Saxidomus giganteus

Beefsteak clam, butter, or Washington clam

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

Taxonomy: Originally described as *Venerupis gigantea*, other synonyms include conflicts of taxonomic genus-species gender agreement, as *Saxidomus* is feminine (article 31.2, ICZN): *S. gigantea* (e.g., Paul et al. 1976; Robinson and Breese, 1982; Bendell 2014), as well as *Venus maxima*.

Description

Size: Adults average 10 cm in length (Paul et al. 1976; Kozloff 1993).

Color: Shell exterior is whitish, but can also have patches of blackish discoloration; juvenile exterior is sometimes tan in color (Kozloff 1993). The shell interior is also white.

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).). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well-developed hinge teeth. There are 22 local families, and members of the Veneridae have three cardinal teeth on each valve (see Fig 302, Kozloff 1993; Plate 396H, Coan and Valentich-Scott 2007) (Fig. 4).

Body:

Color:

Interior: The ligament is completely external, ad is seated on a long, massive nymph, or chondrophore (Fig. 4). The body tissue is rubbery and is "superb for chowder" (Kozloff 1993). Maximal systolic pressure was recorded for *Tresus capax* (see description in this guide) to be 13 cm H_20, which is higher than 11 cm H_20 recorded for *Saxidomus giganteus* (Florey and Cahill 1977).

Exterior:

Byssus:

Gills:

Shell: The shell is oval in shape (Coan and Carlton 1975), and the posterior is truncate (Keen and Coan 1974).

Interior: The valves are similar in shape. The inner ventral margin is smooth (Keen and Coan 1974), and the inner surface is white and porcelaneous. The muscle scars are dark and subequal in size. The pallial line is continuous (but broken by a sinus), not a series of scars (Fig. 3). The flesh is often reddish, hence one common name, the beefsteak clam.

Exterior: Exterior sculpture is with raised concentric growth lines and grooves, with no radial lines (Fig. 1). The valves are very similar, the shell is thick, heavy, and deep (Fig. 2). The most prominent lines representing periods of slowed growth (Kozloff 1993). The valves gape only slightly at posterior end (gape less than 1/4 shell width) (Kozloff 1993). Individuals can retract their siphon, but not feet. The shell microstructure was described for many veneroid clams by Shimamoto (1986), where *Saxidomus* species were characterized by a Type I shell composed of both composite prismatic and crossed lamellar structure (Shimamoto 1986).

Hinge: The hinge is very thick, heavy, and is posterior and external. There are three cardinal hinge teeth, flanked by a long lateral tooth in each valve (Fig. 4).

Eyes:

Foot:

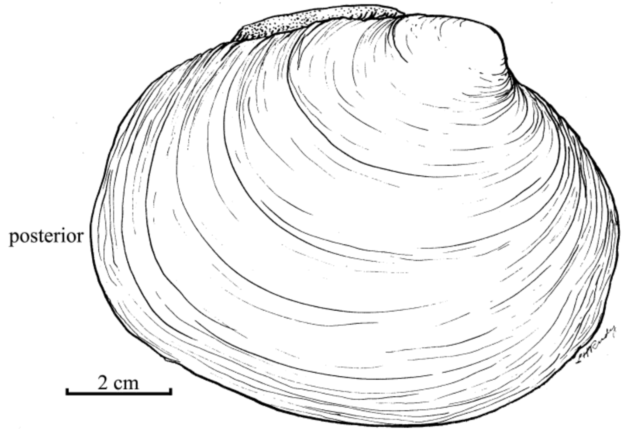
Siphons:

Burrow: Inhabits burrows up to 30 cm deep (Kozloff 1993). The burrow opening is recognizable by a cigar-shaped or deflated figure eight-shaped hole that is 1.2–2 cm long (Jacobson 1975).

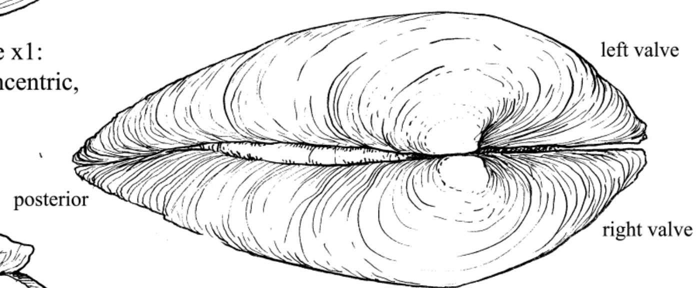
Possible Misidentifications

Veneroida is a large bivalve order, characterized by well-developed hinge teeth,

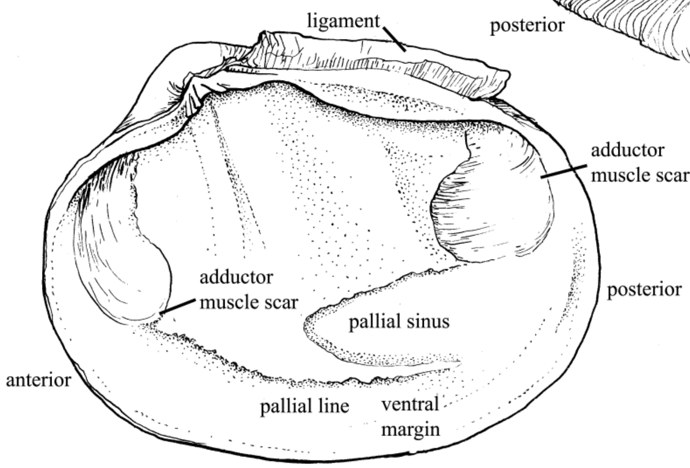
Saxidomus giganteus



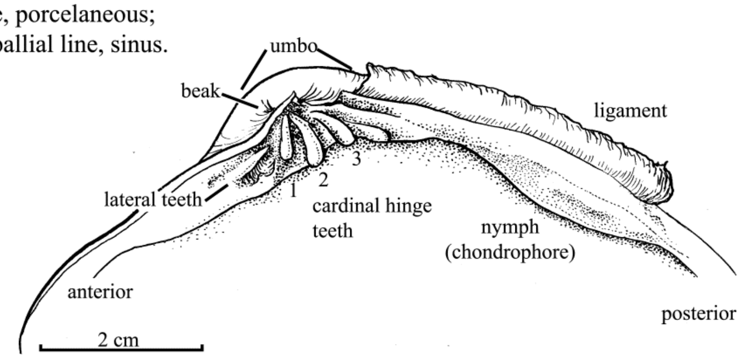
1. *Saxidomus giganteus*, exterior, right valve x1: shell whitish, oval; posterior truncate; concentric, rough ribs close together; valves similar, thick, heavy.



2. Exterior (dorsal view): valves similar, deep; hinge heavy, ligament external.



3. Interior, right valve: margin smooth, surface white, porcelaneous; muscle scars similar; strong pallial line, sinus.



4. Interior, right valve (dorsal region) x1.5: three cardinal hinge teeth; ligament seated on nymph; long lateral teeth.

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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*), *Tivelatultorum*, *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. *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.

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 an 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*. Its shell is more elongate, the ribs heavier, rougher and more conspicuous (Coan and Carlton 1975) and the interior is often marked posteriorly with purple. *Saxidomus nuttalli*, the larger, more southern species, is found in California in the same habitat as *S. giganteus*, but apparently does not extend into Oregon. (*S. nuttalli* is the only *Saxidomus* in Humboldt Bay, however). *Saxidomus nuttalli*, referred to as the "money clam" because of its representation as currency for Californian native American tribes (Ricketts and Calvin 1952), resembles *S. giganteus*, but is larger (ironically, 12.7 compared to 7.6 cm) and has more prominent growth lines and a shell that is purplish at the siphonal end ((Ricketts and Calvin 1952; Kozloff 1993). *Saxidomus nuttalli* is more common in the southern end of its distribution, while *S. giganteus* is more common north (Ricketts and Calvin 1952).

Panopea generosa, the deep-burrowing geoduck, is quadrate, and gapes widely. *Tresus capax*, the gaper clam, (family Mactridae, see description in this guide), is also quadrate, fairly smooth with chalky white shell exterior. The truncated posterior gapes moderately, its ligament is partly internal, the cardinal teeth are "A" shaped, and the shell has a dark, eroded partial covering.

Ecological Information

Range: Type locality is not specified (see Orr et al. 2013). Known range includes the Aleutian Islands, Alaska to Monterey, California; *S. giganteus* is rare in the southern range.

Local Distribution: Locally occurs in bays and estuaries, rarely on open coast or inlets with oceanic influence (Packard 1918). Common from Alaska to San Francisco Bay, California, but rare south of Humboldt bay, California (Kozloff 1993).

Habitat: Occurs in mud or sand (Coan and Carlton 1975), gravelly beaches (Puget Sound, Washington). "Clam gardens", created adjacent to intertidal rock walls constructed by human populations in the Holocene, have four times as many *S. giganteus* and twice as many *P. staminea* (see description in this guide) individuals as non-walled beaches, and transplanted juveniles of the latter species also grow faster (1.7 times faster) in clam gardens (Groesbeck et al. 2014).

Salinity: Occurs in sites with average yearly salinity is 29 (range 24–32, Puget Sound, Washington Goong and Chew 2001).

Temperature: Individuals prefer temperate-cold waters (see **Range**).

Tidal Level: Individuals most commonly collected from just under the sediment surface, but also found up to 30 cm deep.
Associates: Occasionally infested with immature specimens of commensal pea crab *Pinnixa littoralis,* but usually free of symbiotic or parasitic associates (Ricketts and Calvin 1971). Co-occurs with other clams, *Tapes philippinarum* and *Protothaca staminea* as well as the shore crab, *Hemigrapsus* (Nickerson 1977; Goong and Chew 2001). *Protothaca staminea* and *S. giganteus* co-occur on Kiket Island, Washington, where the greatest diversity and richness of other marine invertebrates are found (Houghton 1977). Co-occurs with other clams (e.g., *Tresus capax* and *T. nuttallii*, Gillispie and Bourne 2004; *Sanguinolaria nuttallii*, Peterson and Andre 1980), and the presence of the latter species is negatively effected by *S. nuttallii* (Peterson and Andre 1980).
Abundance: "The most abundant clam of the Northwest" (Ricketts and Calvin 1971), *Saxidomus giganteus* was a commercially harvested species in Puget Sound, Washington (Kozloff 1974). Up to 352 individuals/m^2 were reported from beaches in British Columbia, Canada (Gillespie and Bourne 2005). In British Columbia beaches, assessed in 1993, *S. giganteus* density was as high as 376 individuals/m^2 (Gillispie and Bourne 2004).

Life-History Information

Reproduction: Separate sexes reproduce by free-spawning, external fertilization and development via a free-swimming larva. Oocytes are 80–90 µm in diameter and surrounded by a jelly layer that is 230 µm in diameter (see Fig. 1, Breese and Phibbs 1970). Spawning from March–June has been reported for the Oregon coast (Fraser 1929; Robinson and Breese 1982; Kabat and O'Foighil 1987). Gametogenesis occurs in fall months and is complete by August and September in the Strait of Georgia (Fraser 1929). Like *Protothaca staminea*, spawning in response to dense algal blooms has been reported (Robinson and Breese 1982). There is considerable variation in spawning times, even in neighboring beds with variable water temperatures. Polar body formation occurs 60 minutes post fertilization and cleavage begins 30 minutes later; trochophore larvae develop after 24 hours, which become bivalve veliger larvae 24 hours later (18˚C, see Fig. 1, Breese and Phibbs 1970).
Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. 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 (see Fig. 1, Caddy 1969). 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, Caddy 1969; Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Veliger larvae of *S. giganteus* are free-swimming for up to 30 days and grow approximately 7 µm per day (Breese and Phibbs 1970). They are straight hinge (see Fig. 4, Brink 2001) until they are 160 µm in length after 2 weeks (Fraser and Smith 1928). They have an anterior end that is longer and more pointed than the posterior, which is broadly rounded (Brink 2001). Throughout development, the umbo and both ends (ant and post) become broadly rounded and larvae are longer than they are tall. Larvae metamorphose at about 230 µm and (Brink 2001) have a pelagic duration of 4 wks (Fraser and Smith 1928; Kabat and O'Foighil 1987). Optimal growth and survival for larvae were obtained at 15˚C, salinity 20–29, when fed a mixture of three algal species (settlement at 20–25 days when larvae were 230–250 µm, Bourne 1971).
Juvenile: Juvenile growth was 18 µm per day for 150 days post metamorphosis (Breese and Phibbs 1970, see also Walne 1973).

Longevity: To 20 years or more (Paul et al. 1976; Haderlie 1980).
Growth Rate: There is little growth of young individuals immediately after settling. Instead juveniles grow considerably the following spring (Fraser and Smith 1928). Growth rates varied for clams collected in different sites around Puget Sound, Washington, with oldest clams (e.g., 30 years) being 95–140 mm in length (Goong and Chew 2001, see also Gillespie and Bourne 2005). Growth rates are measured by annular rings, which are formed during periods of slowed growth, usually in winter months (Paul et al. 1976). Periods of growth may be slowed by reduction in salinity (Gillikin et al. 2005) and growth may be density dependent (Kline 1982). Specimens reached 65 mm in length after 8–9 years on Porpoise Island, southeast Alaska (Paul et al. 1976). At three beaches in British Columbia where populations were measured in 1993, individuals 40–71 mm in length were 8 years old, 24–93 mm were 2–16 years, and 25–67 mm were 2–12 years old; estimating that individuals 6.5 years old are approximately 63 mm in length (Gillispie and Bourne 2004). Legal catch size is 63 mm in length, which occurs when individuals are approximately 6–10 years old (Gillispie and Bourne 2004).
Food: A filter-feeder, that feeds by straining material from currents of water that are pumped through the gills. The ingestion and concentration of toxic algae (e.g., from the genera *Alexandrium*, *Gymnodinium*, *Pyrodinium*, Smolowitz and Doucette 1995) leads to paralytic shellfish poisoning, rendering the clams dangerous for human consumption (Kitts et al. 1992; Kitts and Smith 1992). Clams accumulate toxins in their siphon tips, in part, to reduce predation (Price and Lee 1972; Smolowitz and Doucette 1995). This suite of neurotoxins (50 structural variants) are collectively known as saxitoxins as they were first isolated from *S. giganteus* (Oshima et al. 1977; Vale 2010) and the chemical composition of this toxin was described by Schantz et al. (1974).
Predators: Known predators include sting rays, fishes, shore birds (e.g., gulls, Maron 1982), drilling snails, and sea otters (Kvitek and Oliver 1992; Kvitek et al. 1993, but see reduction in sea otter predation due to presence of saxitoxin, Kvitek et al. 1991). Predation by crab species, which break open the shells of many bivalves, is reduced by a larger and thicker shell, an inflated shell shape with steep ventral margin, and the ability to burrow deeply. Other bivalves (e.g., *Protothaca staminea*, see description in this guide) also close tightly, further reducing predation, however, the narrow posterior gape in *S. giganteus* allows for potential breaking by crab claws (Boulding 1984). *Octopus dofleini* are known to prey upon *S. giganteus* by drilling holes in their shells; increased shell thickness may reduce predation as incomplete boreholes were observed on thicker shelled clams (Ambrose et al. 1988). *Saxidomus giganteus* was historically (e.g., Burchell et al. 2013) and is currently a commercially important and harvested species; the most important food clam in British Columbia, Canada (Bourne 1971; Haderlie 1980; Kozloff 1993, see also Fig. 1 Gillispie and Bourne 2005). The fishery in southeast Alaska began in 1930 with a harvest of 11,340 kg (Paul et al. 1976) and in the Broughton Archipelago, British Columbia, Canada harvests as high as 500,000 kg were reported in 1970 (Dunham et al. 2006). (see Bechtol and Gustafson 1998 for commercial summary).
Behavior:

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