
Nutricola tantilla

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Veneridae

Taxonomy: Originally described under the name *Venus (Trigona) tantillus* based on shell structure characters by Gould in 1853, this species was transferred to the genus *Transennella* in 1884 by Dall. The latter genus is routinely seen in manuscripts (e.g., see Kabat 1986; Lindberg 1990; Gallucci and Kawaratani 1975; Falese et al. 2011). However, according to Bernard (1982), the genus *Transennella* is limited to warm and tropical regions of east and western America and he designated the new genus, *Nutricola* (for diagrammatic comparison of the two genera, see Fig. 1–2 Bernard 1982; but see Lindberg 1990). Members of the genus *Transennella* are characterized by a hinge with three cardinal teeth, an elongated anterior lateral tooth on the left valve, an angular pallial sinus, and a grooved inner ventral shell margin (Gray 1982). Two varieties of *N. tantilla* were noticed in 1970 (Gray 1982). Together, these varieties were previously synonymized with the sympatric species, *N. confusa* (designated in 1982 by Gray). But upon investigation of morphological characters of internal anatomy and shell morphology, a neotype of *N. tantilla* was designated (Gray 1982). Common synonyms for *N. tantilla* include: *Venus tantillus*, *Transennella tantilla* and other known synonyms include *Venus rhyssomia* and *Psephis tantillus* (Gray 1982).

Description

Size: A relatively small clam, adults up to 5–6 mm in length (Kozloff 1993). The illustrated specimen (Figs. 1–2) is 3.5 mm in length, 3.0 mm tall, and 1.6 mm in diameter. The weight can be determined by clam length: $\log \text{ weight (mg)} = -0.85598 + 3.09033 \log \text{ length (mm)}$; the average dry weight of the largest individuals collected in False Bay, Washington was 30.2 mg (Pamatmat 1966).
Color: Cream in color, with posterior (end that bears the siphons) one third of shell a purple brown color that radiates from the beak

(Fig. 1). Shell interior is creamy white, with same purple or brown coloration. There is occasionally a radial strip anteriorly (Oldroyd 1924; Kozloff 1993) (Figs. 3–4).

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). *Nutricola tantilla* is a small venerid species, that is unique among venerids by its **byssus**, and an umbo that is situated almost exactly between anterior and posterior ends such that the clam looks like an isosceles triangle from the side (see Fig. 352, Kozloff 1993) (Fig. 1).

Body:

Color:

Interior: The ligament is completely external; there is no resilifer or internal ligament (Fig. 2).

Exterior:

Byssus: Byssal threads are fine and clear (Fig. 1a) and used for attachment to substrate, which is rare in Veneridae (Narchi 1970, 1971). Byssal gland in middle of foot, and threads also join young in brood pouch.

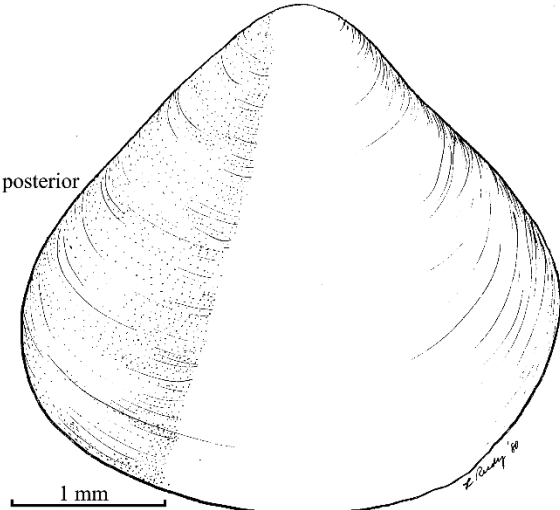
Gills:

Shell:

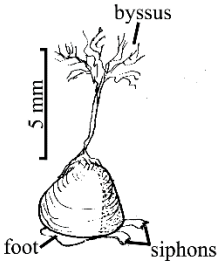
Interior: Ventral margin is smooth, i.e., not crenulated. The margin is with a few oblique grooves on inner ventral margin, but these are visible only with very high magnification. The pallial sinus is rounded, bent anteriorly, and parallel to the ventral margin; not bent sharply upward (Fig. 3).

Exterior: Overall shell shape is not unlike a rounded isosceles triangle (Kozloff 1993) (Fig. 1). Shape is elongate or oval, heavy, solid, slightly longer than high, and clearly triangular. Anterior and posterior dorsal margins are straight. The beaks are almost central, barely anterior to midline, often eroded (Kozloff 1974). The surface sculpture is with fine concentric grooves only, no other sculpture (Kozloff 1974). The valves

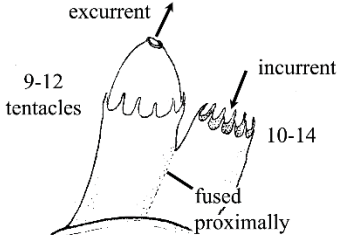
Nutricola tantilla



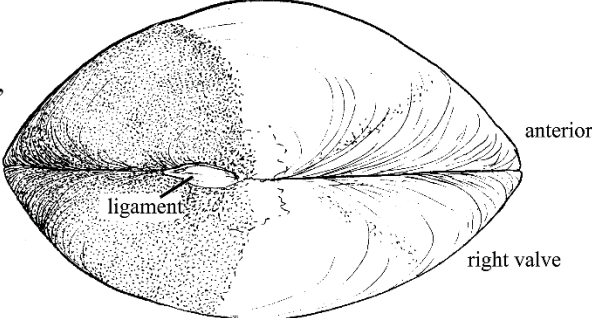
1. *Nutricola tantilla*, right valve (L:3.5mm, D:1.6mm, H:3.0mm) x28: shell solid, triangular; posterior third purple; fine concentric sculpture; no periostracum.



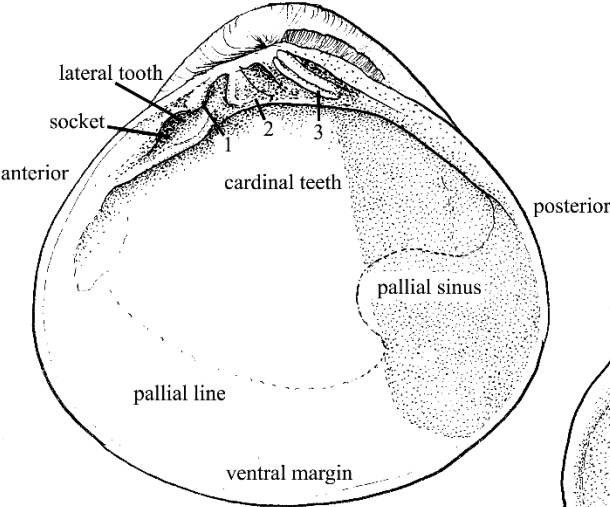
1a. Live clam x4



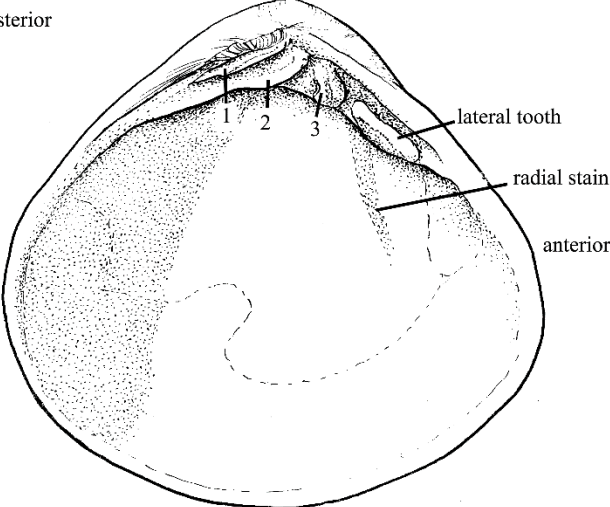
1b. Siphons



2. Exterior (dorsal view): valves equal; beaks almost central; ligament external; no gape to valves.



3. Interior, right valve: three divergent cardinal teeth, one anterior lateral tooth, socket; pallial sinus rounded; purple stain posteriorly; smooth ventral margin.



4. Interior, left valve: three cardinal teeth, one anterior lateral tooth; anterior radial purple stain.

are equal and not gaping. There is no rough periostracum, but byssal attachments (see **Byssus**) may cover part of surface.

Hinge: The hinge area has three divergent cardinal teeth in each valve (Figs. 3–4). The lateral teeth are conspicuous and there are anterior teeth in both valves. There is a socket for the lateral tooth in the right valve (Fig. 3).

Eyes:

Foot: The foot is large, and can bury individuals rather quickly.

Siphons: Siphons are short, sensitive, and extend only a few mm from body. The excurrent and incurrent siphons are fused proximally, with long tentacles that are flexible. There are 9–12 tentacles on the excurrent siphon and 10–14 on the incurrent (a defining character of this species, Maurer 1967b) (Fig. 1b).

Burrow: Individuals are hardly buried and found just under surface of sand (upper 1 cm layer) (Pamatmat 1969; Kozloff 1993); burial too deep leads to mortality in *N. tantilla* (Gallucci and Kawaratani 1975). The presence of byssal threads in this species may be explained by a need to maintain location despite a shallow burrow (Narchi 1970).

Possible Misidentifications

Veneroida is a large bivalve order, characterized by well-developed hinge teeth, including most heterodonts. The family Veneridae is characterized by a hinge without lateral teeth, ligament that is entirely external, radial ribs on shell exterior, and three cardinal teeth on each shell valve. There are 12–16 species reported locally in this family within the genera *Nutricola*, *Saxidomus*, and *Leukoma*, with two species in each, and *Gemma gemma*, *Irusella lamellifera*, *Tivela stultorum*, *Venerupis philippinarum*, *Mercenaria mercenaria*, *Callithaca tenerrima*, each with a single species represented locally.

Nutricola species are small, with shells usually less than 10 mm in length. This genus is defined by a small, ovate shell, inconspicuous beaks, a sunken ligament, and ventral shell margins with weak longitudinal ridges; the genus originated in the Miocene (Bernard 1982). *Gemma gemma* also has a

small shell, but it is triangular in shape compared to *Nutricola* species with elongate or oval shells. *Tivela stultorum* also has a triangular shell, but individuals are larger than *G. gemma* and have a smooth shell surface with shiny periostracum. *Gemma gemma*, the small (about 2.5 mm) purple-marked Atlantic bivalve, can be common in bay mud (for comparison of *N. tantilla* (as *V. tantillus*) and *G. gemma*, see Bernard 1982 and Narchi 1971). It is triangular, and no longer than high, its left hinge lacks the characteristic anterior lateral tooth of *N. tantilla* and **byssus**. Its ventral margin is finely crenulate, not smooth and its pallial sinus is bent sharply upward, not rounded and angled anteriorly. *Gemma* often has *Enteromorpha* attached to its posterior and it can be found in the same habitat as *N. tantilla* (e.g., Puget Sound, Washington) but in California (Tomales Bay, California) it occupies a different niche (Narchi 1971). *Nutricola tantilla* has a shell that is white in color and siphons that are fused (or nearly so) at the tips. *Nutricola confusa* has a shell that is purple in color, siphons that bear a conspicuous cleft as well as conspicuous anterior lateral teeth, which are weak in *N. tantilla*. *Gemma* species also have a series of tiny teeth along the inside lower margin of one valve, which are lacking in *N. tantilla* (Kozloff 1993).

Nutricola tantilla has purple markings, an eroded beak, and clearly marked concentric lines on its shell. Its hinge plate is wide, its anterior tooth well-developed, and it has split siphons (for half their length), with flexible tentacles (9–12 on the excurrent, 10–14 on the incurrent siphon, Fig. 1b)). *Nutricola confusa* is all white, without purple on the posterior, with only an occasional brown slot anterior to its beaks. The beaks are prominent, not eroded and the shell sculpture is faint, consisting of numerous fine lines. The hinge plate is narrow, and the anterior tooth is thin and lamellar. This species has siphons fused for almost their whole length, and short stiff siphon tentacles, with 10–14 tentacles on the excurrent siphon, 11–16 on the incurrent one (Maurer 1967b). *Nutricola confusa*, also occurs from Coos Bay, Oregon to central California, and is the same size, but lacks the distinctive purple color of the shell evident in *N. tantilla*

(see **Color**) (Russel and Huelsenbeck 1989; Kozloff 1993). The two species are very similar, but differ in the shell shape, degree of siphon fusion and tentacle number (Falese et al. 2011). (For full comparative morphology of the two species, see Gray 1982.)

The remaining species have shells larger than 10 mm in length. Some species have shell sculpturing that is dominated by commarginal ribs with fine radial ridges and others have shells that have radial ridges with inconspicuous, or not predominating, commarginal ribs. Of those in the former category, *I. lamellifera* has widely spaced commarginal lamellae and a shell that is short compared to *M. mercenaria* and *C. tenerrima*. The two latter species have elongated shells, no anterior lateral teeth and valves that do not gape. *Saxidomus* species also have an elongate shell, when compared to *I. lamellifera*, but they possess anterior lateral teeth and valves that are separated by a narrow gape, posteriorly. *Saxidomus nuttalli* and *S. giganteus* can be differentiated as the former species has a elongate and thinner shell as well as a narrow escutcheon (not present in *S. giganteus*). The shell sculpturing in *S. giganteus* also appears smooth as the commarginal ribs are thin, low and tightly spaced, while the opposite is true for *S. nuttalli*.

The venerid species without predominately commarginal ribs include *V. philippinarum* and members of the genus *Leukoma*. *V. philippinarum*, the introduced Japanese cockle (see Fig. 1a *Leukoma staminea*, description in this guide), with strong radial ribs and a prominent ligament, elongate oval shell and, like *N. tantilla*, a purple stain in the interior. *Leukoma* species differ from *V. philippinarum* by having an inner ventral margin that is not smooth, a ligament that is not prominent and fused siphons. *Leukoma staminea* has shell sculpturing that is dominated by numerous radiating ribs, with faint commarginal ridges and the opposite is true for its congener (i.e., dominant radiating and commarginal ridges).

Ecological Information

Range: Type locality is Santa Barbara, California. Known range includes the

northeast Pacific from Sitka, Alaska, to southern California (Oldroyd 1924).

Local Distribution: Local distribution includes sites in Coos Bay and the South Slough channel edge).

Habitat: Sand or sandy mud in protected bays. This specimen was collected from clean sand at the channel edge. They are often in other shells, where they attach by byssal threads. The presence of **byssus** may limit the ability of this species to spread geographically. They are also found among eelgrass (e.g., *Zostera* spp., *Phyllospadix* spp.) roots (Obreski 1968), and in firm mud or sandy gravel (Smith 1960). They are nearly always in top centimeters of the sediment (Smith 1960). *Nutricola tantilla* can tolerate turbidity by remaining closed for long periods to avoid the deleterious effects of sediment burial (Maurer 1967b). The largest number of *N. tantilla* were observed in a combination of silt and clay habitats, with sediment size less than 63 μm , although individuals were also observed in fine (> 63 μm), medium (> 250 μm , and coarse (> 500 μm) sand (see Table 1 Tomales Bay, California, Maurer 1967b).

Salinity: Full seawater, collected at salinities of 30.

Temperature: Cold to temperate waters (e.g. 8–11°C, Pamatmat 1969), as indicated by geographical range.

Tidal Level: Low intertidal, top 2.5 cm of sand and mud (Kabat and O'Foighil 1987), as well as offshore down to 35 m (Keen and Coan 1974). Most dense at mean lower low water (False Bay, Washington, Pamatmat 1969).

Associates: Heavily infested by the trematodes, *Telolecithus pugetensis* and *Parvaterma* (Obreski 1968; Ruiz 1991). In *Telolecithus pugetensis*, *N. tantilla* is the first, and sometimes the second, intermediary host. *Nutricola tantilla* ingests trematode eggs, which, as sporocysts, destroy much of its visceral mass and gonads; infected adults are sterile (Tomales Bay, DeMartini and Pratt 1964). Gametes are reduced and sometimes completely removed by the presence of parasitic trematode larvae (Kabat 1985, 1986; Kabat and O'Foighil 1987). *Nutricola tantilla* occasionally, co-occurs with the congener *N. confusa* and the clam, *Macoma inquinata*. Parasitism by the digenetic trematode,

Parvatrema borealis, leads to genetic resistance over time (Grosholz 1994).

Abundance: Individuals most dense at mean lower low water in troughs between sandbars. *Nutricola tantilla* can be one of the numerically dominant animals (Puget Sound, Washington). The local density was measured as 1,500–2,500/m² (South Slough, Coos Bay) (Asson, pers com.).

Life-History Information

Reproduction: Reported as a protandrous hermaphrodite by some (Hansen 1953; Gray 1982; Kabat and O’Foighil 1987) and dioecious by others (see Lutzen et al. 2015); viviparous. Individuals broods young within chamber: eggs and young of all stages can be found in the brood chamber between inner gill and body wall, i.e., the inner demibranch (see Fig. 2, Kabat 1985; Falese et al. 2011) (*Nutricola* = “little nurse”, Bernard 1982). A single brood can contain individuals spanning a range of developmental stages (Kabat 1985; Russell and Huelsenbeck 1989; Falese et al. 2011). Sperm of *Nutricola* are modified, i.e., long and needle-shaped heads, the tail of *N. tantilla* is longer and wider than those of the congener, *N. confusa* (see Fig. 2, Geraghty et al. 2008; Falese et al. 2011), they are packaged into a spermatozeugmata (see Fig. 1 Falese et al. 2011). Males elicit what is called “spermcasting” in which they broadcast spawn sperm while females retain eggs, which are later fertilized within the female brood chamber (Geraghty et al. 2008; Falese et al. 2011). The sperm most likely enters the female chamber via the siphon (Geraghty et al. 2008) and females likely store sperm within nonepithelial tissue until use (Lutzen et al. 2015). The head piece that is 17–18 µm in length and flagellum 48 µm long (for sperm cell ultrastructure, see Lutzen et al. 2015); oocytes are approximately 250 µm in diameter (Hansen 1953; Kabat and O’Foighil 1987). Gametes are released into space between the inner gill and visceral mass where they are brooded until they are released as juveniles (Kabat and O’Foighil 1987; Brink 2001). Brood size estimates vary from with up to 40 (Kozloff 1993) to 300 (Kabat and O’Foighil 1987) embryos per brood, in a mass surrounded by an envelope, and is dependent on the size of the individual

brooding (number of embryos increases in proportion to the adult length cubed, Kabat 1985). Nearly all large clams, which are mostly female, will have broods throughout the year. There is no clear spawning period, but young are released only during summer months (Hansen 1953; Kozloff 1993; Kabat and O’Foighil 1987). *Nutricola tantilla* are among the smallest clams, and males and females are found in equal numbers (Hansen 1953). Their fecundity is affected by, what are sometimes sterilizing, trematode sporocysts (see **Associates**, DeMartini and Pratt 1964). Broods observed in early spring (May–June) in False Bay, Washington (Gray 1982).

Larva: Development takes place in mantle cavity (see **Reproduction**) and the size of adult determines number of the young. Larvae are without a velum, or pelagic stage (Hansen 1953). The oldest larval stage was approximately 650 µm in length (Hansen 1953). Some bivalve species (e.g. *Mytilus edulis*, *Macoma balthica*) have two dispersal periods. The initial larval dispersal and settlement into the benthos, is followed by potential dispersal from the benthos by thread drifting on water currents via mucous threads by juveniles (i.e., “thread drifting”, Martel and Chia 1991).

Juvenile: Males reach sexual maturity at 3.5–4mm in length, while females mature at larger sizes, 3.5–7 mm in length (Kabat and O’Foighil 1987). The smallest adults with eggs were 3.2 mm in length (Pamatmat 1966).

Longevity: *Nutricola tantilla* longevity is probably a little over one year (Hansen 1953; Kabat and O’Foighil 1987).

Growth Rate: In four months, individuals grow 4 mm and from 2.6 mg to 30 mg (September); the total weight gain per individual is 0.953 mg per month (Hansen 1953; Pamatmat 1966). In 2000, Jacobs et al. found, through in-situ hybridization, that gene expression involved in early development of cells surrounding the shell valves appears to have a single evolutionary origin for skeletogenesis in all bilaterian phyla (see Jacobs et al. 2000).

Food: *Nutricola tantilla* is a suspension feeder that eats small particles (not a deposit feeder) (Norchi 1971). Feeding may primarily

occur at night (Obreski 1968). Common foods include diatoms in the following genera: *Navicula*, *Coscinodiscus*, as well as *Nitzschia* and *Melosira* (Maurer 1967b).

Predators: Known predators include fish (e.g., *Cymatogaster* (surf perch)) and trematodes (see also **Associates**) (DeMartini and Pratt 1964), shorebirds, and some gastropods (Obreski 1968). The nonindigenous green crab, *Carcinus maenas*, also preys upon and reduces the population density of both *N. tantilla* and *N. confusa* (Grosholz et al. 2000).

Behavior: Individuals can bury themselves in less than a minute if disturbed (Norchi 1971), but they can be found on or near the surface when feeding.

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