Penitella penita

Common piddock

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Myoida
Family: Pholadidae

Taxonomy: The taxonomies of both pholad species in this guide (*Z. pilsbryi* and *Penitella penita*) are extensive and complicated, including many synonyms and overlapping descriptions (for full list of synonymies see Kennedy 1974). *Penitella penita* was originally described as *Pholas penita* by Conrad in 1837. The current name was designated by Gabb in 1869 and the most common synonym seen today is *Pholadidea penita*. However, *Pholadidea* species differ from those in the genus *Penitella* by having a mesoplax that is divided longitudinally into two pieces, a feature not present in the latter genus (see *Penitella*, Kennedy 1974)

Description
Size: Individuals to 70–95 mm in length and 50 mm in height (Turner 1955; Haderlie and Abbott 1980; Kozloff 1993). The illustrated specimen (from Coos Bay) is 40 mm long, 18 mm high (Fig. 1).
Color: White, inside and out (Haderlie and Abbott 1980; Kozloff 1993).
General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Myoid bivalves are burrowers and borers, with long siphons and hinges with few teeth (Coan and Valentich-Scott 2007). Members of the Pholadidae bore into a variety of substrates, possess no pallets on siphon tips and have an anterior end that is pointed or curved with no notch (contrast to Teredinidae species, e.g. *Bankia setacea*, this guide) (see Plate 427F, 430D, Coan and Valentich-Scott 2007). While most pholad species are intertidal or subtidal, some can be found boring into wood at great depths (e.g. 7,250 meters *Xylophaga*, Kennedy 1974; Reft and Voight 2009; Voight 2009; Marshall and Spencer 2013).
Body:

Color: Foot and mantle white (Turner 1955).
Interior:
Exterior:
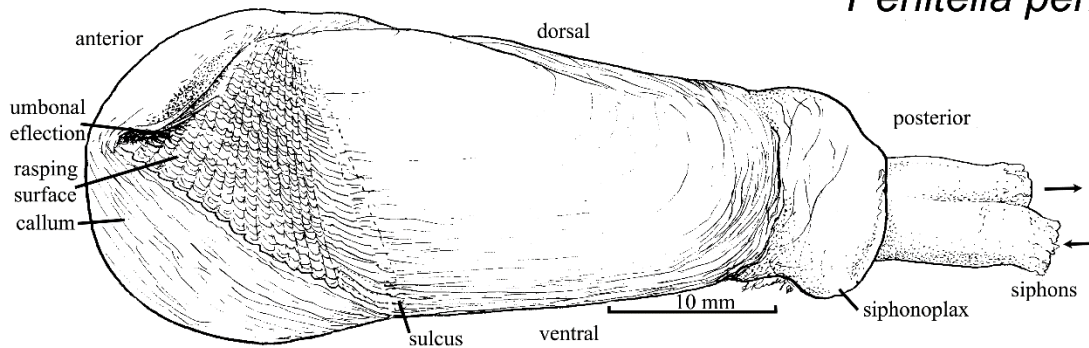**Byssus:**
Ctenidia:
Shell: Shell shape is elongate, and divided into two distinct parts (Fig. 1). Shell anterior becomes worn away from burrowing abrasion (Evans and LeMessurier 1972), the addition of new shell creates a rough and bulbous anterior (Kozloff 1993). No periostracum is present.

Interior: Divided into three areas by pallial lines. The pallial sinus and posterior is with a large posterior muscle scar. The anterior muscle scar and accessory are unusually dorsal and a ventral muscle scar is also present (Fig. 4). An apophysis (myophore) is a short, narrow, spoon-shaped structure of each valve, which serves as an extra muscle attachment site for powerful grinding muscles (Keen 1971) (Fig. 4). In *P. penita* it is "weakly blade-like" (Turner 1955).
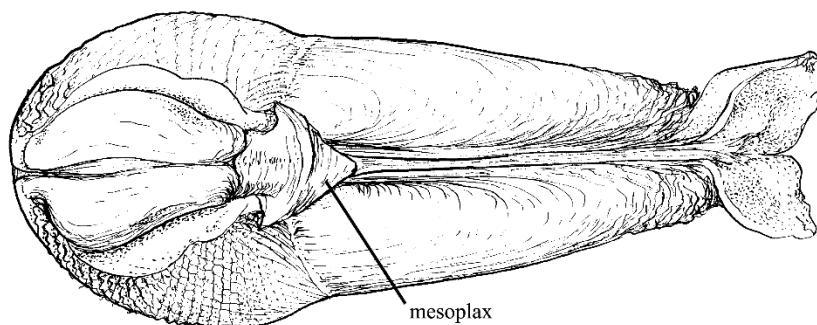
Exterior: The shell anterior is rounded, bulbous, and with rasp-like radial and concentric striae. These heavy file-like denticulations consist of a triangular rasping section which covers less than 1/2 valve area (Fig. 1, 3) (Kozloff 1993). The posterior is wedge-shaped, with regular concentric striations only, and a truncated end. Valves gape does not extend to the middle of the shell (*Penitella,* Keen and Coan 1974). A callum is present in adults (but not in young (Fig. 5)) at the anterior end (Fig. 1). Umbones are not prominent and umbonal reflection (where umbones turn posterior, Fig. 1) are closely appressed for the entire length (Coan and Valentich-Scott 2007). Siphonoplax is brown, membranous, heavy, flexible flaps, and is not lined with calcareous granules (Coan and Valentich-Scott 2007).

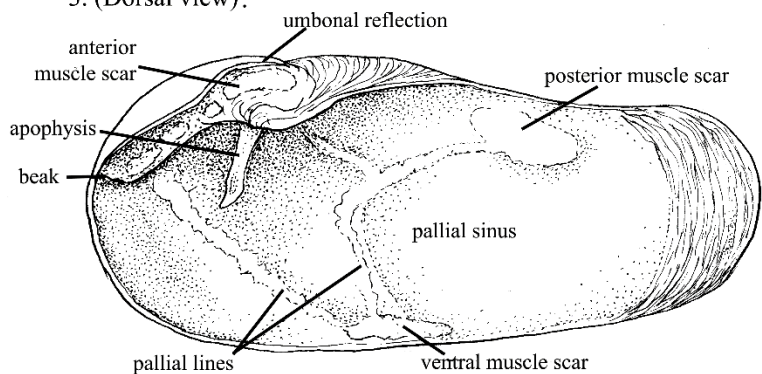**Hinge:** No hinge teeth or ligament present.

Penitella penita

Figure 1 labels: anterior, dorsal, posterior, umbonal reflection, rasping surface, callum, sulcus, ventral, siphons, siphonoplax, 10 mm

1. *Penitella penita* (L:40mm,W:18mm) x3: elongate shell divided into two distinct parts by umbonal-ventral sulcus; bulbous anterior with callum and rasping surface, posterior with concentric striae, truncate end; siphonoplax: heavy, brown flaps; siphons long, white, smooth.
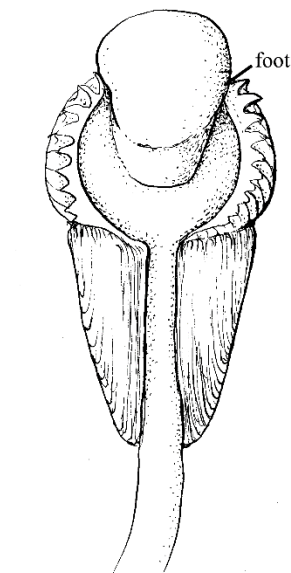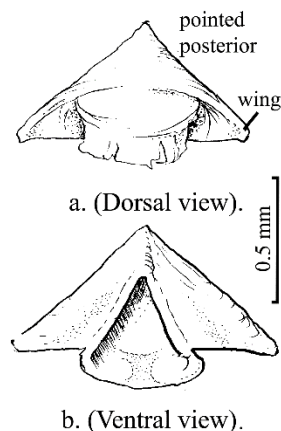
2. Mesoplax x4.5·

Figure 2 labels: pointed posterior, wing, 0.5 mm

a. (Dorsal view).

b. (Ventral view).

3. (Dorsal view).

Figure 3 label: mesoplax

4. Interior, right valve:
white; divided into three sections by two pallial lines; three muscle scars; apophysis: long, spoon-shaped.

Figure 4 labels: umbonal reflection, anterior muscle scar, posterior muscle scar, apophysis, beak, pallial sinus, pallial lines, ventral muscle scar

5. Young (dorsal view) x3:
no callum: foot exposed.

Figure 5 label: foot

Eyes:

Foot: Foot atrophies in adult individuals after the callum seals the shell anterior (Haderlie and Abbott 1980).

Siphons: Long, white, and retractible. The tips are marked with small red spots, but not solidly, red-tipped smooth. No warts or orange chitinous patches are present. No pallets are on siphon tips (compare to Teredinidae, e.g., *Bankia setacea*, this guide). Inhalant siphons with six large, and several small branched cirri around aperture (Turner 1955).

Burrow: (for burrow shape, see Fig 1B, Evans 1968d). Burrows are pear- (Haderlie 1981b) or cone-shaped (Evans and Fisher 1966; Evans 1968d). Burrows into stiff clay, sandstone, soft rock, shale and concrete (Haderlie and Abbott 1980; Kozloff 1993), up to 15 cm below the surface (at least 3 times the shell length). Burrowing mechanism is like that of the common local pholad, *Zirfaea pilsbryi* (see description in this guide): The foot is sucker-like and attaches to the substrate so that the shell can rotate slowly and create a cylindrical burrow. Shell valves rock back and forth by contractions of anterior and posterior adductor muscles. Individuals rotate after each stroke, making a cylindrical burrow (Lloyd 1896; Ricketts and Calvin 1952; Haderlie and Abbott 1980). Estimated burrowing rates varied with substrate type from 50 mm/year (soft substrates) to 50 mm/12 years (hard substrates, Evans 1968b), i.e., harder rock leads to a shallower burrow (Evans 1970). In Monterey, California, Haderlie (1981a) reported boring rates of 32 mm/year (2.6 mm/month). (see also **Habitat** and **Behavior.**)

Pholadidae-specific character

Mesoplax: A small accessory plate on dorsal edge (Fig. 2) has no accessory plates (e.g., protoplax. metaplax, hypoplax) present. The mesoplax is pointed posteriorly, and truncate anteriorly, with swept back lateral wing-like projections (Turner 1955).

Possible Misidentifications

There are several families of burrowing clams and the Pholadidae can be distinguished by their distinctively marked body areas (Fig. 1). Members of the Teredinidae and Pholadidae can be found locally. They can be distinguished by the absence of pallets on siphon tips in the latter family as well as an anterior end that is not notched, as in the Teredinidae. The Pholadidae includes 10 species locally, within the following genera: *Barnea* (*B. subtruncata*), *Chaceia* (*C. ovoidea*), *Netastoma* (*N. rostratum*), *Parapholas* (*P. californica*), *Penitella* (five local species) and *Zirfaea* (*Z. pilsbryi*). The genus *Zirfaea* is characterized by adults that burrow into sand or mud, the absence of a callum in mature individuals, and a shell sculpture that is divided into two distinct zones (see Plates 427C, 429D, Coan and Valentich-Scott 2007). The genus *Barnea*, for example, also lacks a callum, but does not have these two distinct zones. All other local genera are characterized by the presence of a callum and all except *Netastoma* have a myophore as well. *Parapholas* species have shell sculpture with three distinct zones, where members of *Chaceia* and *Pentilla* have two. None of the other local burrowing clams (e.g. in the genera *Hiatella. Entodesma, Barnea, Petricola, Bankia*) have distinct body areas or the bulbous, denticulated anterior of *Penitella.*

The genus closest to *Penitella*, and most likely to be confused with it, is *Zirfaea*. As mentioned above, *Penitella*'s valves are also divided into two distinct sections, but it differs in having a calcareous anterior callum, or accessory plate (in the adult) as well as a posterior which gapes only at the end, not to the middle of the shell (it has no anterior gape) and the apophysis is narrow, not broad. No *Penitella* species have a siphon longer than its body (Evans and Fisher 1966) and all *Penitella* species have retractable siphons. There are five species of *Penitella* in our area (see Coan and Valentich-Scott 2007).

Penitella conradi is very small and is found in *Mytilus* or *Haliotus* (abalone) shells. It has a siphonoplax lined with coarse granules (*Zirfaea* has no siphonoplax) (Evans and Fisher 1966) and can bore into nephrite (Monterey, California, Wilson and Kennedy 1984). *Penitella penita* has a heavy membraneous siphonoplax, a calcified callum and a distinctive **mesoplax**. Its

anterior rasping surface covers less than half the valve area (Kozloff 1974) (Fig. 1, 3). It can be up to 70 mm in length. *Penitella fitchi* also has a heavy siphonoplax, but has a callum with a gap. This is a rare species, found low in the intertidal up to 25 meters deep. *Penitella turnerae* is larger than *P. penita* (to 125 mm), and less common. It is stout, and like *Zirfaea* lacks a siphonoplax. It has a distinctive, rounded mesoplax, however, and its long, white, retractable siphons are tipped with solid red. Like *Zirfaea*, it has a strongly angled anterior ventral edge, but unlike *Zirfaea*, *P. turnerae* has a callum. *Penitella richardsoni* (=*gabbi*, Kennedy 1989) is also small (up to 75 mm) with a warty, creamy-lemon colored siphon and it is not common. It is different from the other members of this genus as its umbone reflection is not appressed to the anterior end, a character also found in *C. ovoidea*. *Penitella richardsoni* differs from *C. ovoidea* by having a callum that does not gap and an more elongated shell (Coan and Valentich-Scott 2007). A new species of *Penitella*, *P. hopkinsi*, was described from Alaska, but it not yet reported in our area (Kennedy and Armentrout 1989). With adult specimens, it should be easy to tell *Penitella* from *Zirfaea* because the latter species has a long, non-retractable siphon and a membraneous covering of the anterior, instead of a calcareous callum. Small shells without the callum could be young *Penitella* as well as mature *Zirfaea* and size at maturity varies greatly with environmental condition.

Ecological Information
Range: Type locality is San Diego, California (Turner 1955). Eastern Pacific distribution includes the Gulf of Alaska (e.g., Chirikof Island) to Pequena, Baja California. The first presence of *P. penita* in the fossil record is in the Oligocene in California (for pholad palaeoecology see Kennedy 1974, 1993) and fossil pholad beds can be observed at 2–15 meters above the high tide line on cliffs in Coos Bay and southward (Evans 1968d).
Local Distribution: Coos Bay distribution at Pigeon Point, Fossil Point, and Coos Head. Other Oregon sites include Yaquina and Netarts Bays (Turner 1955).

Habitat: Individuals found in open coast habitats as well as exposed bays (Haderlie and Abbott 1980), where they bore into mud and rock and prefer northeast surfaces, where algae and light are reduced (similar to barnacles). The ability of *P. penita* to utilize a wide variety of substrates leads to the wide geographic distribution (Evans 1968d). Harder substrates produce individuals with heavier, less elongate shells and larger muscles (Evans and LeMessurier 1972). The substrate also affects the burrowing speed, as harder rock leads to individuals that burrow and grow more slowly. For example, individuals in soft rock may mature (and stop burrowing) at three years, while those in harder rock may mature as late as 21 years. Such timing corresponds to burrowing speeds that are 4 (hard substrate) to 50 mm (soft substrate)/year (Haderlie and Abbott 1980). Substrate type (e.g., hard versus soft) has been shown to alter the piddock shell shape, size and hardness (Evans 1968c; Tajima and Kondo 2003). Piddock burrows have the ability, particularly when individuals are present in large numbers, of compromising the stability of shorelines throughout their lifetimes (e.g., *Pholas dactylus*, *Barnea candida*, *B. parva*, Pinn et al. 2005; Davidson and de Rivera 2012). The ability of *P. penita* to burrow into a variety of substrates (e.g., clay, sandstone, cement, Coan and Valentich-Scott 2007) renders it a significant species in the erosion and destruction of marine structures (e.g., jetties). For example, erosion from physical factors leads to roughly 0.5 mm substrate eroded/year while that due to erosion from *P. penita* is 12 mm/year (Fossil Point, Coos Bay, Evans 1968a).
Salinity: Collected at salinities of 30.
Temperature: Cold to temperate waters.
Tidal Level: Intertidal and subtidal (Evans 1967), with a broad distribution vertically, individuals are found as high as +0.6 m (Coos Bay, Evans 1968a) and as low as -91 m (Kofoid and Miller 1927).
Associates: Other nestling and burrowing invertebrates utilize the burrows of *Penitella penita* (e.g. polychaetes *Thelepus*, *Halosydna*, clams *Hiatella*, *Entodesma*, *Zirfaea*, Coos Bay, Table 2, Evans 1967).
Abundance: Often co-occurs with other pholads (e.g., *Zirfaea pilsbryi*, *Penitella* spp.,

Netastoma rostratum) (Haderlie 1979). In Oregon, *Penitella penita* accounted for up to 90% of all boring species in the low intertidal and has been called the most common and widely distributed rock boring clam in the eastern Pacific (Evans 1968d). However, in California, *P. penita* was less abundant than the congeners, *P. conradi* and *P. richardsoni* (Haderlie and Abbott 1980). Fossil records (El Rosario, Baja California) suggest densities as high as 200 individuals/m^2 (Ledesma-Vazquez and Johnson 1994).

Life-History Information
Reproduction: Reproductive strategies are variable among the Pholadidae (e.g., reproduction in *Barnea candida* includes hermaphroditic, dioecious, oviparous and larviparous, Evans 1970). *Penitella penita* is dioecious and oviparous. Sexual maturity is postponed until growth stops (Evans 1970), as individuals become sexually mature once callum is formed and their foot atrophies (Haderlie and Abbott 1980). Gonad morphology in mature individuals suggests gamete development in February, ripe gametes in June and spawning in July (Fossil Point, Coos Bay, Evans 1970). The development of *P. penita* has not yet been described. Boyle and Turner (1976) described the reproduction and development of the east coast pholad, *Martesia striata.* This species spawns in February and eggs are translucent white and 45–46.8 µm in diameter (33°C, Turner and Johnson 1968; 21°C, Boyle and Turner 1976).
Larva: Bivalve development, including members of the Pholadidae, generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. However, in the deep water pholad genus, *Xylophaga*, species brood larvae until late veliger stages (Kennedy 1974; Voight 2009). Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the "D" shaped shell. This initial shell is

called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.) Larvae of *P. penita* are free swimming with a pelagic duration of two weeks (Haderlie and Abbott 1980) with peaks in settlement occurring from August to September (Evans 1970). The development of other pholads (e.g. *Barnea truncata*, Chanley 1965; *Cyrtopleura costata*, Chanley and Andrews 1971; *Martesia striata*, Boyle and Turber 1976) proceeds as planktotrophic veliger larvae. After 24 hours, *M. striata* larvae are straight hinge veligers (68 µm in length and 59 µm in height, Boyle and Turner 1976). After eight days, they are umbo larvae (129–224 µm) and they are pediveligers by 28–32 days (224–236 µm) post fertilization. Metamorphosis in *M. striata* occurs after 48–53 days (see Table 1, Figure 1, Boyle and Turner 1976). (see also Campos and Ramorino 1990 for planktonic pholad larvae from Chile).
Juvenile: Average time to maturity is 33 months and metamorphosis is marked by the resorption of the foot (Evans 1968a, 1970). This species is unusual in having determinate growth where, at about three years, individuals metamorphoses into non-boring adults (about 55 mm in length). Crowding may induce early metamorphosis (Evans 1968d). Anterior end of juveniles is soft (without callum), while animal is actively burrowing. Exposed foot is circular and has developed as a suction disc (Fig. 5).
Longevity: Lives until substrate surrounding the burrow erodes enough to make it subject to predators. Longevity is thus dependent on erosion rate and varies with rock hardness (Haderlie and Abbott 1980). At Fossil Point, erosion process takes about six years following metamorphosis (nine years total lifespan, Evans 1970).
Growth Rate: Once they settle, growth proceeds at a rate of 22 growth bands/year (Haderlie and Abbott 1980). Growth occurs in

two distinct phases: the first where individuals are actively boring and growing, and the second where both boring and growth stops (Evans 1970).

Food: A suspension feeder, *P. penita* uses long siphons and gills to filter food.

Predators: Flatworms *Stylochoplana, Notoplana inquieta,* where worms enter the shell, eat the flesh, and lay eggs (Evans 1967). Additionally, interference from *Botula californiensis*, which settles on the burrow entrance may lead to the death of *P. penita* individuals (Evans 1967). Other invertebrates predators include *Ceratostoma foliatum, Roperia poulsoni* (Haderlie and Abbott 1980).

Behavior: Pholads are the most efficient burrowers of the seven families of rock-boring bivalves (Evans 1968a). Grinding is assisted by keeping algae out of burrow with sea water, by loosening rock grains, and by ciliary currents which flush out cavity (Keen 1971). The callum shape is determined by the contours of the burrow and, in artificial burrows, the callum can be rather square (versus pear-shaped, Haderlie 1981b).

Bibliography

1. BOYLE, P. J., and R. D. TURNER. 1976. Larval development of wood boring piddock *Martesia striata* (L.) (Mollusca: Bivalvia: Pholadidae). Journal of Experimental Marine Biology and Ecology. 22:55-68.
2. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In:* Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
3. CAMPOS, B., and L. RAMORINO. 1990. Larvae and postlarvae of Pholadacea from Chile (Mollusca, Bivalvia). Revista de Biologia Marina. 25:15-64.
4. CHANLEY, P. E. 1965. Larval development of a boring clam, *Barnea truncata*. Chesapeake Science. 6:162-166.
5. CHANLEY, P. E., and J. D. ANDREWS. 1971. Aids for identification of bivalve larvae of Virginia. Malacologia. 11:45-119.
6. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
7. DAVIDSON, T. M., and C. E. DE RIVERA. 2012. Per capita effects and burrow morphology of a burrowing isopod (*Sphaeroma quoianum*) in different estuarine substrata. Journal of Crustacean Biology. 32:25-30.
8. EVANS, J. W. 1967. Relationship between *Penitella pentia* (Conrad, 1837) and other organisms of the rocky shore. The Veliger. 10:148-151.
9. —. 1968a. Factors modifying the morphology of the rock-boring clam, *Penitella penita* (Conrad, 1837). Journal of Molluscan Studies. 38:111-119.
10. —. 1968b. Growth rate of the rock-boring clam *Penitella penita* (Conrad 1837) in relation to hardness of rock and other factors. Ecology. 49:619-628.
11. —. 1968c. The effect of rock hardness and other factors on the shape of the burrow of the rock-boring clam *Penitella penita* (Conrad 1837) (Family Pholadidae). Palaeogeography, Palaeoclimatology, Palaeoecology. 4:271-278.
12. —. 1968d. The role of *Penitella penita* (Conrad 1837)(Family Pholadidae) as eroders along the Pacific coast of North America. Ecology. 49:156-159.
13. —. 1970. Sexuality in rock-boring clam *Penitella penita* (Conrad 1837). Canadian Journal of Zoology. 48:625-627.
14. EVANS, J. W., and D. FISHER. 1966. A new species of *Penitella* (family Pholadidae) from Coos Bay, Oregon. The Veliger. 8:222-224.
15. EVANS, J. W., and M. H. LEMESSURIER. 1972. Functional micromorphology and circadian growth of the rock-boring clam *Penitella penita*. Canadian Journal of Zoology. 50:1251-1258.
16. HADERLIE, E. C. 1979. Range extension for *Penitella fitchi* Turner,

1955 (Bivalvia, Pholadidae). Veliger. 22:85-85.

17. —. 1981a. Growth rates of *Penitella penita* (Conrad, 1837), *Chaceia ovoidea* (Gould, 1851)(Bivalvia, Pholadidae) and other rock boring bivalves in Monterey Bay. Veliger. 24:109-114.

18. —. 1981b. Influence of terminal end of burrow on callum shape in the rock boring clam *Penitella penita* (Conrad, 1837)(Bivalvia, Pholadidae). Veliger. 24:51-53.

19. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In:* Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.

20. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In:* Reproduction and development of marine invertebrates of the northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.

21. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.

22. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.

23. KENNEDY, G. L. 1974. West American Cenozoic Pholadidae. Memoirs of the San Diego Society of Natural History. 8:1-128.

24. —. 1989. Status of *Penitella gabbii* (Tryon, 1863) in the Eastern and Western Pacific, and description of the previously misidentified Eastern Pacific species (Bivalvia, Pholadidae). Veliger. 32:313-319.

25. —. 1993. New Cretaceous and Tertiary Pholadidae (Mollusca, Bivalvia) from California. Journal of Paleontology. 67:397-404.

26. KENNEDY, G. L., and J. M. ARMENTROUT. 1989. A new species of chimney-building *Penitella* from the Gulf of Alaska (Bivalvia, Pholadidae). Veliger. 32:320-325.

27. KOFOID, C. A., and R. C. MILLER. 1927. Biological section, p. 188-343. *In:* Marine Borers and their Relation to Marine Construction on the Pacific Coast. Final Report of the San Francisco
Bay Marine Piling Committee, San Francisco,. Final Report of the San Francisco
Bay Marine Piling Committee, San Francisco.

28. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.

29. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.

30. LEDESMA-VAZQUEZ, J., and M. E. JOHNSON. 1994. Late pliocene abrasion platform from the Cantil Costero formation of Baja California. Ciencias Marinas. 20:139-157.

31. LLOYD, F. E. 1896. On *Pholadidea penita*, and its method of boring. Science. iv:188-190.

32. MARSHALL, B. A., and H. G. SPENCER. 2013. Comments on some taxonomic changes affecting marine bivalvia of the New Zealand region recently introduced in Huber's Compendium of Bivalves, with some additional taxonomic changes. Molluscan Research. 33:40-49.

33. PINN, E. H., C. A. RICHARDSON, R. C. THOMPSON, and S. J. HAWKINS. 2005. Burrow morphology, biometry, age and growth of piddocks (Mollusca: Bivalvia: Pholadidae) on the south coast of England. Marine Biology. 147:943-953.

34. REFT, A. J., and J. R. VOIGHT. 2009. Sensory structures on the siphons of wood-boring bivalves (Pholadidae: Xylophagainae: *Xylophaga*). Nautilus. 123:43-48.

35. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.

36. TAJIMA, T., and Y. KONDO. 2003. The relationship between functional shell morphology and nature of the bored substratum in the family Pholadidae (Bivalvia). Fossils (Tokyo):5-19.

37. TURNER, R. D. 1955. The family Pholadidae in the western Atlantic and the eastern Pacific. II. Martesiinae, Jouannetiinae and Xylophaginae. Johnsonia (Harvard Unviersity). 3:65-160, 80-85.

38. TURNER, R. D., and A. C. JOHNSON. 1968. Biology of marine wood-boring mollusks, p. 259-301. *In:* Marine borers, fungi and fouling organisms of wood. E. B. G. Jones and S. K. Eltringham (eds.). Organization for Economic Cooperation and Development, Paris.

39. VOIGHT, J. R. 2009. Diversity and reproduction of near-shore vs offshore wood-boring bivalves (Pholadidae: Xylophagainae) of the deep eastern Pacific Ocean, with three new species. Journal of Molluscan Studies. 75:167-174.

40. WILSON, E. C., and G. L. KENNEDY. 1984. The boring clam, *Penitella conradi*, (Bivalvia: Pholadidae) in nephrite from Monterey County, California. Nautilus. 98:159-162.