Scaphandridae. **A–B.** ***Scaphander interruptus*** Dall, 1890, (A) 22 mm (LACM 73-109.5), Costa Rica (photo: Jenny McCarthy), (B) 19 mm (LACM 74-18.4), Peru (photo: Jenny McCarthy). **C.** ***Scaphander willetti*** Dall, 1919, 12 mm (USNM 216405), Forrester Island, Alaska (photo: USNM). **D.** ***Cylichnium cylindrellum*** (Dall, 1908), 33 mm (LACM 95-126.3), Santa Barbara, California (photo: Jenny McCarthy).

Cylichnium cylindrellum (Dall, 1908)

(Figure 18D)

Scaphander cylindrellus Dall, 1908: 239, pl. 8, fig. 1. Holotype USNM 110563. Peru, 5,200 m.

Description. Shell to 33 mm, somewhat cylindrical, with nearly parallel sides; aperture as long as shell, wider anteriorly, constricted posteriorly; apex sunken, convex; lip raising above apex in some specimens; sculpture with fine spiral grooves crossed by microscopic axial lines only present in the spiral grooves. Live animal unknown.

Distribution. Santa Barbara County, California to Peru; 3,600–5,200 m. Uncommon.

Scaphander Montfort, 1810

(Figures 18A–C)

Scaphander Montfort, 1810: 234. Type species (OD): *Bulla lignaria* Linnaeus, 1767. Northeast Atlantic.

Description. Shell external, solid, oblong, tapered posteriorly, with spire concealed by callus; surface with thin periostracum, microsculpture of spiral lines or series of pits; aperture as long as shell, narrow above, wider below.

Remarks. Species of *Scaphander* are typically found from the subtidal to below 4,000 m. They burrow into soft sediments aided by ciliary movement on the cephalic shield. Species of *Scaphander* are generalist bottom feeders, ingesting mud and sand with diatoms, foraminiferans, and small animals such as bivalves, small sea urchins, polychaetes, scaphopods, gastropods, and gastropod shells containing sipunculids.

***Scaphander interruptus* Dall, 1890**
(Figures 18A–B)

Scaphander interruptus Dall, 1890: 297, pl. 12, fig. 12. Syntypes USNM 97075. Chile, 1,920 m.

Description. Shell to 22 mm, involute, oval; aperture as long as shell, wider anteriorly, constricted posteriorly; lip rising slightly above apex; sculpture of spiral lines of oval pits, with alternating rows of wider, narrower pits. Live animal unknown.

Distribution. Point Arguello, Santa Barbara County, California, to Chile; 1,025–4,100 m. Uncommon.

***Scaphander willetti* Dall, 1919**
(Figure 18C)

Scaphaner willetti Dall, 1919: 299. Holotype USNM 216405. Forrester Island, Alaska.

Description. Shell to 12 mm, involute, oval, narrower posteriorly; aperture as long as shell, much wider anteriorly, constricted posteriorly; lip not rising above apex; sculpture of faint spiral lines of oval pits. Live animal unknown.

Distribution. Forrester Island, Alaska; depth not specified. Rare.

Remarks. Known only from the holotype. The specimen is broken in front.

Retusidae Thiele, 1926 (1925–1926)
(Figure 19)

Description. Shell oval to elongate, small, with some fine spiral sculpture; nucleus hyperstrophic (ultradextral), often concealed; columella smooth or with only weak folds; live animal able to withdraw completely into shell; radula absent; gizzard with three lobate plates.

Remarks. Species of Retusidae have been reported feeding on foraminiferans and juvenile hydrobiid gastropods. They are typically very small animals found from shallow estuaries to the deep sea. Four species are recognized in the northeast Pacific. Diversity is unremarkable.

***Retusa* Brown, 1827**
(Figure 19)

Retusa Brown, 1827: pl. 38, fig. 19. Type species (M): *Bulla obtusa* Montagu, 1803. Northeast Atlantic.
Coleophysis Fischer, 1883 (1880–1887): 555. Type species (M): *Bulla truncatula* Bruguière, 1792 (1789–1792). Northeast Atlantic and Mediterranean.
Cylichnina Monterosato, 1884: 143. Type species (SD, Crosse 1885: 141): *Cylichna laevisculpta* Granata-Grillo, 1877. Mediterranean.
Sulcularia Dall, 1921 [not Rafinesque, 1831]: 61, 202. Type species (M): *Retusa xystrum* Dall, 1919. San Diego, California.
Sulcoretusa Burch, 1945: 16 [replacement name for *Sulcularia* Dall, 1921].
Mamilloretusa Nordsieck, 1972: 36. Type species (OD) *Bulla mammillata* Philippi, 1836. Mediterranean.

Description. Shell external, fragile, with parallel or convex sides; spire visible or not; aperture longitudinal, narrow, anteriorly rounded; inner lip thickened; columella simple, with no folds; operculum absent. Live animal with large headshield, posterior end divided into two projecting lobes; radula absent; gizzard with three lobate plates.

Remarks. Gosliner (1996) noted that *Sulcoretusa* was based solely on conchological characters and synonymized it with *Retusa*. *Retusa montereyensis* and *R. xystrum* are often included in *Sulcoretusa*, but there is no evidence that species with marked spiral lines are monophyletic. *Cylichnina*, which was previously used for *Retusa umbilicata* was synonymized with *Retusa* by Thompson (1976). A revision of Retusidae is needed to clarify the genus-level taxonomy.

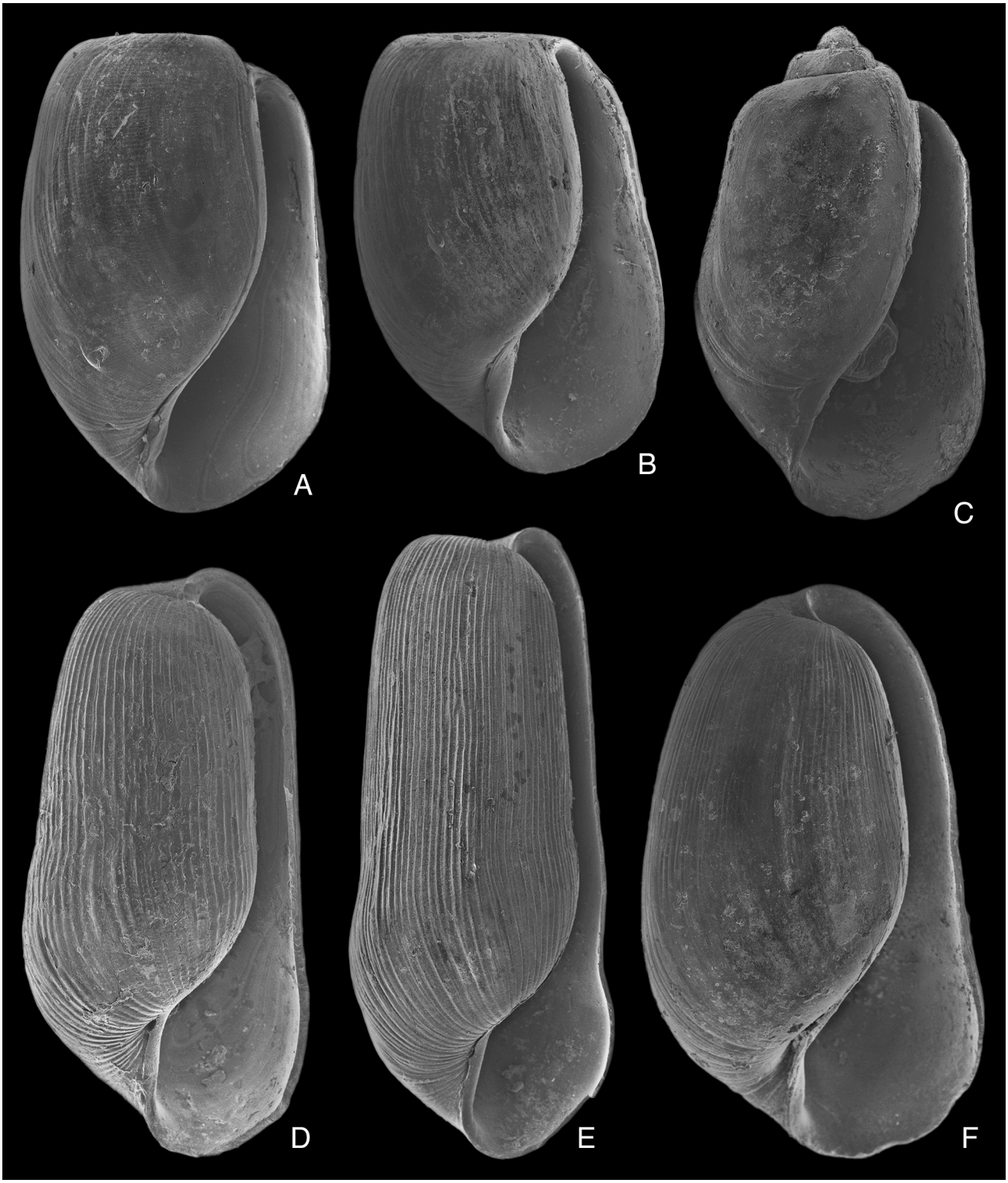

FIGURE 19. Retusidae (images: Ángel Valdés). **A–C.** ***Retusa obtusa*** (Montagu, 1803), (A) 2.2 mm (LACM 1967-138.1) Vancouver Island, British Columbia; (B) 3.1 mm (LACM 1957-12.77) Kasitsna Bay, Alaska; (C) 3.2 mm (LACM 1986-293.4) Amchitka Island, Alaska. **D,** ***Retusa montereyensis*** Smith & Gordon, 1948, 2.2 mm (LACM 1960-23.36) Pacific Grove, California. **E.** ***Retusa xystrum*** Dall, 1919, 3.6 m (LACM 1971-94.28) Cedros Island, Baja California. **F.** ***Retusa umbilicata*** (Montagu, 1803), 2.8 mm (LACM 1987-339.10) Dry Bay, Alaska.

***Retusa obtusa* (Montagu, 1803)**
(Figure 19A–C)

Bulla obtusa Montagu, 1803: 223–224, pl. 7, fig. 3. Syntypes (14) RAMM Moll4073-4087. Locality not mentioned in original description.

Description. Shell to 5 mm, fragile, oval, wider anteriorly, right side convex, left side slightly concave; protoconch partially visible; apex truncate or elevate; aperture slightly shorter than shell, wider anteriorly narrowing abruptly at about 1/2 of length; columellar margin thickened with rudimentary fold; umbilicus closed; sculpture of faint growth lines; color uniformly dirty white, often with thin, brown periostracum.

Distribution. Arctic Ocean to the Gulf of Alaska; intertidal to 360 m. Uncommon.

Remarks. Lemche (1948) noted that this broadly distributed Arctic species has forms with flat spires, such as *R. obtusa*, and others with protruding spires, such as *R. turrita* (Møller, 1842) and *R. pertenuis* (Mighels, 1843), and all possible intermediate forms. Lemche (1948) recognized only the species *R. obtusa*, placing *R. pertenuis* and other names not included here as synonyms or forms. The type series of *R. obtusa* (RAMM Moll4073-4087) includes a combination of forms with elevate spires and with flat apices. Similar variation occurs in specimens from the Bering and Chukchi Seas and, therefore, only *R. obtusa* is here recognized. However, certain populations seem to be consistent, thus it is likely that *R. obtusa* may constitute a species complex. The northeast Pacific forms illustrated here (Fig. 19C) may also constitute different species.

***Retusa montereyensis* Smith & Gordon, 1948**
(Figure 19D)

Retusa (*Sulcularia*) *montereyensis* Smith & Gordon, 1948: 217–218, pl. 3, fig. 11. Holotype CASIZ 065596. Monterey, California.

Description. Shell to 3 mm, fragile, elongate, wider anteriorly, narrower posteriorly; apex umbilicated, aperture lip forming rounded wing connected to columellar margin; aperture as long as shell, wider anteriorly, narrowing abruptly at about 1/4 of length; columellar margin slightly thickened; columella simple, with no folds; umbilicus closed; sculpture of strong, simple axial lines; color uniformly whitish.

Distribution, Monterey Bay, California; 15–46 m. Rare.

***Retusa xystrum* Dall, 1919**
(Figure 19E)

Retusa xystrum Dall, 1919: 297. Holotype USNM 273985. San Pedro, Los Angeles County, California.

Description. Shell to 4 mm, fragile, elongate, wider anteriorly, narrower posteriorly; apex umbilicate, aperture lip forming rounded wing connected to columellar margin; aperture as long as shell, wider anteriorly, narrowing abruptly at about 1/4 of length; columellar margin slightly thickened; columella simple, with no folds; umbilicus closed; sculpture of strong, simple axial lines; color uniformly whitish.

Distribution. Redondo Beach, Los Angeles County to San Diego, California; 1–90 m. Rare.

Remarks. Very similar to *R. montereyensis* but consistently with more delicate spiral lines and more elongate shell. Records from the Gulf of California are likely *R. paziana*. The species is often included in *Sulcoretusa*.

***Retusa umbilicata* (Montagu, 1803)**
(Figure 19F)

Bulla umbilicata Montagu, 1803: 222–223, pl. 7, fig. 4. Type material unknown, not at NHMUK or RAMM. Falmouth Harbour, England.

Description. Shell to 3 mm, fragile, oval, wider anteriorly, right side convex, left side slightly concave; apex

deeply umbilicate, with aperture lip slightly rising from right side; aperture as long as shell, wider anteriorly narrowing gradually at about 1/3 of length; columellar margin slightly thickened; columellar simple, with no folds; umbilicus closed; sculpture of faint growth lines; color uniformly dirty white.

Distribution. Arctic Ocean and Gulf of Alaska; 119–152 m. Rare.

Remarks. Lemche (1948) listed additional synonyms and made comparisons to related species. This is species is often included in *Cylichnina*, but there is no evidence *Cylichnina* is a monophyletic group.

Rhizoridae Dell, 1952
(Figure 20)

Description. Shell external, thin, delicate, elongate, with only one whorl visible; aperture longitudinal, anteriorly rounded; operculum absent. Live animals with short headshield, posterior end divided into two short projecting lobes; jaws, radula, gizzard plates absent.

Remarks. Previously considered a synonym of Retusidae, Oskars *et al*. (2015) reinstated Rhizoridae to the family-level based on molecular evidence. Little is known about the diet and biology of members of Rhizoridae. They are typically very small animals found from shallow estuaries to the deep sea. For species are recognized in the northeast Pacific. Diversity is unremarkable.

***Volvulella* Newton, 1891**
(Figure 20)

Volvula A. Adams, 1850: 558 [not Gistel, 1848]. Type species (SD, A. Adams 1862: 154): *Bulla acuminata* Bruguière, 1792 (1789–1792). Eastern Atlantic.
Volvulella Newton, 1891: 268 [replacement name for *Volvula* A. Adams].
Paravolvulella Harry, 1967: 141. Type species (OD): *Volvulella* (*Paravolvulella*) *texasiana* Harry, 1967. Gulf of Mexico.

Description. Shell external, thin, delicate, elongate, with only one whorl visible; umbilicus absent; aperture longitudinal, anteriorly rounded, bending apically over apex; parietal wall forming extension (spine in some species) covering apex; operculum absent. Live animals with short headshield, posterior end divided into two short projecting lobes; jaws, radula, gizzard plates absent.

Remarks. Harry (1967) introduced the subgenus *Paravolvulella* for species with a deep rounded sinus in the apical end of the outer lip, resulting in the presence of a truncate junction with the spine (e.g., *V. panamica* Dall, 1919). Because there are no anatomical or phylogenetic evidence to support this distinction, *Paravolvulella* is here regarded as a synonym of *Volvulella*. For a discussion of the taxonomic status of *Volvulella* see Valdés & Camacho-García (2004).

Animals live subtidaly and to several hundred meters depth; mainly in tropical oceans, few species reach temperate regions. Species are rarely abundant.

***Volvulella californica* Dall, 1919**
(Figure 20B–C)

Volvulella californica Dall, 1919: 298. Lectotype (Harry 1967: 143) USNM 211303. Santa Rosa Island, California, 97 m.

Description. Shell to 4.4 mm, fragile, oval, with convex sides; aperture long, wider anteriorly, narrowing gradually at ~1/4 of length; aperture bended apically over apex, with parietal wall forming conical spine completely covering apex; columellar margin thickened; sculpture of faint irregular spiral grooves; color uniformly pale brown. Live animal unknown.

Distribution. Santa Cruz, California to Todos los Santos Bay, Baja California Sur, Mexico; 27–553 m. Rare.

Remarks. Gosliner (1996) considered *V. californica* to be distinct from *V. cylindrica* because it is consistently devoid of sculpture and is pyriform in shape, whereas *V. cylindrica* has a sculpture and is far more cylindrical. Harry (1967) argued that the lack of sculpture in *V. californica* is probably due the specimens examined having been weathered.

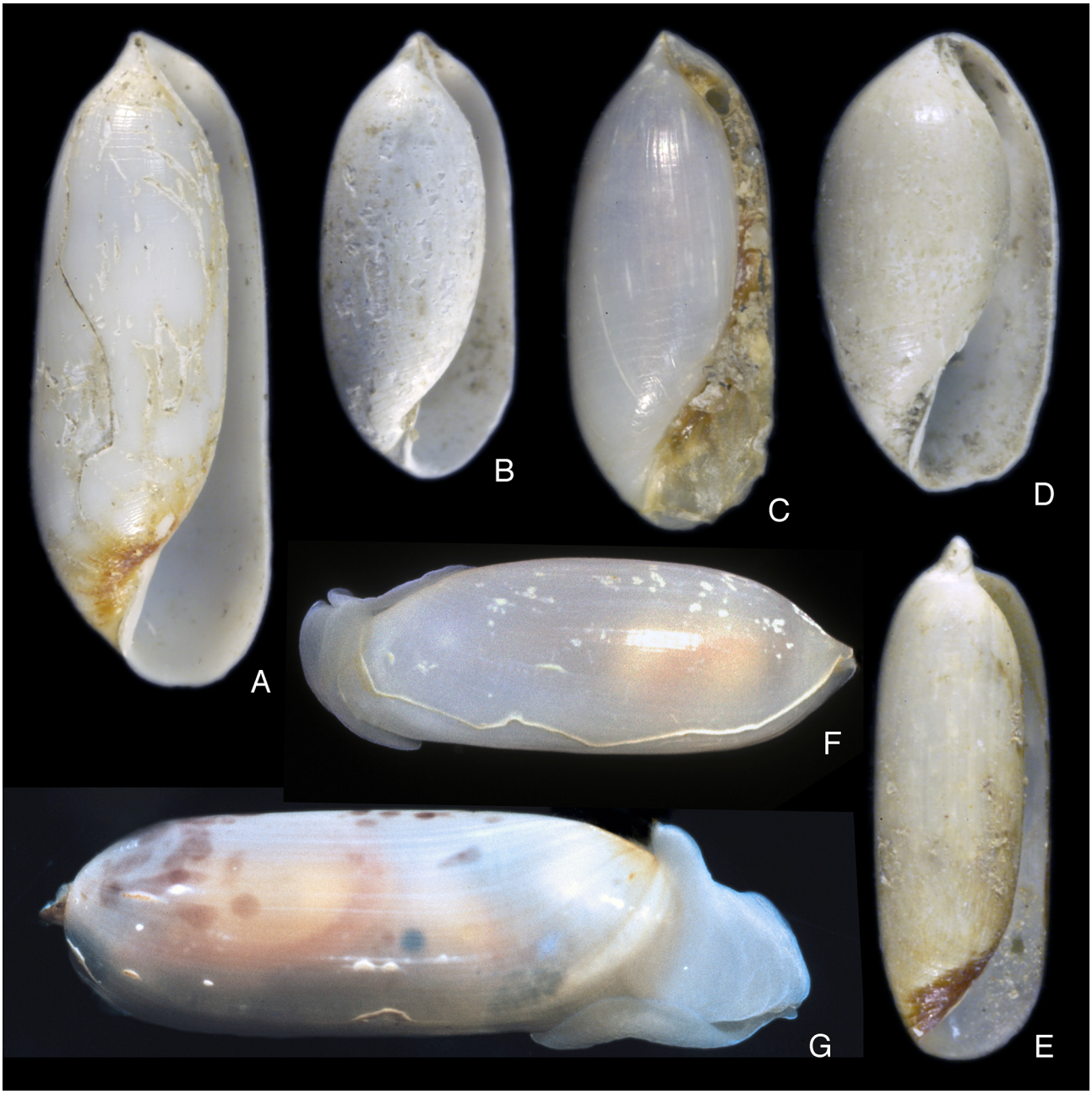

FIGURE 20. Rhizoridae. **A.** ***Volvulella cylindrica*** (Carpenter, 1864), 9 mm (LACM 1941-19.20) San Clemente Island, California (photo: Jenny McCarthy). **B–C.** ***Volvulella californica*** Dall, 1919, (B) 4.1 mm (LACM 157885), San Pedro, California, (C) 5 mm (LACM 157886) Redondo Beach, California (photos: Jenny McCarthy). **D.** ***Volvulella catharia*** Dall, 1919, 4 mm (LACM 1941-44.13) Cedros Island, Baja California (photo: Jenny McCarthy). **E.** ***Volvulella panamica*** (Dall, 1919), 4.8 mm (LACM 1940-104.57) Laguna Beach, California (photo: Jenny McCarthy). **F.** ***Volvulella cylindrica*** (Carpenter, 1864), live animal, British Columbia (photo: Ron Long). **G.** ***Volvulella panamica*** (Dall, 1919), live animal, California (photo: Gary McDonald).

Volvulella catharia **Dall, 1919**
(Figure 20D)

Volvulella catharia Dall, 1919: 298. Lectotype (Harry 1967: 143) USNM 211784. Panama Bay, Panama, 113 m.

Description. Shell to 4 mm, fragile, oval, with convex sides; aperture long, wider anteriorly, narrowing gradually at ~1/4 of length; aperture bended apically over apex, with parietal wall forming short, blunt

protuberance; columellar margin thickened; sculpture of irregular spiral grooves; color uniformly pale brown. Live animal unknown

Distribution. Southern California to Panama; 37–457 m. Rare.

***Volvulella cylindrica* (Carpenter, 1864)**
(Figure 20A, F)

Volvula cylindrica Carpenter, 1864: 647. Holotype RM 2364. Santa Barbara, California.
Volvulella cooperi Dall, 1919: 297. Lectotype (Harry 1967: 142) USNM 105501. Laguna Ojo de Liebre (= Scammon's Lagoon), Baja California, Mexico.
Volvulella callicera Dall, 1919: 299. Lectotype (Harry 1967: 142–143) USNM 194176b. Galapagos Islands.
Volvulella lowei Strong & Hertlein, 1937: 164, pl. 35, fig. 2. Holotype CASIZ 0065971. Puerto Escondido, Gulf of California.

Description. Shell to 5.5 mm, fragile, elongate, with nearly parallel sides; aperture long, wider anteriorly, narrowing gradually at ~1/5 of length; aperture bent apically over apex, with parietal wall forming conical spine completely covering apex; spine long, curved in some specimens, shorter, straight in others; columellar margin thickened, with small protuberance; sculpture of irregular spiral grooves crossed by numerous fine growth lines; spiral grooves near anterior, posterior ends more conspicuous, separated from each other by wider gaps than those in center; color uniformly shiny whitish. Live animal unknown.

Distribution. Vancouver Island, British Columbia, to Panama and the Galapagos Islands; 0–55 m, rarely to 230 m (D. Cadien, pers. comm.). Locally common.

Remarks. Harry (1967) reviewed this species and provided the synonymy above. Valdés & Camacho-García (2004) studied numerous specimens from Costa Rica confirming the wide range of shell morphological variation in this species.

***Volvulella panamica* Dall, 1919**
(Figure 20E, G)

Volvulella panamica Dall, 1919: 298. Lectotype (Harry 1967: 143) USNM 212654. Panama Bay.
Volvulella tenuissima Willett, 1944: 71, pl. 4, fig. 1. Holotype LACM 1073. Redondo Beach, California, 137 m.

Description. Shell to 5.5 mm, fragile, elongate, with nearly parallel sides; aperture long, wider anteriorly, narrowing gradually at ~1/5 of length; aperture bending apically over apex, with parietal wall forming short spine completely covering apex; spine sharp, narrow because of sinus on posterior end of spire; columellar margin thickened, with small protuberance; sculpture of irregular spiral grooves crossed by numerous fine growth lines; spiral grooves near anterior, posterior ends more conspicuous, separated from each other by wider gaps than those in center; color uniformly shiny whitish.

Distribution. Redondo Beach, Los Angeles County, California to Panama; 37–137 m, rarely to 305 m (D. Cadien, pers. comm.). Common in southern California, rare in the southern part of the range.

Remarks. Often included in *Paravolvulella*, which has been distinguished from *Volvulella* by the presence of a truncate junction with the spine formed by the inner lip.

Philinidae J. E. Gray, 1850
(Figures 21–23, 24A–C)

Description. Shell internal, thin, poorly calcified, variable in shape from flat, open, to bulloid; sculpture smooth or of spiral striae or punctuations. Live animals elongate, with reduced parapodial lobes; radula present; gizzard plates present or absent.

Remarks. The classification of philinids into one or several families and a number of genera is controversial and unsettled (Rudman 1972, Gosliner 1996, 1998, Price *et al.* 2011, Gonzales & Gosliner 2011, Ohnheiser & Malaquias 2013, Chaban & Soldatenko 2009, Chaban 2014, Oskars *et al*. 2015, Valdés *et al.* 2016). Following Valdés *et al.* (2016), Laonidae and Philinorbidae are recognized here, while other philinids with distinct shell morphologies are provisionally regarded as *Philine* s.l. until the taxonomy of this group is

resolved. Found in tropical, temperate and polar regions. Animals commonly burrow in soft sediments where they feed on other benthic organisms unselectively. Six species and one genus are recognized here, diversity is remarkable.

Philine (s.l.) Ascanius, 1772

(Figures 21–23, 24A–C)

Philine Ascanius, 1772: 331. Type species (M): *Bulla aperta* Linnaeus, 1767. South Africa.

Lobaria Müller, 1776: xxix, 226. Type species (M): *Lobaria quadriloba* Müller, 1776 [= *Philine aperta* (Linnaeus, 1767)]. Eastern Atlantic and Mediterranean.

Bullaea Lamarck, 1801: 63. Type species (M): *Philine planciana* Lamarck, 1801 [= *Philine aperta* (Linnaeus, 1767)]. Eastern Atlantic and Mediterranean.

Hermania Monterosato, 1884: 147. Type species (M): *Bulla scabra* Müller, 1784. Norway.

?*Yokoyamaia* Habe, 1950: 50. Type species (OD): *Philine ornatissima* Yokoyama, 1927. Japan.

Choshiphiline Habe, 1958: 120. Type species (M): *Philine pygmaea* Yokoyama, 1922 [= *Philine japonica* Lischke, 1872. Japan.

Globophiline Habe, 1958: 120. Type species (M): *Globophiline kawamurai* Habe, 1958. Japan.

Philingwynia Nordsieck, 1972: 22. Type species (OD): *Philine monterosati* Jeffreys *in* Monterosato, 1874. Mediterranean.

Retusophiline Nordsieck, 1972: 20. Type species (OD): *Philine lima* Brown, 1827. British Isles.

?*Praephiline* Chaban & Soldatenko, 2009: 206. Type species (OD): *Philine finmarchica* M. Sars, 1858. North Atlantic and adjacent Arctic Ocean.

Description. Shell internal, thin, fragile, ovate to subquadrate; sculpture absent or of spiral striae or punctuations; only one whorl visible; spire sunken; aperture very large; columella simple, reduced. Live animals usually white, headshield occupying between 1/2–2/3 of body length; parapodial lobes reduced; posterior shield normally with median notch; radula with 1–3 lateral teeth, sometimes denticulate; reproductive system monaulic, with long prostate; penis unarmed.

Remarks. At least two moderately large species in this genus that are native to Japan are now established in Californian waters. Molecular data has proven critical to determine the origin and identity of these species (Krug *et al.* 2012). Two recently described species, *Philine wareni* Valdés, Cadien & Gosliner, 2016 and *Philine harrisae* Valdés, Cadien & Gosliner, 2016 are known only from preserved specimens with damaged shells and are not illustrated here.

Philine auriformis Suter, 1909 [introduced species]

(Figures 21A–B, 24A)

Philine constricta auriformis Suter, 1909: 257–258, pl. 11, figs 14–17. Lectotype (Boreham 1959) NPCNZ TM 1192, Akaroa Harbour, New Zealand, 4–6 fathoms.

Description. Shell to 20 mm, large, oval, nearly as broad posteriorly (at apex) as anteriorly; lip flaring roundly above apex, sometimes flaring at lower right; sculpture of fine punctate striae. Live animal to 40 mm, uniformly white; cephalic shield broad, longer than posterior shield; posterior shield notched; lateral radular teeth broad, with 30–50 denticles; gizzard plates spindle-shaped with approximately same size, shape; each plate with two long indentations on dorsal side; penial papilla small, hammer-shaped; penial sac pyriform; prostate convoluted branching into short muscle connecting to end of penial sac.

Distribution. Native to New Zealand introduced to the northeast Pacific from Coos Bay, Coos County, Oregon to San Diego, California; 5–300 m. Locally very common.

Remarks. For ecology and biotic interactions see Cadien & Ranasinghe (2001).

Philine orientalis A. Adams, 1854 [introduced species]

(Figures 21C–D, 24B)

Philine orientalis A. Adams, 1854: 94–95. Syntypes (3) NHMUK 20080105. Eastern Seas.

Philine argentata Gould, 1859: 139. Holotype USNM 1680. “Hakodadi Bay” [=Hakodate, Japan].

Philine japonica Lischke, 1872: 105–106. Holotype LMA 111211a. Tokyo, Japan.

Philine striatella Tapparone-Canefri, 1874: 109–110, pl. 2, fig. 9. Type material unknown. “Jokohama” [=Yokohama, Japan].

Description. Shell to 20 mm, large, oval, nearly as broad posteriorly (at apex) as anteriorly; lip flaring roundly above apex; sculpture of growth lines, sometimes fine punctate striae. Live animal to 40 mm, uniformly white; cephalic shield longer than posterior shield; posterior shield with or without notch; parapodial lobes thick, muscular; radular teeth broad with 35–42 small denticles; gizzard plates spindle-shaped with small to medium shallow pores; paired plates broad filling entire anterior portion of body, unpaired plate much shorter, narrower; penial sac ovoid; penial papilla hammer-shaped with subequal lobes, supported above cushion-shaped base by stalk; prostate convoluted branching into long ejaculatory duct extending to, or far beyond, buccal mass.

Distribution. Native to southeast Asia (cited from Japan, Taiwan and Malaysia), introduced to the San Francisco Bay Area, from Bodega Bay, Sonoma County to San Mateo County, California; 0–300 m. Locally common.

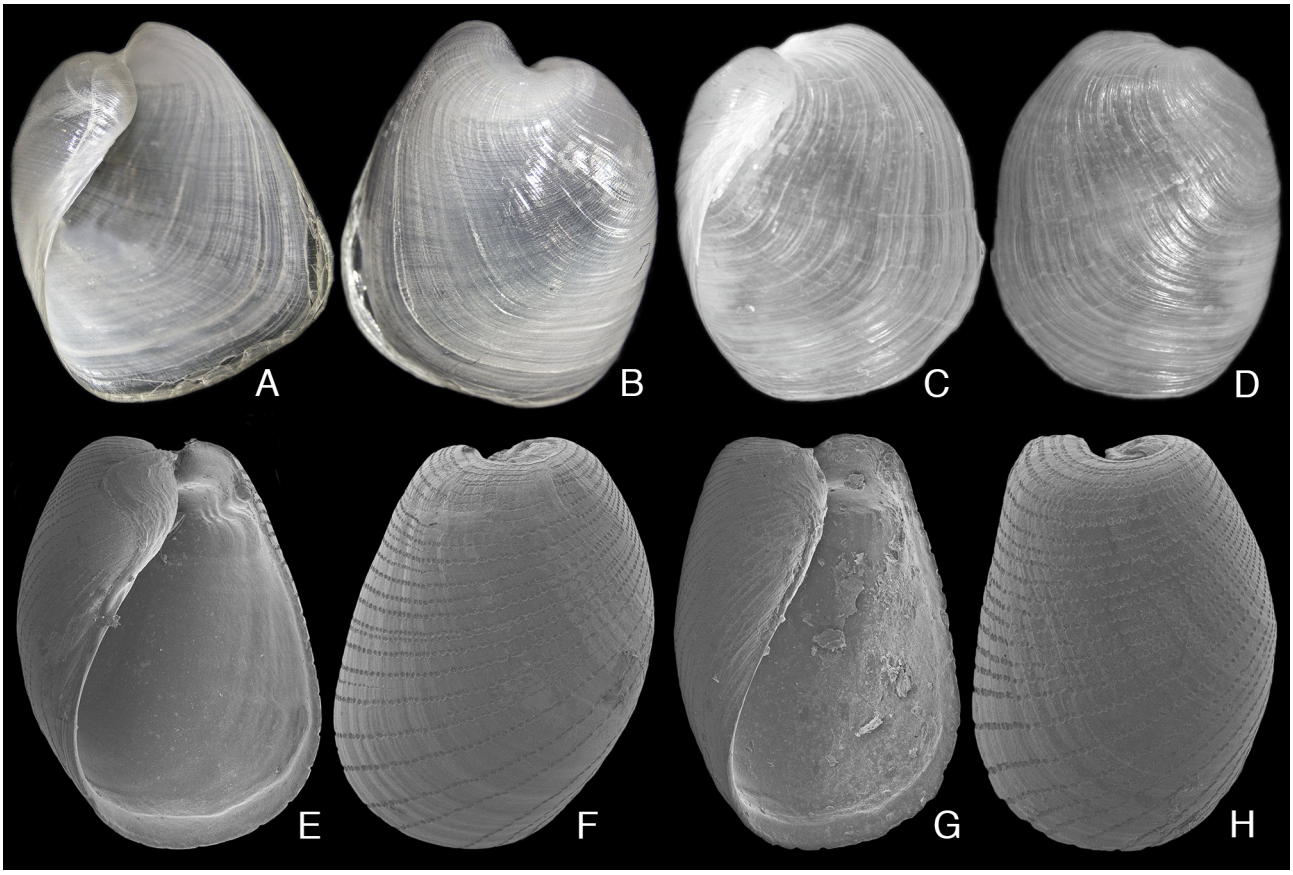

FIGURE 21. Philinidae. **A–B.** ***Philine auriformis*** Suter, 1909, 10 mm (CPIC00783), Los Angeles, California (photos: Ángel Valdés). **C–D.** ***Philine orientalis*** A. Adams, 18 mm (LACM96-11) Foster City, California (photos: Sabrina Medrano). **E–H.** ***Philine bakeri*** (Dall, 1919), (E–F) 1.6 mm (LACM69-32.40) Santa Cruz Island, California (images: Ángel Valdés); (G–H) 1.6 mm (LACM77-110.9) Santa Catalina Island, California.

Philine bakeri **Dall, 1919**
(Figures 21E–H)

Philine bakeri Dall, 1919: 300. Holotype USNM 225194. Coronado del Sur Island, Baja California, Mexico.

Description. Shell to 2 mm, small, elongate, narrower posteriorly (at apex) than anteriorly; apex flat, with no spire; lip edge straight in apertural view; sculpture of conspicuous punctate striae. Live animal unknown.

Distribution. Pacific Grove, Monterey County, California to San Juanico Bay, Baja California, Mexico; 3–76 m. Rare.

Remarks. Callus deposition on the inner whorl near the spire of 2 mm shells indicates that these specimens are mature. Abbott (1974) stated that the shell of this species is buried in a body of 35 mm length

but gave no source; this claim is most likely a mistaken reference to *Philinorbis albus*, the only native species in southern California have such a large body size. Gosliner (1996) correctly distinguished *P. bakeri* from *Philinorbis albus* (as *P. alba*), but also suggested that *P. bakeri*, *P. polystrigma* (which he redescribed) and *Laona californica* (as *P. californica*) are similar and require further study. However, *L. californica*, is easily distinguishable by the unique net-like sculpture of its shell; the shell of *P. polystrigma* is more globose with densely punctuate striae.

***Philine hemphilli* Dall, 1919**
(Figure 22A–D)

Philine hemphilli Dall, 1919: 301. Holotype USNM 211753. San Quintin Cape, Baja California, Mexico, 656 m.
?*Woodbridgea williamsi* Berry, 1953: 422, fig. 8. Holotype CASIZ 64608. Colorado Point, SW of Guaymas, Sonora, Mexico.

Description. Shell to 5 mm, small, globose, oval; apex with involute spire; lip not rising above apex; sculpture of faint growth lines, with no punctuate striae. Live animal unknown.

Distribution. Hawkins Island, Alaska, to Cedros Island, Baja California, Mexico; 9–975 m. Rare.

Remarks. The southern species *P. williamsi* is morphologically similar and could constitute a synonym.

FIGURE 22. Philinidae (images: Ángel Valdés). **A–D.** ***Philine hemphilli*** Dall, 1919, (A–B) 3.2 mm (LACM41-337.6), San Miguel Island, California; (D–E) 3.4 mm (LACM71-158.48), Cedros Island, Baja California. **E–F.** ***Philine ornatissima*** Yokoyama, 1927, 3.2 mm (LACM 178889), Palos Verdes, California. **G–H.** ***Philine polystrigma*** (Dall, 1908), 4.5 mm (LACM 178892), Tillamook, Oregon.

***Philine ornatissima* Yokoyama, 1927**
(Figures 22E–F, 24C)

Philine ornatissima Yokoyama, 1927: 408, pl. 46, fig. 6. Holotype UMUT CM 23626. Tokyo, Pleistocene.

Description. Shell to 4 mm, flat, elongate; wide aperture broad; outer lip with distinct apical wing; sculpture composed of very large punctuations arranged in spiral lines. Live animal to 12 mm; body elongate, white; cephalic shield longer than posterior shield; posterior shield with two posterior broad extensions; parapodial lobes thick, muscular; radular with two outer, one inner lateral tooth per half-row; lateral teeth broad, with strong denticles, outer teeth elongate; gizzard plates oval, with no punctuations, thicker centrally; reproductive system with very elongate prostate branched into long loop. Anatomy described by Gulbin & Chaban (2009), Gosliner (1996), Valdés *et al*. (2016).

Distribution. Japan, Russia and California, from Oceano, San Luis Obispo County to Point Loma, San Diego County; 8–222 m. Rare.

Remarks. This species was described from Pleistocene fossils from Japan and reported alive from several localities in East Asia (Gulbin & Chaban 2009). Gulbin & Chaban (2009) and Valdés *et al*. (2016) indicated that the northeast Pacific specimens referred to as *Philine* sp. A (Cadien 1988) and *Philine* sp. 1 (Gosliner 1996) belong to the same species. This species is often placed in the genus *Yokoyamaia* Habe, 1950.

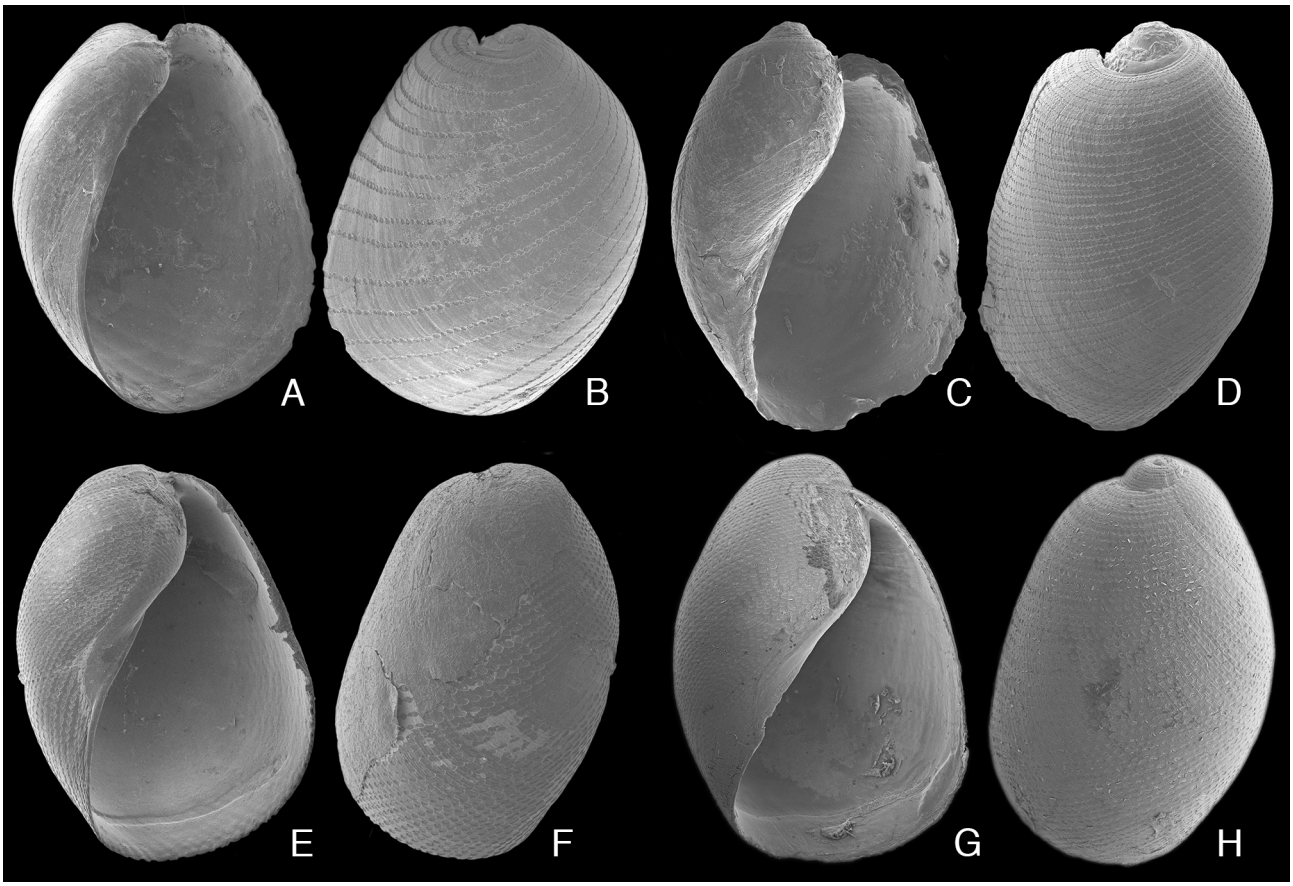

FIGURE 23. Philinidae (photos: Ángel Valdés). **A–D.** ***Philine baxteri*** Valdés, Cadien & Gosliner, 2016, (A–B) 2.7 mm (LACM 57-12.82), Kenai Peninsula, Alaska; (C–D) 2.9 mm (LACM 86-354.8), Aleutian Islands, Alaska.

Philine polystrigma **(Dall, 1908)**
(Figures 22G–H)

Clistaxis? *polystrigma* Dall, 1908: 246. Holotype USNM 110649. San Diego, 92 m.

Description. Shell to 4.5 mm, small, globose, oval to elongate, wider anteriorly; apex with involute spire; lip not rising above apex; sculpture of faint punctuate striae densely packed. Live animal unknown.

Distribution. Point Chehalis, Grays Harbor County, Washington to San Diego, California; 128–4,100 m. Rare.

Remarks. Dall (1908) stated that the animal is contained within the shell, but the dried holotype shows mantle tissue enveloping the lip, thus the shell is internal as indicated by Gosliner (1996).

***Philine baxteri* Valdés, Cadien & Gosliner, 2016**
(Figures 23A–D)

Description. Shell to 3 mm, bulloid, elongate; aperture broad; spire short, well-formed in some specimens; sculpture composed of conspicuous spiral lines, formed by partially fused punctuations. Live animal unknown; radula formula 2.1.0.1.2; lateral teeth broad, with strong denticles, outer teeth hook-shaped; gizzard plates absent.

Distribution. Aleutian Islands, Bearing Sea and Gulf of Alaska, 0–148 m. Uncommon.

Laonidae Pruvot-Fol, 1954
(Figures 25A–D)

Description. Shell rounded to quadrangular; smooth or with chain-like or net-like sculpture; parietal wall protruding into posterior half of aperture; gizzard non-muscularized, lacking plates.

Remarks. Molecular evidence shows Laonidae is genetically distinct from Philinidae and includes animals lacking gizzard plates, typically with a net-like sculpture on the shell (Oskars *et al*. 2015). Only one species is known from the northeast Pacific.

***Laona* A. Adams, 1865**
(Figures 25A–D)

Laona A. Adams, 1865: 324. Type species (M): *Laona zonata* A. Adams, 1865. Japan.
Ossiania Monterosato, 1884: 147. Type species (OD): *Philine scutulum* Lovén, 1846. Northeast Atlantic.

Description. Same as for Laonidae.

***Laona californica* Willett, 1944**
(Figure 25A–D)

Philine californica Willett, 1944: 72, pl. 14, fig. 4. Holotype LACM 1074. Redondo Beach, Los Angeles County, California, 91 m.

Description. Shell to 5.5 mm, elongate, inflated; spire sunken; aperture very large, oval, narrowing posteriorly; outer lip extending above apex; columellar slightly thickened; inner lip twisted, flattened at intersection with body whorl; sculpture of fine axial striations crossed by spiral lines forming net-like pattern; color white with light brown band.

Distribution. Southern California; 48–208 m. Rare.

Remarks. Willett (1944) placed *P. californica* in the "section" *Laona* because of the "latticed" or net-like sculpture of the shell. Valdés *et al*. (2016) confirmed this species belongs to *Laona* as defined by Oskars *et al*. (2015).

Philinorbidae Oskars, Bouchet & Malaquias, 2015
(Figures 24D–E, 25E–F)

Description. Shell internal, rounded, with lip extending well above apex; sculpture smooth or with spiral lines. Live animals with broad, rhomboid cephalic shield; pallial lobe elongate, lacking posterior notch; gizzard non-muscular, with reduced brown chitinous gizzard plates, sometimes absent; radula with short, broad, hook-shaped inner lateral teeth, smooth or with fine denticulation along inner edge; penial atrium embedded in tissue anteriorly to body cavity.

Remarks. Molecular data indicate that members of Philinorbidae are distinct from Philinidae (Oskars *et al*. 2015). According to Oskars *et al*. (2015) the anatomy of these species suggests a close relationship with the northeast Pacific species *Philine alba*, and consequently is here included in Philinorbidae. Only one genus, *Philinorbis*, is currently included in this family, which is represented in the northeast Pacific by a single species. Diversity is unremarkable.

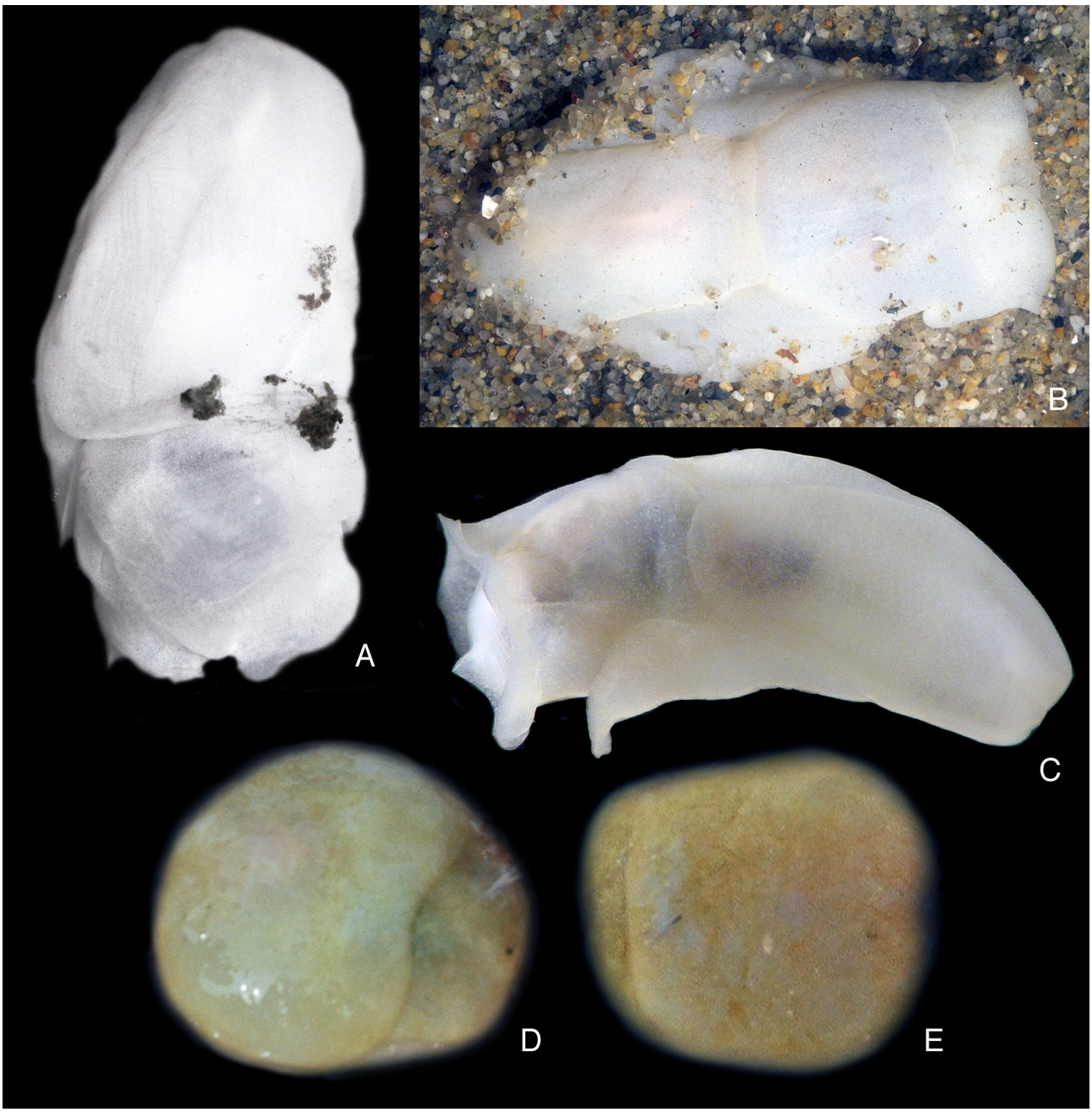

FIGURE 24. Philinidae and Philinorbidae. **A.** ***Philine auriformis*** Suter, 1909, Los Angeles, California (photo: Ángel Valdés. **B.** ***Philine orientalis*** A. Adams, 1854, Bodega Bay, California (photo: Terry Gosliner). **C.** ***Philine ornatissima*** Yokoyama, 1927, Los Angeles, California (photo: Leslie Harris). **D–E.** ***Philinorbis albus*** (Mattox, 1958), San Diego, California, (photos: Megan Lilly), (D) dorsal view, (E) ventral view.

Philinorbis **Habe, 1950**
(Figure 24D–E, 25E–F)

Philinorbis Habe, 1950: 52. Type species (M): *Philinorbis teramachii* Habe, 1950. Japan.
?*Pseudophiline* Habe, 1976: 154. Type species (OD): *Pseudophiline hayashii* Habe, 1976. Japan.

Description. Same as for Philinorbidae.

Remarks. The synonymy of *Philinorbis* and *Pseudophiline* is controversial (Chaban 2011, Chaban 2016, Oskars *et al*. 2015, Valdés *et al*. 2016).

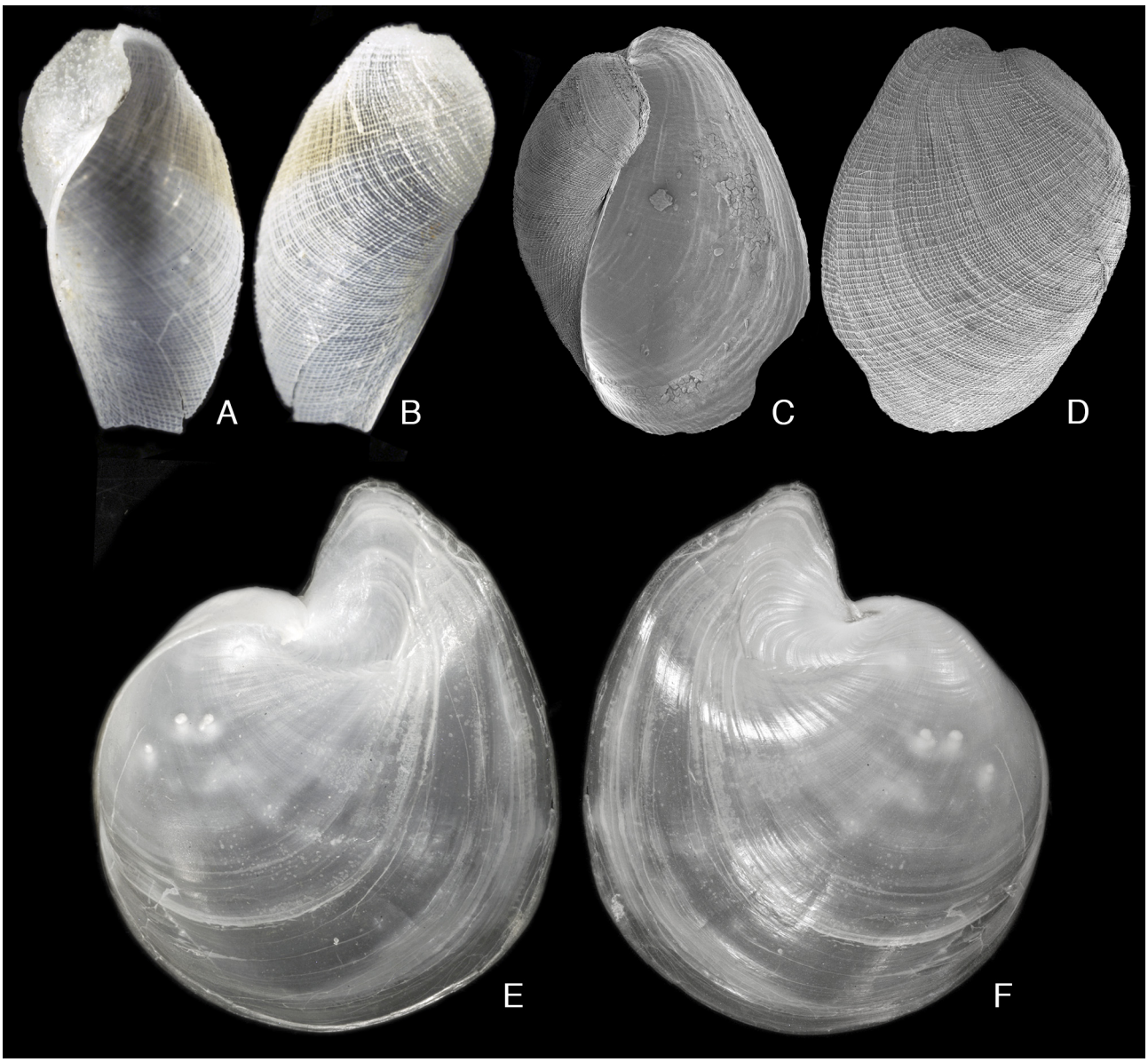

FIGURE 25. Laonidae and Philinorbidae. **A–D.** ***Laona californica*** Willett, 1944 (images: Ángel Valdés), (A–B) Holotype, 5.5 mm (LACM 1074), Redondo Beach, California; (C–D) 4.6 mm (LACM 41-228.4), Seal Beach, California. **E–F.** ***Philinorbis albus*** (Mattox, 1958), 28.1 mm (LACM 10592), Gaviota, California (photo: Sabrina Medrano).

Philinorbis albus **(Mattox, 1958)**
(Figures 24D–E, 25E–F)

Philine alba Mattox, 1958: 98, pl. 33, figs 1–3. Holotype LACM 2072. Santa Catalina Island, California, 64 m.

Description. Shell to 30 mm, smooth; inner whorl reduced, uncoiled, bearing weak shelly projection for muscle attachment; lip flaring above, left of remnant of shell axis, anterior extension of lip projecting 90º from remnant of shell axis; periostracum thin. Live animal to 60 mm, creamy white, smooth, elongate; cephalic shield longer than posterior shield.

Distribution. Monterey Bay, California to central Baja California, Mexico and Galapagos Islands; 36–274 m. Currently rare, very common before the introduction of *P. auriformis*.

Remarks. Mattox (1958) and Price *et al*. (2011) provided full anatomical descriptions of this species.

Aglajidae Pilsbry, 1895 (1895–1896) (1847)
(Figures 26–27)

Description. Shell internal, completely or partially calcified, flattened, often coiled; head with sensory cilia; posterior shield with short to moderate caudal lobes or elongate 'flagellum'; radula absent.

Remarks. The phylogenetic systematics of this group was examined by Camacho-García *et al*. (2014) and Zamora-Silva & Malaquias (2017). Aglajidae was placed in the official list and ruled to have precedence over Doridiidae J. E. Gray, 1847 by ICZN (1977: Opinion 1079). Algajids are carnivorous, active predators, feeding primarily on other benthic invertebrates including sea slugs. Most species are tropical, including some radula-bearing taxa, and are typically brightly colored. Four species occur in the northeast Pacific, one of them was introduced. Diversity is unremarkable.

***Aglaja* Renier, [1807]**
(Figures 26A–B, 27A)

Aglaja Renier, [1807]: pl. 8. Type species (SD, Suter 1913): *Aglaja tricolorata* Renier, [1807]. Mediterranean.
Doridium Meckel, 1809: 33 [rejected ICZN 1977: Opinion 1079]. Type species (SD, Gray 1847: 161): *Doridium membranaceum* Meckel, 1809 [= *Aglaja tricolorata* Renier, [1807]]. Mediterranean.

Description. Shell completely calcified; narrow or flaring into wing. Live animal with rounded headshield; posterior shield with elongate 'flagellum'; single pair of sensory mounds on head.

Remarks. Camacho-García *et al*. (2014) indicated that *Aglaja* was nested within *Chelidonura* s.l. and suggested these two names would probably need to be synonymized. However, Zamora-Silva & Malaquias (2017) split *Chelidonura* into several genera and retained *Aglaja* as valid. Because support values for critical nodes in both studies are low, further research is needed to resolve the status of several Aglajidae genera.

***Aglaja ocelligera* (Bergh, 1893)**
(Figures 26A–B, 27A)

Doridium ocelligerum Bergh, 1893: 212–213, pl. 10, fig. 10, pl. 12, figs 5–6. Type material lost, not at USNM. Sitka Harbor, Alaska.
Doridium adellae Dall,1894: 73–74. Holotype USNM 128336. Eagle Harbor, Puget Sound, Washington.
Chelidonura phocae Er. Marcus, 1961: 8–9, pl. 1, figs 18–24. Holotype unknown, not found at MZUSP (C. Cunha, pers. comm.), Paratype CASIZ 020302. Tomales Bay, California.

Description. Shell to 3 mm, internal, calcified, fragile; spire flattened with elongate wing; protoconch visible. Live animal to 20 mm, elongate, narrow; posterior end of body with two tails, left tail more elongate expanding into long 'flagellum'; cephalic shield occupies ~2/3 of body; color white to dark grey-black with numerous orange-white spots, sometimes with opaque white dots.

Distribution. Sitka, Alaska to San Diego Bay, California; 0–218 m, on mud flats, in shallow water. Scarce.

***Melanochlamys* Cheeseman, 1881**
(Figures 26C–E, 27B–C)

Melanochlamys Cheeseman, 1881: 224. Type species (OD): *Melanochlamys cylindrica* Cheeseman, 1881. New Zealand.

Description. Shell completely calcified, coiled, flaring into short apical wing. Live animal with rounded headshield; posterior shield with short caudal lobes; single pair of sensory mounds on head.

Remarks. *Melanochlamys* is monophyletic (Camacho-García *et al*. 2014, Zamora-Silva & Malaquias 2017) and mainly distributed in temperate regions. There are only two species in the Eastern Pacific, one of them (*M. ezoensis*) is non-native in San Francisco Bay (Cooke *et al*. 2014). Species are distinguished based on the male reproductive anatomy and shell morphology (Cooke *et al*. 2014). Species of *Melanochlamys* appear to feed on polychaetes and/or nematodes on soft bottoms.

FIGURE 26. Aglajidae. **A–B.** ***Aglaja ocelligera*** (Bergh 1893), (A) light specimen, California (photo: Leslie Harris), (B) most common spotted form, La Jolla, California (photo: Kevin Lee). **C–D.** ***Melanochlamys diomedea*** (Bergh, 1893), (C) dark specimen, California (photo: LACM archives), (D) light specimen, California (photo: LACM archives). **E.** ***Melanochlamys ezoensis*** (Baba, 1957), Chiba, Japan (photo: Yayoi Hirano). **F–I.** ***Navanax aenigmaticus*** Cooper, 1862, Long Beach, California, color variation (photos: Ángel Valdés), (F) juvenile specimen, (G) typical lined adult, (H) spotted adult often referred to as *Navanax polyalphos*, (I) typical spotted adult.

***Melanochlamys diomedea* (Bergh, 1893)**
(Figures 26C–D, 27B)

Doridium diomedeum Bergh, 1893: 211–212, pl. 11, fig. 1. Type material lost, not at USNM. St. Paul Island, Alaska, and Yukon Harbor, Kitsap County, Washington.
Aglaja nana Steinberg & Jones, 1960: 73–75, pl. 16, figs 1–4. Holotype USNM 575426. Richmond Yacht Harbor, Contra Costa County, California.

Description. Shell to 5 mm, broad, relatively flat; spire small; sculpture of irregular growth lines; body whorl large, with distinctive flat, broad external rim on posterior-right hand side; posterior process elongate, directed backward, separated from spire by deep notch. Live animal to 15 mm, elongate, narrow; posterior end of body with two blunt tails; cephalic shield occupies ~1/3 body; color translucent pale grey with brown or black pigment, varying among individuals in density, coverage.

Distribution. Fairmount Island, Alaska, to Newport Bay, Orange County, California; 0–100 m. Locally common.

Remarks. Feeds on nematodes on sand and mud bottoms in bays, estuaries and open coast.

***Melanochlamys ezoensis* (Baba, 1957) [introduced species]**
(Figures 26E, 27C)

Aglaja ezoensis Baba, 1957: 10, fig. 3. Holotype OMNH Mo 34829. Akkeshi, Hokkaido, Japan.

Description. Shell to 3 mm, broad, relatively deep; spire small, with large, ventral, irregular process; sculpture of irregular growth lines; body whorl large with distinctive, sharp indentation of posterior-left hand side; posterior process short, curved, directed backward, separated from spire by shallow notch. Live animal to 13 mm, elongate, narrow; cephalic shield occupies more than ½ of body; color brownish grey, mottled with dark pigment; opaque white spots all over body, typically concentrated on anterior, posterior ends of cephalic shield, anterior end of visceral region, posterior tails.

Distribution. Introduced in San Francisco Bay. Native range from Lake Onneto, Hokkaido, Japan, and Peter the Great Bay, Russia, to Katsuura, Chiba Prefecture, Japan; intertidal. Uncommon.

Remarks. This species occurs on sand and mud bottoms in bays and estuaries.

***Navanax* Pilsbry, 1895 (1895–1896)**
(Figures 26F–I, 27D–E)

?*Posterobranchaea* d'Orbigny, 1837 (1834–1847): 201–203. Type species (M): *Posterobranchaea maculata* d'Orbigny, 1837 (1834–1847) [?= *Navanax aenigmaticus* (Bergh 1893)]. Eastern Pacific.
Strategus Cooper, 1862 [not *Strategus* Kirby *in* Kirby & Spence, 1828]: 202. Type species (M): *Strategus inermis* Cooper, 1862. California.
Navarchus Cooper, 1863 [not *Navarchus* Filippi & Vérany, 1859]: 58 [replacement name for *Strategus*].
Navanax Pilsbry, 1895a: 131 [replacement name for *Navarchus*].

Description. Shell calcified basally or completely, flat, flaring into wing. Live animal with quadri-lobed headshield; posterior shield with elongate caudal lobes; two pairs of sensory mounds present on head; buccal mass large, bulbous, muscular.

Remarks. Camacho-García *et al*. (2014) indicated that *Navanax* was nested within *Chelidonura* s.l. and suggested these two names would probably need to be synonymized. However, Zamora-Silva & Malaquias (2017) split *Chelidonura* into several genera and retained *Navanax* as valid. *Posterobranchaea* could constitute a senior synonym of *Navanax*, but Schrödl (2007) and Ornelas-Gatdula *et al*. (2012) were unable to determine its identity with certainty. *Navanax* are active predators of other sea slugs. There are four valid species worldwide; two represented in the Eastern Pacific, but only one in the area covered by this chapter.

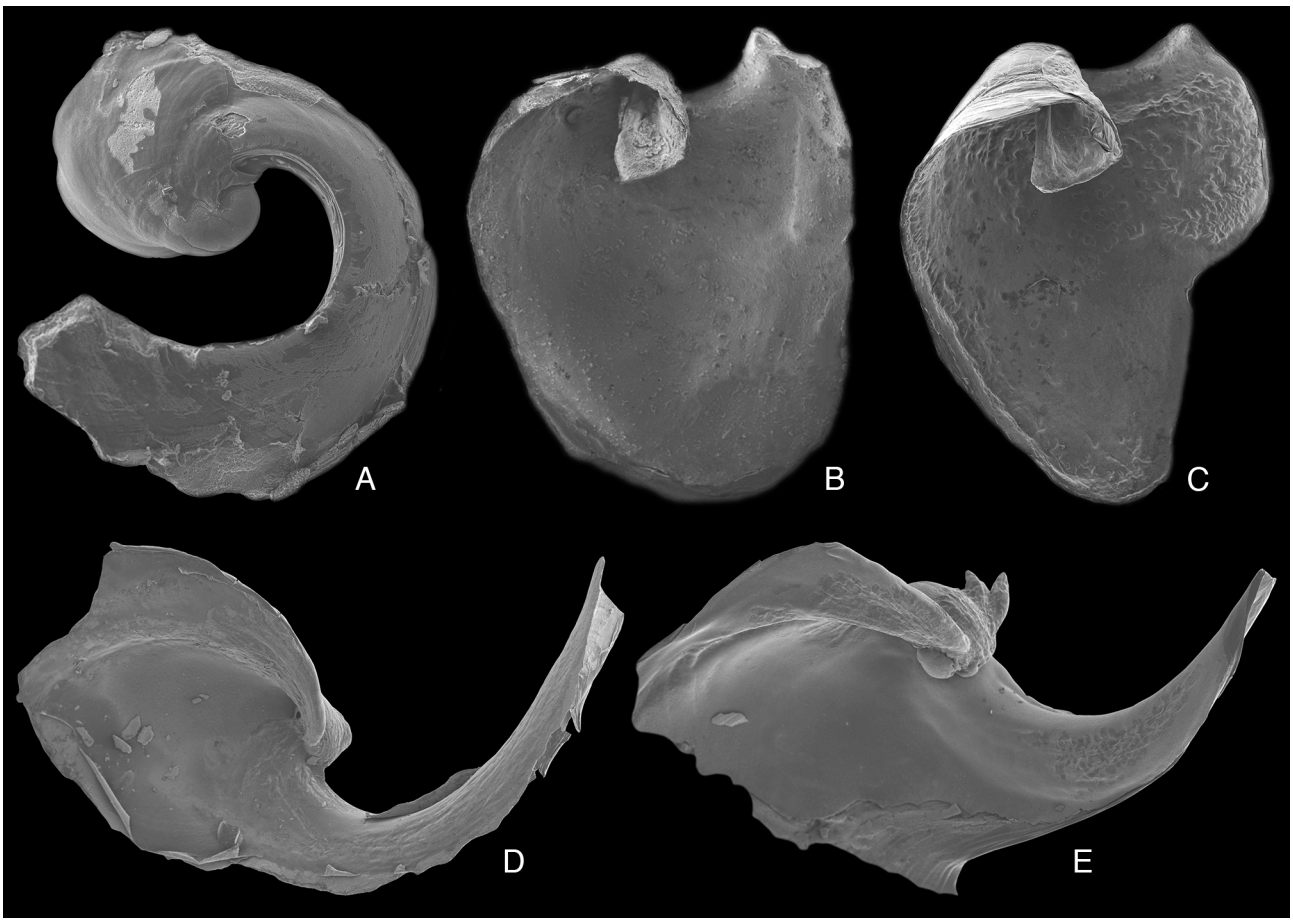

FIGURE 27. Aglajidae (images: Ángel Valdés). **A.** ***Aglaja ocelligera*** (Bergh 1893), 2 mm (LACM 1939-79.17), California. **B.** ***Melanochlamys diomedea*** (Bergh, 1893), 4.2 mm (CPIC00700), San Juan Islands, Washington. **C.** ***Melanochlamys ezoensis*** (Baba, 1957) 2.5 mm (CPIC00905), Hokkaido, Japan. **D–E.** ***Navanax inermis*** Cooper, 1862, (D) 4.5 mm (LACM72-118), Baja California; (E) 3.5 mm (LACM153-2), San Benito Islands, Baja California.

Navanax inermis (Cooper, 1862)

(Figures 26F–I, 27D–E)

Strategus inermis Cooper, 1862: 202–203. Type material unknown. San Diego Bay, California.

Doridium purpureum Bergh, 1893: 209–211, pl. 12, fig. 7. Type material unknown, not at USNM. Santa Catalina Island, California.

Aglaja bakeri MacFarland, 1924: 391–395, pl. 11, figs 5–6, pl. 12, figs 12, 16–17. Holotype CASIZ 020294. San Marcos Island, Mexico.

?*Chelidonura polyalphos* Gosliner & Williams, 1971: 424–433, figs 1–8. Holotype CASIZ 020369. San Carlos Bay, Mexico.

Description. Shell to 20 mm, flat, with thin, elongate apical wing; body whorl reduced, sometimes with two apical spines. Live animal to 225 mm (often half that size), elongate, narrow; posterior end of body with two elongate, triangular tails; body color dark brown-grey with complex, variable pattern of white lines or spots; parapodial margin with yellow-orange marginal line, submarginal band of bright blue spots; blue spots occasionally present on head.

Distribution. Bolinas Lagoon, Marin County, California to Nayarit, Mexico; 0–30 m. Locally abundant.

Remarks. *Navanax polyalphos* could be a color variant. It is found on mudflats and sand bays where it feeds voraciously on *Bulla gouldiana* and *Haminoea* spp., swallowing its prey whole.

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