
Entodesma navicula

The rock-dwelling entodesma

Phylum: Mollusca

Class: Bivalvia, Heterodonta, Euheterodonta

Order: Anomalodesmata

Family: Pandoroidea, Lyonsiidae

Taxonomy: The Anomalodesmata is a well supported monophyletic group of bivalves that has previously been regarded as a subclass (e.g., Coan and Scoot 1997; Dreyer et al. 2003), however, recently authors suggest it should no longer be designated as such and, instead, be included as a basal lineage of the Heterodonta (Harper et al. 2006; Healy et al. 2008). The generic designations within the Lyonsiidae have also been unclear historically, including as few as one and as many as twelve genera (Prezant 1980, 1981b). Lyonsiid subgeneric and specific designations are often based on variable characters (e.g., periostracal color, shell shape and sculpture) leading to several synonyms and subgenera that were abandoned altogether by Prezant (1980, 1981b). *Entodesma navicula* has been referred to by its junior synonym, *Entodesma saxicola* (Yonge 1976; Haderlie 1980; Prezant 1981b; Harper et al. 2009 and references therein) due to its morphological similarity to a species described from Japan with an older name. Based on taxonomic priority (Coan and Scott 1997; Harper et al. 2009). *Entodesma navicula* was originally described in the genus *Lyonsia*, but was later transferred to *Entodesma*, a genus designated in 1845 by Philippi.

Description

Size: Lyonsiidae is a very large bivalve family (Oldroyd 1924) and *Entodesma navicula* is one of the largest species within it, with individuals reaching 150 mm in length (Quayle 1970). The illustrated specimen (from Coos Bay) is only 60 mm in length and 40 mm in width.

Color: Shell exterior is white, but also bears abundant brown color, and transversely striated periostracum. The shell interior is pink and nacreous (i.e., pearly).

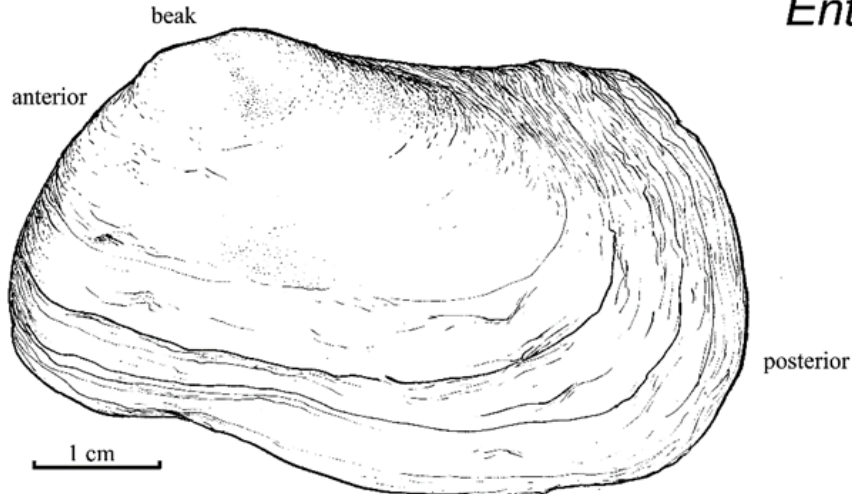
General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). The Pholadomyoidea are characterized by a shell that has nacreous interior and inconspicuous hinge teeth (if present at all). The Lyonsiidae are unique among the, exclusively marine, group Anomalodesmata due to their attachment to hard surfaces with byssal threads (Dreyer et al. 2003; Harper et al. 2005). *Entodesma* species are distinct within the Lyonsiidae in their habit to attach to rocks and nestle into crevices. This behavior renders their shells thick and of variable shape, and their byssus strong (Prezant 1981b, 1981c).

Body: Broadly rounded externally, and with thick shell and variable morphology. The left valve often larger and extending longer than right (Lyonsiidae, Prezant 1981b). (See Fig. 1, Morton 1981 for external anatomy (as *E. saxicola*) and Fig. 13, Prezant 1981b for general internal anatomy of *Entodesma* species)

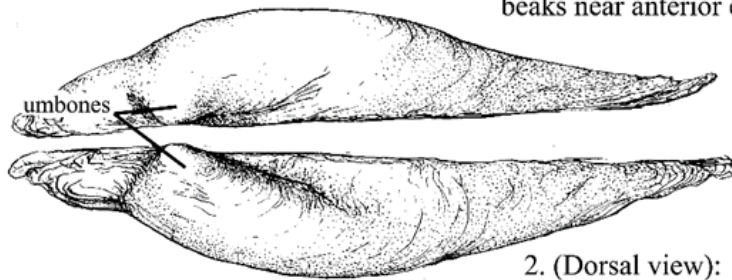
Color:

Interior: Ligament is internal (Lyonsiidae, Coan and Valentich-Scott 2007), small, extends ventrally, and is reinforced with a large lithodesma or ossicle, which is a calcareous plate (Fig. 3) (see Fig. 1, Yonge 1976). The lithodesma is only found in members of the Anomalodesmata and, it has been suggested, that its presence allows for the ca-

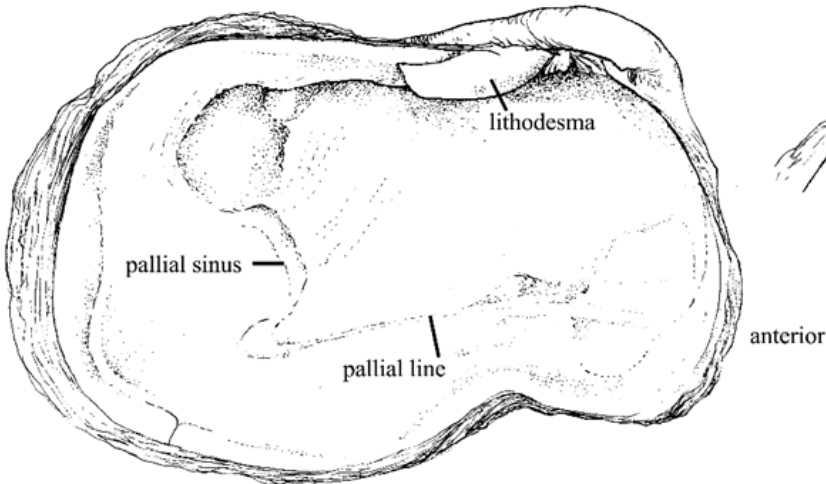
Entodesma navicula



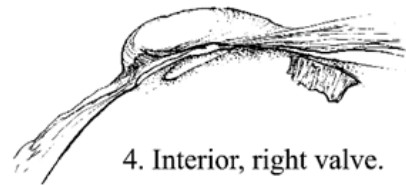
1. *Entodesma navicula* (L:60mm) x2:
shell oblong, deformed; concentric striations, rough periostracum;
beaks near anterior end, posterior truncate.



2. (Dorsal view):
beaks large, incurved; umbones not touching; posterior gaping.



3. Interior, left valve:
pearly, iridescent; hinge area without teeth of chondrophore;
lithodesma reinforces internal ligament, pallial line solid,
pallial sinus present but obscure.



4. Interior, right valve.

capacity for greater shell width, especially among the Lyonsiidae (Yonge 1976). The lithodesma is particularly large among the *Entodesma* (Prezant 1981b). A secondary dorsal ligament is sometimes observed in members of the Lyonsiidae (see Yonge 1976). Internal anatomy is described in detail by Morgan and Allen (as *E. saxicola*, 1976).

Exterior:

Byssus: Uses byssal threads to attach to substratum (e.g., floats, pilings, rock). Members of the *Entodesma* often have a byssal notch at the ventral posterior shell edge (Morgan and Allen 1976; Prezant 1981b). Byssal gland is located in the **Foot** and produces very strong byssal threads (Morgan and Allen 1976; Prezant 1981b). *Entodesma navicula* possesses a single pair of byssal muscles, posteriorly, compared to other byssally attached bivalves (e.g., *Mytilus*) that possess three pairs (Morgan and Allen 1976).

Gills: Large gills are deeply plicate (i.e., folded) and comprise approximately 230 plicae (Morgan and Allen 1976).

Shell: Overall shell shape is oblong, with valves longer than they are tall, and shells can be strongly deformed due to nestling habit. The posterior is gaping and truncated. The genus *Entodesma* contains the thickest shelled species within the family Lyonsiidae. *Entodesma* and *Lyonsia* species have the capacity to adhere particles to their shell exterior, due to the presence of arenophilic radial mantle glands along the mantle edge (see **Juvenile**) (Morgan and Allen 1976; Yonge 1976; Prezant 1981b, 1981d; Lutaenko 2012). Periostracum may extend beyond the shell edges (up to 1 cm, Morgan and Allen 1976) and bear radial striations (Prezant 1981b).

Interior: (see Fig. 1, Morgan and Allen 1976.) All Lyonsiids have shell interior that is nacreous (Morgan and Allen 1976),

thus, the shell interior in *E. navicula* is pearly and iridescent. The pallial line is also solid and not in patches (Coan and Valentich-Scott 2007), and the pallial sinus is obscure and angular (Oldroyd 1924) (Fig. 3). The two adductor muscle scars are conspicuous (Prezant 1981b) and of equal size (although anterior may be slightly smaller than posterior, see Prezant 1981b), but differ in shape (Fig. 3). The shell microstructure is distinct in Lyonsiid bivalves and is described for *E. navicula* by Harper et al. (2009) as homogeneous, allowing for some shell flexibility to adapt to varying substrates (Prezant 1980, 1981b, 1981c; Harper et al. 2009).

Exterior: The exterior is rough, with concentric striations, and coarse or irregular ribs (Keen and Coan 1974), but not radial ribs. The ventral margins flex, and gape and the left valve is slightly larger than right (Oldroyd 1924). The shell is brittle and breaks easily. Periostracum covers the shell exterior and is coarse and often cracks the shell as it dries, which can be prevented in collecting by applying a lubricant like Vaseline (Keen 1971).

Hinge: No true teeth or chondrophore present (Fig. 3). The beaks are large, incurved (Oldroyd 1924), and close to anterior end (Fig. 2). The umbones do not touch (Keen and Coan 1974) (Fig. 2).

Eyes: *Entodesma* species lack photoreceptors (Prezant 1981b).

Foot: Due to their habit of attaching to various substrata, the foot is reduced, small, and cylindrical (*Entodesma*, Morgan and Allen 1976; Prezant 1981b). The foot is not used for locomotion in *E. navicula* such that it resembles *Mytilus* species (Morgan and Allen 1976).

Siphons: Siphons are short and muscular (Prezant 1981b), but not red-tipped (compare to *Hiatella arctica* description in this guide).

Burrow: Individuals do not create a burrow per se, but are often nestled into the aban-

doned burrows of other invertebrates (e.g., pholads).

Possible Misidentifications

There are five bivalve subclasses based on morphology and fossil evidence and one of those is the diverse Heterodonta. The monophyletic group Anomalodestmata comprises at least one sixth of all bivalves families (Harper et al. 2006), which are widely diverse and found in specific marine niches (Morgan 1981). They are characterized by a nacreous shell, a ligament with a lithodesma (ossicle), as well as a variety of characters of internal anatomy (see Dreyer et al. 2003). Family designations within this group have been difficult to interpret taxonomically due to the extreme variation in morphology and life habits of groups (see Fig. 2, Harper et al. 2006; Healy et al. 2008).

Three bivalve families including the, potentially diphyetic (see Dreyer et al. 2003) Lyonsiidae, Hiatellidae, and Thraciidae are characterized by their lack of dorsal margin ears or projecting teeth or chondrophores, and two adductor muscles. In thraciids the ligament can be both internal and external and the pallial line is continuous; in hiatellids (see *Hiatella arctica* in this guide) the ligament is always external and the pallial line is broken into patches (see below). On the other hand, in the lyonsiids the pallial line is continuous, as in thraciids, but the ligament is always internal, unlike thraciid species (Coan and Valentich-Scott 2007).

The Lyonsiidae is a distinct family consisting up to 45 species comprising three genera (*Lyonsia*, *Entodesma*, *Mytilimeria*), with the latter two having evolved from a *Lyonsia*-like ancestor (Prezant 1981a, 1981b; Harper et al. 2009). (For characters with which to differentiate these genera, see Prezant 1981b and 1981c) *Entodesma* species bear the thickest shell among these three genera (Prezant 1981c).

Representatives of each genera occur locally, including *Mytilimeria nuttallii*, *Lyonsia californica*, *Entodesma pictum* (= *E. inflatum*), and *E. navicula* (= *E. saxicola*). *Entodesma navicula* have a thick shell and anterior end that is one third the total shell length as well as a heavy periostracum. *Entodesma pictum*, on the other hand, has a thin shell, thin periostracum and an anterior end that is less than one third the total length. The shell of *E. pictum* is also smaller, lighter in color and more regular in shape than *E. navicula*. The shell shape in *Entodesma* species is irregular due to their nestling habits and attachment to the substratum. *Mytilimeria nuttallii* has a circular shell outline. In *Lyonsia californica*, the shell and periostracum are thin and elongate with a conspicuous posterior end (Pimenta and Oliveira 2013). The latter species tends to occur in protected muddy bays and the former in the rocky intertidal among ascidians (e.g. *Cystodites*, Kabat and O'Foighil 1987; Harper et al. 2009).

Of the nestling or burrowing clams of our estuarine rocky intertidal, most of the pholads can be immediately distinguished from *Entodesma* by their file-like denticulations anteriorly, and by the two distinct sections of each valve (see *Penitella penita*, *Zirfaea pilsbryi* in this guide). The nestling habit of some clams can distort shell shape and make identification difficult (see *Protothaca staminea* in this guide).

Species from other bivalve families that may be confused with *E. navicula* include *Hiatella arctica*, *Petricola carditoides*, and *Platydodon cancellatus*. *Hiatella arctica* (= *Saxicava*) is a very similar, often deformed nestling clam. It can be most easily distinguished from *E. navicula* by its white, porcelain-like interior (Keen and Coan 1974) (not pink and pearly), and by its broken pallial line (see Plate 429B, Coan and Valentich-Scott 2007). It also has very distinctive red-tipped siphons (Kozloff 1993), which are not found in *E. navicula*. *Pe-*

tricola carditoides has an external ligament and 2–3 cardinal hinge teeth, as well as some radial sculpture, and lives in pholad burrows. It is chalky white, with purple-tipped siphons (Kozloff 1993), and usually is narrower posteriorly than anteriorly. A myid clam, *Platyodon cancellatus*, is another rock dweller, but it is a burrower, not a nestler (Quayle 1970; Coan and Valentich-Scott 2007). It has a chondrophore and tooth in its hinges, fine, almost lamellar concentric exterior sculpture, and a white interior with a well-developed pallial sinus (Kozloff 1974).

Juveniles of the families Clavagellidae and Penicillidae (“watering pot bivalves”) are morphologically similar to members of the Lyonsiidae (Morton 2007).

Ecological Information

Range: Type locality is Vancouver Island, British Columbia (as *E. saxicola*, Dall 1916). Known range extends in the north Pacific in the Kurile Islands and northern Japan down through the Aleutian Islands in Alaska to San Diego, California (Harper et al. 2009).

Local Distribution: Local distribution includes sites in Coos Bay, including Fossil Point.

Habitat: Occurs among rocks and in crevices and abandoned pholad burrows. Individuals also found attached by byssus to floats and pilings.

Salinity: Collected at salinities of 30.

Temperature:

Tidal Level: Intertidal and subtidal to 60, or even 82 meters deep (Keen and Coan 1974; Harper et al. 2009).

Associates: Co-occurs with other nestling and burrowing molluscs (e.g., *Hiatella*, *Zirfaea*, *Penitella*).

Abundance: Common in Puget Sound, Washington. Individuals are present, but not common, in Oregon (Quayle 1970).

Life-History Information

Reproduction: All members of the Anoma-

lodesmata are believed to be hermaphroditic (Healy et al. 2008). *Entodesma navicula* is a hermaphroditic species, with external fertilization and planktonic larvae. Eggs and sperm are emitted alternatively (Quayle 1970). Although the development of this species has not been described, other members of the Anomalodesmata are free-spawners, primarily in summer months. These include *Lyonsia bracteata*, which is a simultaneous hermaphrodite with oocytes that are 120 μm and surrounded by a thick egg jelly; *Mytilimeria nuttallii*, is also a simultaneous hermaphrodite that free-spawns in July with oocytes that are also 120 μm in diameter (Kabat and O’Foighil 1987). The sperm morphology of the family Lyonsiidae is of modified (or elongated) morphology (see Fig. 6, Healy et al. 2008). Ova have been observed within the suprabranchial chamber of the gills in several *Entodesma* species and larvae have a short pelagic duration (Prezant 1981b).

Larva: Larval development has not been described for *E. navicula*.

Juvenile:

Longevity: Arenophilic mantle glands (which produce a secretion that allows for material to be adhered to shell surface, over the periostracum, Morton 1987) are often present in juvenile *Entodesma* species, but these are usually lost by adulthood, shell thickness increases (Prezant 1981b). These glands develop within the mantle, but the specific location has been debated (either the outer fold (Prezant 1981c, 1981d) or the middle and inner folds (Morton 1987)), and secrete shell through the periostracum.

Growth Rate:

Food: A suspension feeder. Ciliary currents move water across gills and all incoming particles move toward the ventral margin of the inner demibranch before they move anteriorly to the mouth (Yonge 1952; see Fig. 4, Morgan and Allen 1976).

Predators:

Behavior: Individuals adapt to their particular rocky niche by changing shell shape with grows, leading to shells with highly irregular morphology.

Bibliography

1. 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.
2. COAN, E. V., and P. H. SCOTT. 1997. Checklist of the marine bivalves of the northeastern Pacific Ocean. Santa Barbara Museum of Natural History Contributions in Science. 1:1-28.
3. 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.
4. DALL, W. H. 1916. A review of some bivalve shells of the group Anatinacea from the west coast of America. Proceedings of the United States National Museum. 49:441-456.
5. DREYER, H., G. STEINER, and E. M. HARPER. 2003. Molecular phylogeny of Anomalodesmata (Mollusca : Bivalvia) inferred from 18S rRNA sequences. Zoological Journal of the Linnean Society. 139:229-246.
6. HARPER, E. M., A. G. CHECA, and A. B. RODRIGUEZ-NAVARRO. 2009. Organization and mode of secretion of the granular prismatic microstructure of *Entodesma navicula* (Bivalvia: Mollusca). Acta Zoologica. 90:132-141.
7. HARPER, E. M., H. DREYER, and G. STEINER. 2006. Reconstructing the Anomalodesmata (Mollusca : Bivalvia): morphology and molecules. Zoological Journal of the Linnean Society. 148:395-420.
8. HEALY, J. M., R. BIELER, and P. M. MIK-KELSEN. 2008. Spermatozoa of the Anomalodesmata (Bivalvia, Mollusca) with special reference to relationships within the group. Acta Zoologica. 89:339-350.
9. 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.
10. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
11. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
12. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
13. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
14. LUTAENKO, K. A. 2012. Transportation of bivalve shells with attached algae in Ussuriysky Bay (Sea of Japan). Byulleten' Dal'nevostochnogo Malakologicheskogo Obshchestva. 15-1:154-164.
15. MORGAN, R. E., and J. A. ALLEN. 1976. On the functional morphology and adaptations of *Entodesma saxicola* (Bivalvia, Anomalodesmacea). Malacologia. 15:233-240.
16. MORTON, B. 1981. The Anomalodesmata. Malacologia. 21:35-60.
17. —. 1987. The mantle margin and radial mantle glands of *Entodesma saxicola* and *Entodesma inflata* (Bivalvia, Anomalodesmata, Lyonsiidae). Journal of Molluscan Studies. 53:139-151.

- 18.—. 2007. Evolution of the watering pot shells (Bivalvia: Anomalodesmata: Clavagellidae and Penicillidae). Records of the Western Australian Museum. 24:19-64.
19. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
20. PIMENTA, A. D., and C. D. DE CASTRO OLIVEIRA. 2013. Taxonomic review of the genus *Lyonsia* (Pelecypoda: Lyonsiidae) from east coast of South America, with description of a new species and notes on other western Atlantic species. American Malacological Bulletin. 31:75-84.
21. PREZANT, R. S. 1980. Taxonomic revisions of marine Lyonsiidae bivalvia. Bulletin of the American Malacological Union. 46:75-75.
- 22.—. 1981a. Arenophilic mantle glands, shell ultrastructure, taxonomy, and evolution of the Lyonsiidae (Bivalvia: Anomalodesmata). Vol. Ph.D. University of Delaware.
- 23.—. 1981b. Comparative shell ultrastructure of Lyonsiid bivalves. Veliger. 23:289-299.
- 24.—. 1981c. Taxonomic re-evaluation of the bivalve family Lyonsiidae. Nautilus. 95:58-72.
- 25.—. 1981d. The Arenophilic radial mantle glands of the Lyonsiidae (Bivalvia, Anomalodesmata) with notes on Lyonsiid evolution. Malacologia. 20:267-289.
26. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
27. 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 University Press, Stanford.
28. YONGE, C. M. 1976. Primary and secondary ligaments with the Lithodesma in the Lyonsiidae (Bivalvia, Pandoracea). Journal of Molluscan Studies. 42:395-408.

Updated 2016

T.C. Hiebert