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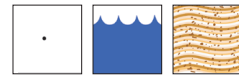
40 ~ NUCULANIDAE

INFRA- and SUPRABRANCHIAL CHAMBERS, perforated by slitlike pores. Incurrent and excurrent water flows are posterior. The STOMACH is TYPE I. The MIDGUT is long and variously convoluted. The HINDGUT passes through the ventricle of the heart, and leads to a sessile rectum. Nuculanids are GONOCHORISTIC; a PERICALYMMMA larva is assumed. The nervous system is not concentrated. STATOCYSTS in adults are closed, with STATOLITHS. ABDOMINAL SENSE ORGANS are absent.

Nuculanids are INFAUNAL in mud and sand of high organic content, lying partly buried with the rostrum protruding just above the surface. The planar foot allows plowing and rapid burrowing. Although primarily DEPOSIT FEEDERS through action of the palp proboscides, rhythmic contractions by the gills have been described as setting up a pumping action that can create water flow sufficient for supplemental SUSPENSION FEEDING. One species from hydrothermal vents is known to possess sulfide-oxidizing endosymbiotic bacteria.

The family Nuculanidae is known since the Devonian and is represented by at least 7 living genera and 200–250 species, inhabiting all seas but most common in the deep sea.

Ledella sublevis A. E. Verrill & Bush, 1898 – Polished Nut Clam



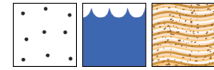
Elongated oval, with short roundly pointed rostrum, whitish, smooth. Massachusetts to Florida, Bermuda, West Indies, South America (Uruguay). Length 4 mm.

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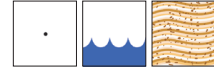
42 ~ NUCULANIDAE

***Nuculana acuta* (Conrad, 1832) – Pointed Nut Clam**



Elongated trigonal, with sharply pointed rostrum, white with light yellow periostracum, with shallow groove from umbo to ventral margin at both ends of valve, with coarse subequal commarginal ridges extending across posterior ridge. Eastern Canada to Florida, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 6 mm (to 10 mm).

***Nuculana concentrica* (Say, 1824) – Concentric Nut Clam**



Elongated trigonal, with sharply pointed, upturned rostrum, semiglossy yellowish white, with shallow groove from umbo to ventral margin at both ends of valve, with fine commarginal grooves not extending across posterior ridge, smooth at umbo and dorsal center. Florida, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 7 mm (to 18 mm).

***Nuculana jamaicensis* (d'Orbigny, 1853) – Jamaican Nut Clam**



Elongated trigonal, with sharply pointed rostrum, white, with strong rounded ridge on posterior slope from umbo to tip of rostrum and with radial furrow on anterior slope, with strong regular commarginal sculpture. North Carolina, Florida Keys, West Indies, South America (Suriname). Length 3 mm. Note: The sepia-toned drawings are the original illustrations of the species.

***Nuculana cf. semen* (E. A. Smith, 1885) – Seed Nut Clam**



Elongated oval, with short, roundly pointed rostrum that is slightly hooked (indented ventrally), glossy translucent yellowish white, smooth, umbones slightly opisthogyrate. Florida Keys. Length 2 mm. Note: This deepwater species is closest in shape and adult size to *Nuculana semen* (E. A. Smith, 1885), known only from Brazil; its identification has not been confirmed.

***Nuculana verrilliana* (Dall, 1886) – Barbed Nut Clam**



Elongated trigonal, with bluntly pointed rostrum, whitish, with widely spaced slightly elevated commarginal ridges, reflexed at anterior end, which is defined by a rounded indistinct ridge and is more strongly sculptured (even when worn) than the remaining shell. North Carolina to Florida, West Indies, Gulf of Mexico. Length 5 mm.

***Nuculana vitrea* (d'Orbigny, 1853) – Glassy Nut Clam**



Elongated trigonal, with sharply pointed, upturned rostrum, white, with coarse regular commarginal ridges. Florida, West Indies, South America (Colombia). Length 6 mm. Note: The sepia-toned drawings are the original illustrations of the species.



Nuculana acuta



Nuculana concentrica



Nuculana jamaicensis

dorsal



Nuculana cf. semen



Nuculana verrilliana



Nuculana vitrea

dorsal

Family Yoldiidae – Yoldia Clams

Classification

PROTOBRANCHIA Pelseneer, 1889

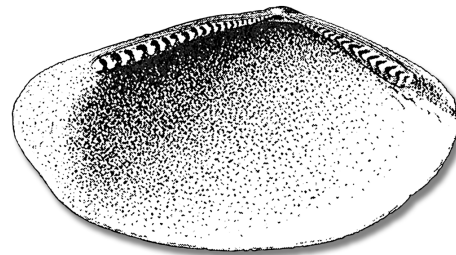
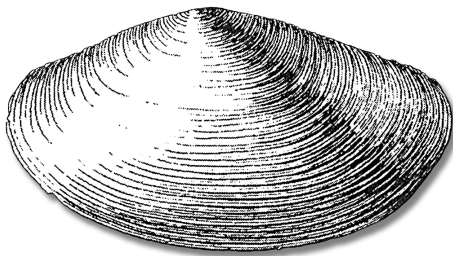
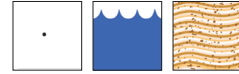
Nuculanoida Carter, Campbell, & Campbell, 2000

Nuculanoidea H. Adams & A. Adams, 1858 [1854]

Yoldiidae Dall, 1908

Featured species

Yoldia liorhina Dall, 1881 – Smooth-nosed Yoldia

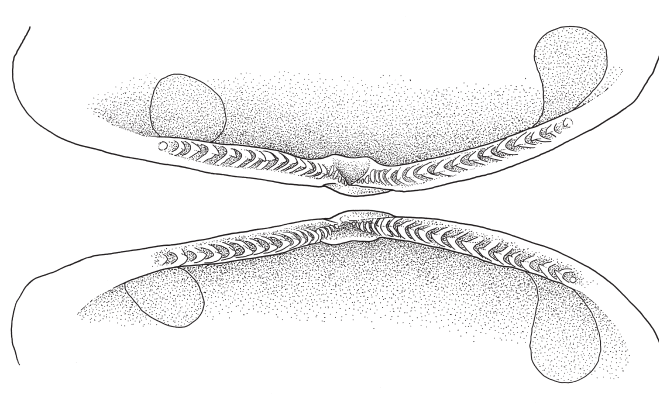


pallial line

Elongated oval, with rounded anterior and posterior ends, light greenish, with slight posterior ridge and numerous commarginal grooves not crossing the ridge, remaining surface smooth and polished; interior glossy. Florida Keys, West Indies, Gulf of Mexico. Length 13 mm. Note: The pallial line is drawn for a specimen of *Yoldia seminuda* Dall, 1871, from off California.

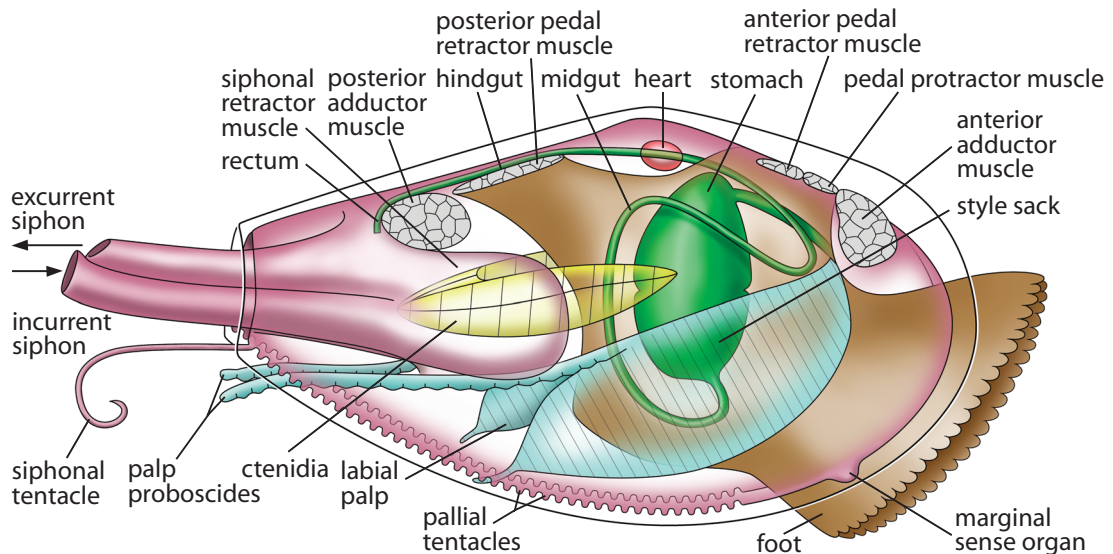
Family description

The yoldiid shell is small to medium-sized (to at least 60 mm), thin-walled, elongated oval, with the posterior end extended or slightly ROSTRATE. It is EQUIVALVE, usually compressed, usually gaping at both ends, and EQUILATERAL or INEQUILATERAL (umbones slightly anterior or posterior), with PROSOGYRATE UMBONES. Shell microstructure is ARAGONITIC and three-layered, with a PRISMATIC outer layer, a CROSSED LAMELLAR or HOMOGENOUS middle layer, and a COMPLEX CROSSED LAMELLAR or homogenous inner layer (in



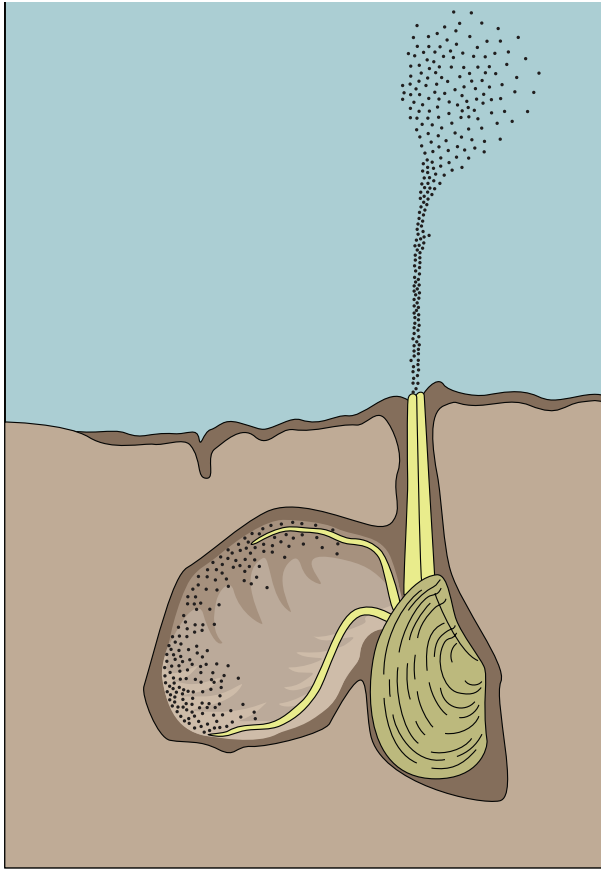
some species also with an innermost prismatic layer). TUBULES are apparently absent. Ex-
teriorly yoldiids are covered by brownish to olive green, varnishlike PERIOSTRACUM.
Sculpture is usually smooth and glossy, with fine commarginal growth lines. LUNULE and
ESCUTCHEON are present or absent. Interiorly the shell is non-NACREOUS. The PALLIAL
LINE has a deep SINUS. The inner shell margins are smooth. The HINGE PLATE is TAX-
ODONT, arched, with anterior and posterior series of chevron-shaped teeth separated by a
subumbonal RESILIFER. The LIGAMENT is SIMPLE, AMPHIDETIC, in some species submarginal
set on FOSSETTES, and can be extended by periostracum; an internal portion (RESILIUM) is
entirely mineralized, and splits in half dorsally with growth.

The animal is ISOMYARIAN; the pedal retractor and protractor muscles are well de-
fined. The MANTLE margins are not fused ventrally. Posterior EXCURRENT and INCURRENT
SIPHONS are short and united; the incurrent siphon is either complete or incomplete (i.e.,
made tubular only by ciliary junctions). A posterior unpaired siphonal tentacle (attached
to the right or left mantle margin) and marginal sense organs on the anteroventral mantle
edge are present. HYPOBRANCHIAL GLANDS in the suprabranchial chamber are small or



absent. The FOOT is large and active with a broad planar sole, with a heavily papillate (stellate) margin. A BYSSAL (pedal?) GLAND and GROOVE is present but the adult is not byssate.

The LABIAL PALPS are large with retractor muscles, terminal filaments, and narrow ciliated PALP PROBOSCIDES attached posterodorsally. A PALP POUCH is absent. The CTENIDIA are PROTOBRANCH, small to medium-sized, posterior, oriented horizontally, and can



rearrange to form a SEPTUM separating INFRA- and SUPRABRANCHIAL CHAMBERS, perforated by slitlike pores. Incurrent and excurrent water flows are posterior. The STOMACH is TYPE I. The MIDGUT is long and convoluted. The HINDGUT passes through the ventricle of the heart, and leads to a sessile rectum. Yoldiids are GONOCHORISTIC and produce PERICALYMMMA larvae. The nervous system is not concentrated, and has fused cerebropleural ganglia (unlike most other protobranch bivalves). STATOCYSTS (closed, with STATOLITHS) have been reported in adult *Yoldia*. ABDOMINAL SENSE ORGANS are absent.

Yoldiids have been biologically investigated more than other protobranchs because they are common, large, and play major roles in the food chains of commercial fish and in bioturbation of the sediment. They are INFAUNAL in mud or sand, and are strong and rapid burrowers. Leaping (under laboratory conditions) was described by Drew (1899b). They DEPOSIT FEED using the palp proboscides predominantly by excavating a subsurface feeding chamber with the labial palps (rejecting feces and PSEUDOFECES through the excurrent siphon into the water column) or less often by sweeping the surface. Yoldiids can also supple-

ment their nutrition by suspension-filtration by the gills, facilitated by the pumping action of the gills.

The family Yoldiidae is known since the Cretaceous and is represented by at least 10 living genera and at least 90 species, inhabiting all seas.

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Family Arcidae – Ark Clams

Classification

AUTOLAMELLIBRANCHIATA Grobben, 1894

Pteriomorphia Beurlen, 1944

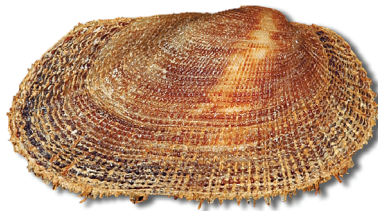
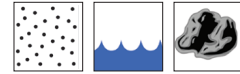
Arcoida Stoliczka, 1870

Arcoidea Lamarck, 1809

Arcidae Lamarck, 1809

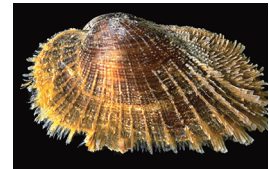
Featured species

Barbatia cancellaria (Lamarck, 1819) – Red-brown Ark



Elongated oval to quadrangular, longer posteriorly, solid, dark purplish brown with wide lighter band at mid-valve, covered by radially tufted yellow-brown periostracum, surface cancellate or weakly beaded; interior brownish with white radial ray (reflecting external colors) and narrow byssal gape, margin smooth, cardinal area narrow (see p. 57), hinge line straight, distal teeth nearly parallel to hinge line. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 16 mm (to 45 mm).

The **periostracum** of living *Barbatia cancellaria* (here from Indian Key) is thick, fibrous, and occasionally hairy, with projections that extend past the shell margins.

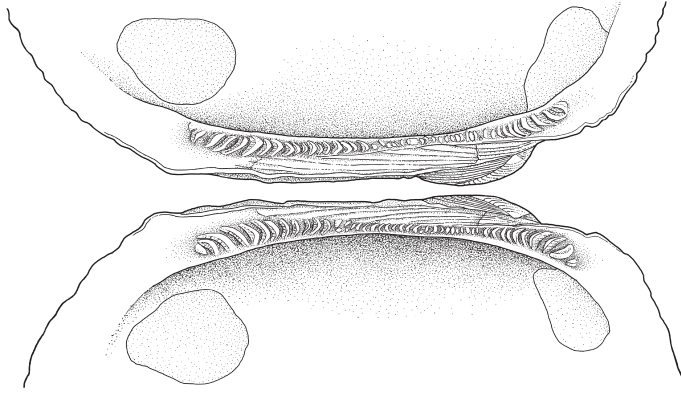


Barbatia cancellaria attaches to hard substrata in shallow water, either at the base of other benthic organisms or under rocks (see additional figure on p. 113).



Family description

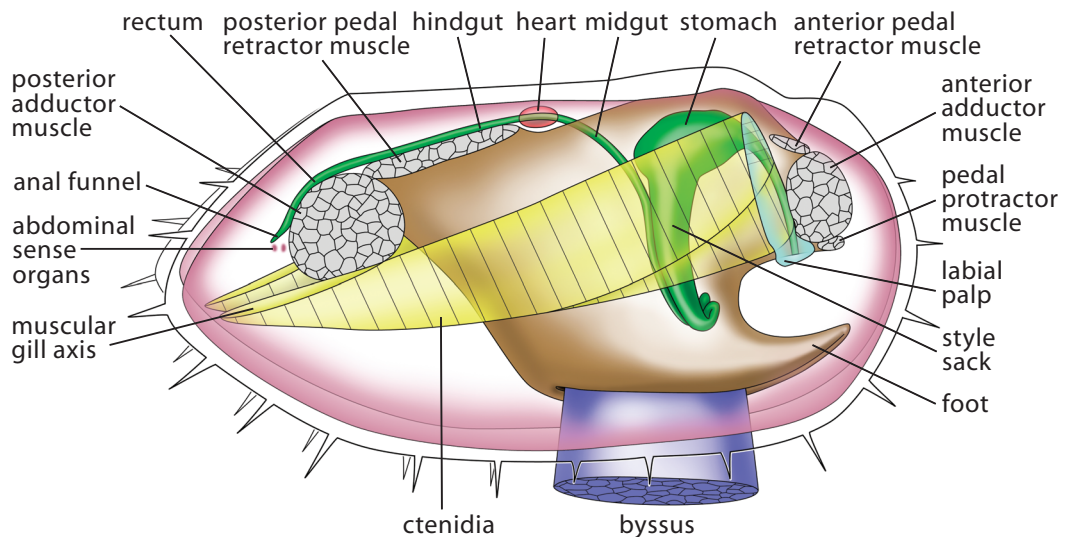
The arcid shell is small to medium-sized (to 125 mm), elongated quadrangular to oval, and thin-walled to solid. It is **EQUIVALVE** to slightly **INEQUIVALVE** (left valve larger), inflated, and in some species ventrally gaping (or at least indented where the byssus emerges). The shell is **EQUILATERAL** or **INEQUILATERAL** (umbones anterior), with **PROSO-**



OPISTHO-, or ORTHOGRATE UMBONES separated by a narrow to wide CARDINAL AREA. Shell microstructure is ARAGONITIC and three-layered, with a PRISMATIC outer layer, a CROSSED LAMELLAR middle layer, and a COMPLEX CROSSED LAMELLAR inner layer. TUBULES are present in some species through all shell layers except the outermost (periostracum). Exteriorly arcids are covered by a thick, fibrous, pilose (occasionally hirsute) PERIOSTRACUM. Sculpture is primarily radial, often with weaker commarginal ridges, or in some species cancellate. LUNULE and ESCUTCHEON are absent. Interiorly the shell

is NON-NACREOUS; in a few species, the inner margin of the posterior adductor muscle scar is reinforced by a raised MYOPHORIC RIDGE. The PALLIAL LINE is ENTIRE. The inner shell margins are smooth or denticulate. The HINGE PLATE is straight or slightly arched, TAXODONT, with numerous perpendicular to oblique teeth, rarely reduced to a few nearly horizontal ridges, and often diminished in size or absent below the umbones. The LIGAMENT occupies the entire cardinal area and is SIMPLE or more typically DUPLIVINCULAR (with superficial chevron-shaped grooves), and AMPHI-, PROSO-, or OPISTHODETIC.

The animal is ISOMYARIAN or HETEROMYARIAN (anterior ADDUCTOR MUSCLE smaller in, e.g., *Bentharca* and *Bathyarca*); the pedal retractor muscles are elongated and well developed, especially posteriorly where the larger posterior pedal retractors have repositioned the pericardial cavity close to the umbones. Pedal protractor muscles underlie the anterior adductor. The MANTLE margins are not fused ventrally except, in some, for a small posterior excurrent aperture; SIPHONS are absent. In some burrowing forms, INCURRENT and EXCURRENT APERTURES are formed by temporary appression of the mantle lobes. The MANTLE margins are muscular and nontentaculate; simple PALLIAL EYES (cup-shaped,



without lens) on the outer folds have been reported for some species, covered by perios-tracum. Deepwater *Bentharca* and *Bathyarca* possess a pair of prominent posterior mantle flaps and mantle flap glands, presumed to protect the gills and help convey PSEUDOFECES from the MANTLE CAVITY. HYPOBRANCHIAL GLANDS have not been reported. The FOOT is elongated and deeply grooved ventrally. A BYSSUS is present in the adult, is often robust, emanates from a conical process within the BYSSAL GROOVE, and can be shed and resecreted for relocation purposes.

The LABIAL PALPS are relatively small to medium-sized, with ridges restricted to the dorsal part. The CTENIDIA are FILIBRANCH (ELEUTHERORHABDIC), HOMORHABDIC, of about equal size, and not inserted into (or fused with) the distal oral groove of the palps (CATEGORY III association). The posterior third of each gill is attached to a muscular stalk originating on the ventral surface of the posterior adductor muscle. CEPHALIC EYES are present. Incurrent and excurrent water flow is mainly posterior, with a secondary anterior incur-rent flow. The STOMACH is TYPE III. The MIDGUT is variable in length and degree of coil-ing. The HINDGUT passes either dorsal to or through the ventricle of the heart, and leads to a rectum with a free ANAL FUNNEL. In species of *Arca*, the heart includes two lateral pericardia, each with its own auricle and ventricle, and divided by the elongated posterior pedal retractor muscle; the ventricles are medially connected. Intracellular hemoglobin is present in the blood (e.g., the Blood Cockle, *Anadara granosa* (Linnaeus, 1758)) in red blood cells unknown elsewhere in the Mollusca. Arcids are GONOCHORISTIC and usually produce planktonic VELIGER larvae; one species of *Lissarca* is known to brood its larvae. The gonad often extends branches into the mantle tissues. The nervous system is not concentrated. STATOCYSTS in adults are present or absent. ABDOMINAL SENSE ORGANS are present.

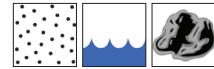
Arcids are SUSPENSION FEEDERS and usually marine, rarely inhabiting estuarine or fresh waters (e.g., Indian *Scaphula nagarjunai* Ram & Radhakrishna, 1984). They can be EPIBYSSATE on coral or rock, or (presumably secondarily) ENDOBYSSATE in sand or mud, or less commonly, rock-boring (e.g., Panamic *Litharca lithodomus* (G. B. Sowerby I, 1833)) by a combination of mechanical and chemical means.

The family Arcidae is known since the Jurassic, is represented by 12 living genera and ca. 250 species, and is widely distributed mainly in intertidal or shallow waters. Some species (e.g., *Anadara granosa*) have been exploited for human food throughout Asia and have been cultured since the seventeenth century in China and the mid-nineteenth century in Japan. Members of the superficially similar Noetiidae differ mainly by characters of the ligament.

References

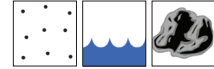
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***Cucullaearca candida* (Helbling, 1779) – White Bearded Ark**



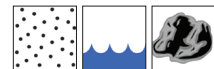
Elongated quadrangular, longer posteriorly, thin-walled, white to beige with brown periostracum, with radial ribs crossing commarginal ridges forming beads (strongest posteriorly) and narrow byssal gape; interior white, margin smooth, cardinal area narrow, hinge line straight, distal teeth nearly parallel to hinge line. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 50 mm (to 54 mm). Formerly in *Barbatia*. Compare *Fugleria tenera*, which is generally more delicate and has a denticulate interior shell margin.

***Fugleria tenera* (C. B. Adams, 1845) – Delicate Ark**



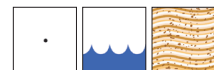
Elongated oval to quadrangular, longer posteriorly, thin-walled, white with thick brown radial periostracum, with radial ribs crossing commarginal ridges forming beads and narrow byssal gape; interior white, margin denticulate, cardinal area narrow (see p. 57), hinge line straight. Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 20 mm (to 35 mm). Syn. *balesi* Pilsbry & McLean, 1939. Formerly in *Barbatia*. Compare *Cucullaearca candida*, which has a smooth interior shell margin. Note: See also image of living animal on p. 57. Also known as Doc Bales' Ark.

***Acar domingensis* (Lamarck, 1819) – White Miniature Ark**



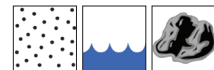
Elongated quadrangular, skewed anterodorsally, anterior end narrowed, posterior end longer with oblique angular ridge, solid, sandy brown to whitish without noticeable periostracum, surface coarsely cancellate, no byssal gape; interior white, margin denticulate, cardinal area narrow (see p. 57), hinge line slightly arched, teeth more numerous posteriorly. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 20 mm. Formerly in *Barbatia*.

***Lunarca ovalis* (Bruguière, 1789) – Blood Ark**



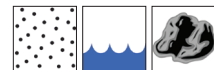
Obliquely oval, umbones slightly anterior of center, inflated, solid, white with thick black-brown periostracum, with 26–35 smooth radial ribs, no byssal gape; interior white, margin coarsely denticulate, cardinal area narrow, hinge line arched, teeth more numerous posteriorly, those near umbones coarse. Massachusetts to Florida, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Uruguay). Length 40 mm (to 56 mm). Formerly in *Anadara*.

***Arca zebra* (Swainson, 1833) – Atlantic Turkey Wing**



Elongated quadrangular, about twice as long as high, longer posteriorly, with V-shaped indented posterior slope and produced posterior auricle, solid, tan to whitish with ragged stripes of reddish to purple-brown, periostracum yellowish brown, coarse and fibrous, with radial ribs crossing commarginal ridges and narrow byssal gape; interior whitish centrally, mottled to solid reddish brown marginally, margin smooth to weakly denticulate, cardinal area wide, hinge line straight. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 60 mm (to 90 mm). Note: See also image of living animal on p. 57.

***Arca imbricata* Bruguière, 1789 – Mossy Ark**



Elongated quadrangular, about twice as long as high, longer posteriorly, with bluntly oblique posterior slope, inflated, solid, brown to greenish with thick brown periostracum, with radial ribs crossing commarginal ridges forming beads and wide byssal gape; interior whitish centrally, mottled brown marginally, cardinal area wide (see p. 57), hinge line straight. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 50 mm (to 64 mm). Syn. *umbonata* Lamarck, 1819.



Cucullaearca candida



Fugleria tenera



Acar domingensis



Lunarca ovalis



Arca zebra

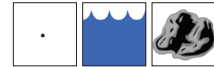
LV cleaned



Arca imbricata

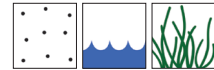
ventral





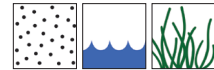
***Anadara baughmani* Hertlein, 1951 – Baughman's Skewed Ark**

Elongated oval, skewed anterodorsally, left valve slightly larger, longer posteriorly, solid, white with brown periostracum, with 28–30 flat radial ribs, smooth or beaded commarginally, anteriormost ribs faintly or not cut medially, interrib spaces with close commarginals, no byssal gape; interior white, margin coarsely denticulate, cardinal area wide, hinge line straight. Florida Keys, Gulf of Mexico, Caribbean Central America, South America (to Uruguay). Length 45 mm. Syn. *springeri* Rehder & Abbott, 1951. Compare *Anadara floridana*, which has more radial ribs that are strongly radially grooved. Note: The valves photographed are of the HOLOTYPE specimen of *Anadara springeri* Rehder & Abbott, 1951, a synonym of *A. baughmani*.



***Anadara floridana* (Conrad, 1869) – Cut-Ribbed Ark**

Elongated oval, left valve slightly larger, longer posteriorly, inflated, solid, white with light to dark brown thick periostracum, with 30–38 medially cut radial ribs crossing commarginal ridges forming weak beads, no byssal gape; interior white, margin coarsely denticulate, cardinal area wide, hinge line straight. North Carolina to Florida, West Indies, Gulf of Mexico, Caribbean Central America, South America (Venezuela). Length 65 mm (to 90 mm). Compare *Anadara baughmani*, which has fewer radial ribs that are faintly or not radially grooved.



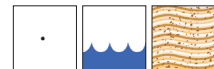
***Anadara notabilis* (Röding, 1798) – Eared Ark**

Oval to quadrangular, longer posteriorly with produced posterior auricle, inflated, left valve slightly larger, solid, white with thick brown periostracum, with 25–27 radial ribs crossed by rounded commarginal ridges, no byssal gape; interior white, margin coarsely denticulate, cardinal area wide (see p. 57), hinge line straight, anterior teeth more densely packed. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 40 mm (to 92 mm).



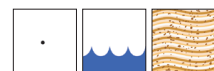
***Anadara transversa* (Say, 1822) – Transverse Ark**

Elongated oval to quadrangular, left valve slightly larger, longer posteriorly, solid, white with light brown periostracum mainly on margins, with 30–35 radial ribs that are beaded on left valve only, no byssal gape; interior white, margin coarsely denticulate, cardinal area narrow, hinge line straight. Massachusetts to Florida, West Indies, Gulf of Mexico, Caribbean Central America. Length 20 mm (to 38 mm).



***Scapharca brasiliiana* (Lamarck, 1819) – Incongruous Ark**

Rounded trigonal, left valve slightly larger, inflated, thin-walled, white with thin light brown periostracum, with 26–28 squared radial ribs crossing barlike beads, no byssal gape; interior white, margin coarsely denticulate, cardinal area trigonal (see p. 57), hinge line straight with slightly arched tooth row. North Carolina to Florida, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 55 mm. Compare *Scapharca chemnitzii*, which is thicker shelled with fewer radial ribs.



***Scapharca chemnitzii* (Philippi, 1851) – Chemnitz's Triangular Ark**

Rounded trigonal, left valve slightly larger, inflated, solid, white with thin light brown periostracum, with ca. 25 squared radial ribs crossed by barlike beads, no byssal gape; interior white, margin coarsely denticulate, cardinal area trigonal, hinge line straight, teeth dense subumbonally. Florida, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Uruguay). Length 30 mm. Compare *Scapharca brasiliiana*, which is thinner shelled with more radial ribs.





Anadara baughmani



Anadara floridana



Anadara notabilis



Anadara transversa

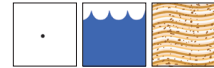


Scapharca brasiliana



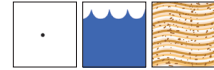
Scapharca chemnitzii

Bathyarca glomerula (Dall, 1881) – Little-Ball Bathyark



Obliquely oval, inflated, solid, whitish with thin periostracum in radial rows, with fine radial ribs crossed by commarginal ridges forming beads, no byssal gape; interior whitish, margin denticulate, cardinal area narrow, hinge line straight, with <12 teeth. North Carolina, Florida Keys, West Indies, Gulf of Mexico. Length 6 mm.

Bentharca sagrinata (Dall, 1886) – Shagreen Ark



Elongated quadrangular, skewed anterodorsally, anterior end narrowed, posterior end longer, solid, whitish with irregular orange rays, with fine radial ribs and few coarse posterior undulations crossed by commarginal ridges, no byssal gape; interior whitish with coarse radial ridges, margin smooth, cardinal area narrow, hinge line straight. Georgia to Florida, West Indies, South America (Colombia). Length 15 mm.

Dorsal views of six species in six genera of Arcidae (*Fugleria tenera*, *Scapharca brasiliana*, *Acar domingensis*, *Anadara notabilis*, *Barbatia cancellaria*, and *Arca imbricata*) illustrate varying configurations of umbones and ligament within the family.

Living *Arca zebra* attaches solidly to the surface of hard substrata with its stout byssus, where algae and other fouling biota camouflage it within its environment. In this position, the intraumbonal area of this specimen (on a rock in the backreef area of Looe Key) shows the zebra-stripe pattern characteristic of this species.

Living *Fugleria tenera* also byssally attaches to rock surfaces using a strong byssus. When detached, an individual (like this specimen at Looe Key) can crawl to a new attachment site on its colorful foot. Hemoglobin has been shown to be the source of soft-tissue pigmentation in some species of arks.



Bathyarca glomerula



Bentharca saginata



Fugleria tenera



Scapharca brasiliana



Acar domingensis



Anadara notabilis



Barbatia cancellaria



Arca imbricata



Family Noetiidae – False Ark Clams

Classification

AUTOLAMELLIBRANCHIATA Grobben, 1894

Pteriomorphia Beurlen, 1944

Arcoidea Stoliczka, 1870

Arcoidea Lamarck, 1809

Noetiidae Stewart, 1930

Featured species

Arcopsis adamsi (Dall, 1886) – Adams' Miniature Ark



dorsal

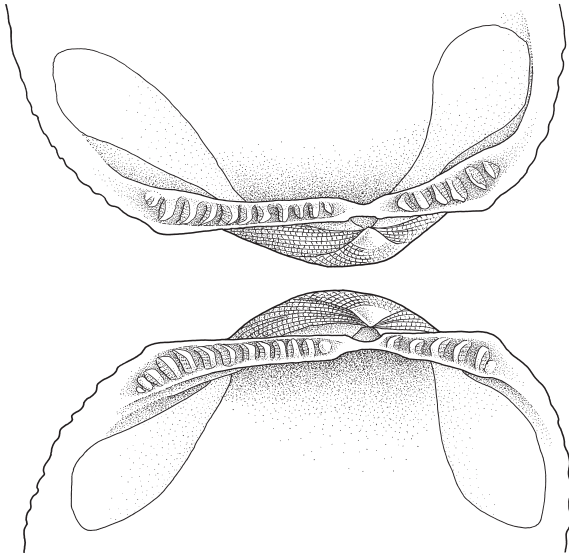
Elongated oval to quadrangular, white to cream with inconspicuous periostracum, surface cancellate, no byssal gape; interior white, margin smooth, cardinal area relatively wide, ligament limited to small, trigonal black patch between umbones. North Carolina to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 12 mm (to 17 mm). Note: Also known as Adams' Cancellate Ark.

A group of *Arcopsis adamsi* crowd closely together on the undersurface of a rock from the bayside of Spanish Harbor Key. When so disturbed, individuals voluntarily release their byssus and relocate away from the light. Discarded byssi show as brown dash-shaped objects on the rock at the lower right and center of this photograph.



Family description

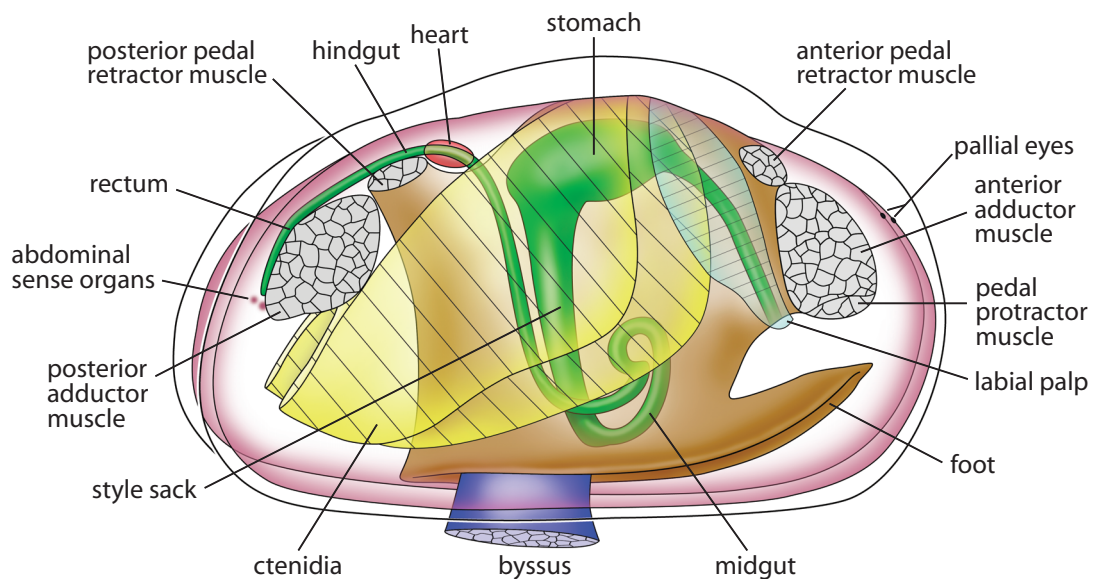
The noetiid shell is small to medium-sized (to 50 mm), quadrangular to trigonal to oval, and solid. It is EQUIVALVE, inflated, and not gaping. The shell is INEQUILATERAL (umbones slightly anterior), with UMBONES PROSO-, ORTHO-, or OPISTHOGRATE and separated by a narrow to wide CARDINAL AREA that is flat or V-shaped. Shell microstructure is ARAGO-



NITIC and three-layered, with a PRISMATIC outer layer, CROSSED LAMELLAR middle layer, and COMPLEX CROSSED LAMELLAR inner layer. TUBULES are present in some species through all shell layers except the outermost (periostracum). Exteriorly noetiids are covered by dense, fibrous, pilose PERIOSTRACUM, in some cases persisting only at the margins. Sculpture is radial or cancellate, usually with dense radial ribs. LUNULE and ESCUTCHEON are absent. Interiorly the shell is non-NACREOUS; one or both adductor muscle scars have a raised inner ridge or shelf (MYOPHORIC RIDGE). The PALLIAL LINE is ENTIRE. The inner shell margins are smooth or denticulate. The HINGE PLATE is straight or weakly arched, TAXODONT, with numerous vertical or rarely oblique teeth, often diminished in size or absent below the umbones. The LIGA-

MENT occupies only part of the cardinal area, is PROSO-, AMPHI-, or OPISTHODETIC, and is modified DUPLIVINCULAR, having "vertical" (i.e., transverse, not chevron-shaped) grooves in dorsal view (a SYNAPOMORPHY of the family).

The animal is ISOMYARIAN or HETEROMYARIAN (anterior ADDUCTOR MUSCLE smaller); the pedal retractor muscles are well developed. Pedal protractor muscles underlie the anterior adductor. The MANTLE margins are not fused ventrally; SIPHONS are absent. In some burrowing forms, EXCURRENT and INCURRENT APERTURES are formed by temporary appression of the mantle lobes. The MANTLE margins are muscular and nontentaculate, and usually have well-developed simple PALLIAL EYES (cup-shaped, without lens) on the outer folds, covered by periostracum, and that are restricted to the anterodorsal margin. HYPO-



BRANCHIAL GLANDS have not been reported. The FOOT is elongated, heeled, and deeply grooved ventrally, and is usually byssate in the adult.

The LABIAL PALPS are relatively small to medium-sized (large in *Didimacar*). The CTENIDIA are FILIBRANCH (ELEUTHERORHABDIC), HOMORHABDIC, of about equal size (outer demibranch slightly smaller), and not inserted into (or fused with) the distal oral groove of the palps (CATEGORY III association). Incurrent and excurrent water flows are posterior, with a secondary anterior incurrent. The STOMACH is TYPE III. The MIDGUT is coiled. The HINDGUT passes through the ventricle of the heart, and leads to a sessile rectum. The heart frequently has a doubled ventricle. Hemoglobin has been documented in the blood of some species (e.g., *Arcopsis adamsi*). Noetiids are GONOCHORISTIC and usually produce planktonic VELIGER larvae. The gonad often extends branches into the mantle tissues. The nervous system is not concentrated. STATOCYSTS are present in adults. ABDOMINAL SENSE ORGANS are present.

Noetiids are marine, and usually free-living as adults, but some species are EPIBYSSATE on coral or rock.

The family Noetiidae is known since the Cretaceous, is represented by 13 living genera and ca. 40 species, and is widely distributed in shallow waters.

Noetia ponderosa (Say, 1822) – Ponderous Ark



Rounded trigonal, almost as high as long, slightly skewed anterodorsally, with strong posterior ridge, inflated, white with brown-black periostracum, with 27–31 squared radial ribs each divided by fine incised line, com-marginal ridges most apparent between ribs, umbones opisthogyrate, no byssal gape; interior white, margin strongly denticulate, cardinal area wide. Virginia to Florida, West Indies, Gulf of Mexico, Caribbean Central America. Length 50 mm (to 60 mm).

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Family Glycymerididae – Bittersweet Clams or Dog Cockles

Classification

AUTOLAMELLIBRANCHIATA Grobben, 1894

Pteriomorphia Beurlen, 1944

Arcoidea Stoliczka, 1870

Arcoidea Lamarck, 1809

Glycymerididae Dall, 1908 [1847]

Featured species

Tucetona pectinata (Gmelin, 1791) – Comb Bittersweet



dorsal

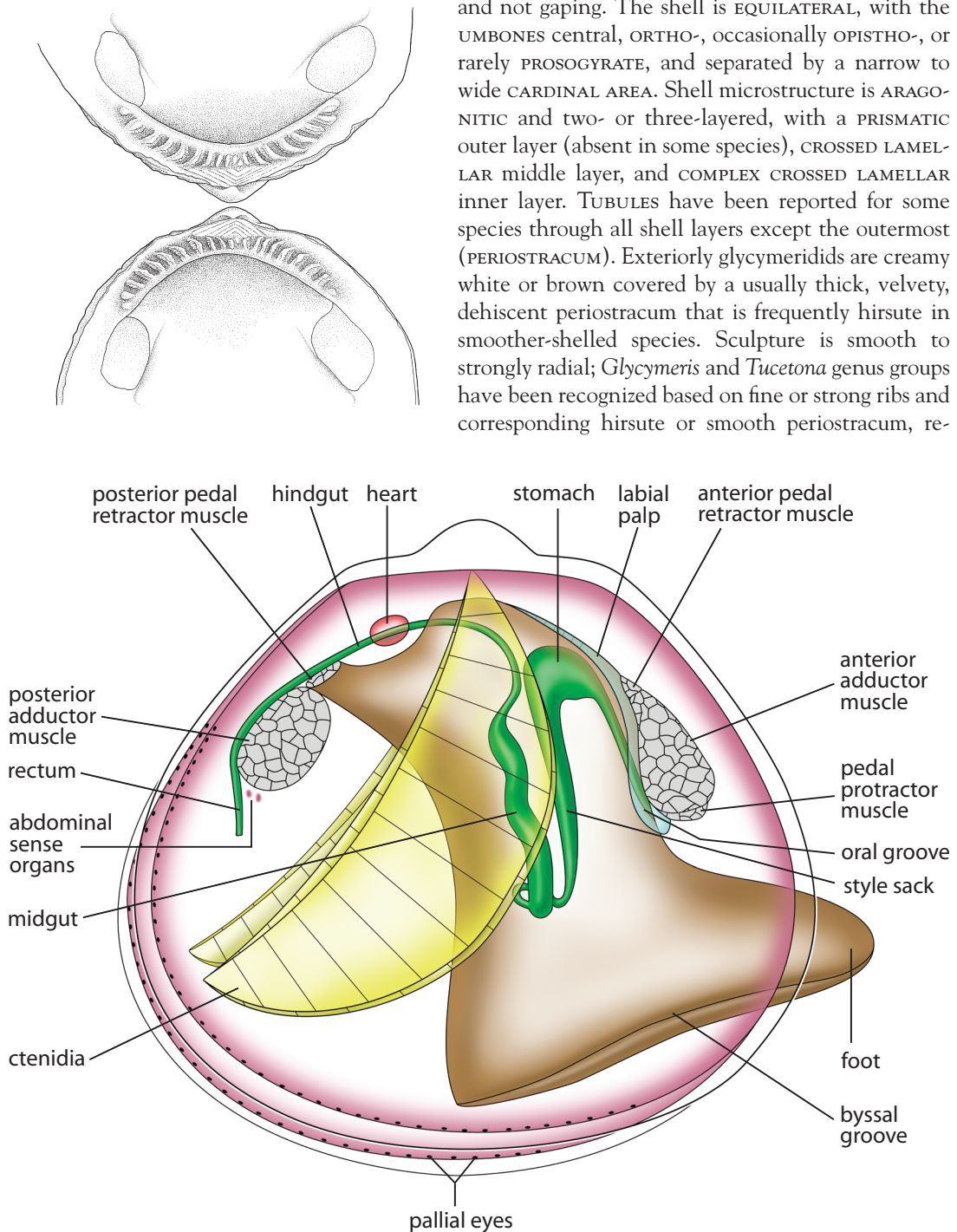
Circular, but ventrally flattened, white to gray with brown patches and irregularly commarginal bands, with 20–40 coarse rounded radial ribs crossed by fine commarginal striae, periostracum inconspicuous, umbones orthogyrate; interior white with brown stain. New Jersey to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Brazil). Length 20 mm (to 31 mm). Formerly in *Glycymeris*. Compare *Tucetona subtilis*, which is ventrally rounded and has more radial ribs.

Tucetona pectinata lives epifaunally on sand or hard-bottom habitats (like these from the bayside of Stirrup Key), with the shell surfaces often fouled by algae.



Family description

The glycymeridid shell is small to medium-sized (to 100 mm), circular to oval to rounded trigonal, in some cases slightly oblique, and solid. It is EQUIVALVE, moderately inflated, and not gaping. The shell is EQUILATERAL, with the UMBONES central, ORTHO-, occasionally OPISTHO-, or rarely PROSOGRATE, and separated by a narrow to wide CARDINAL AREA. Shell microstructure is ARAGONITIC and two- or three-layered, with a PRISMATIC outer layer (absent in some species), CROSSED LAMELLAR middle layer, and COMPLEX CROSSED LAMELLAR inner layer. TUBULES have been reported for some species through all shell layers except the outermost (PERIOSTRACUM). Exteriorly glycymeridids are creamy white or brown covered by a usually thick, velvety, dehiscent periostracum that is frequently hirsute in smoother-shelled species. Sculpture is smooth to strongly radial; *Glycymeris* and *Tucetona* genus groups have been recognized based on fine or strong ribs and corresponding hirsute or smooth periostracum, re-



spectively. LUNULE and ESCUTCHEON are absent. Interiorly the shell is non-NACREOUS; the posterior (in some cases also the anterior) adductor muscle scar has a raised ridge (MYOPHORIC RIDGE) on the inner margin. The PALLIAL LINE is ENTIRE. The inner shell margins are denticulate, with denticles corresponding to the external spaces between ribs. The HINGE PLATE is robust and strongly arched, TAXODONT, with numerous radially arranged, in some species chevron-shaped teeth (the larger of which are commonly crenulate), diminished in size below the umbones and laterally. The LIGAMENT occupies the entire CARDINAL AREA, and is PROSO- or AMPHIDETIC, and DUPLIVINCULAR (with superficial chevron-shaped grooves).

The animal is slightly HETEROMYARIAN (posterior ADDUCTOR MUSCLE smaller, a SYNAPOMORPHY of the family); the pedal retractor muscles are well developed. Pedal protractor muscles underlie the anterior adductor. The MANTLE margins are not fused ventrally; SIPHONS are absent. The MANTLE margins are muscular and nontentaculate; the outer folds have simple PALLIAL ("siphonal") EYES (cup-shaped, without lens) on the posterior margin, covered by periostracum. Temporary EXCURRENT and INCURRENT APERTURES can be formed by appression of the mantle edges. HYPOBRANCHIAL GLANDS have not been reported. The FOOT is large, wedge-shaped, and has a deep BYSSAL GROOVE; the adult is nonbyssate.

The LABIAL PALPS are relatively small, and are extended by a long, unridged oral groove to the mouth. The subumbonal CTENIDIA are FILIBRANCH (ELEUTHERORHABDIC), HOMORHABDIC, of about equal size, and not inserted into (or fused with) the distal oral groove of the palps (CATEGORY III association). CEPHALIC EYES are present. Incurrent and excurrent water flows are posterior, with a secondary anterior incurrent. The STOMACH is TYPE III. The MIDGUT is not coiled and is somewhat enlarged in diameter. The HINDGUT passes through the ventricle of the heart, and leads to a freely hanging or sessile rectum. Hemoglobin has been found in the blood of some species. Glycymeridids are generally GONOCHORISTIC, although evidence suggests that at least one species is a PROTANDRIC HERMAPHRODITE, and produce planktonic VELIGER larvae. The nervous system is apparently not concentrated. STATOCYSTS have not been reported in adults. ABDOMINAL SENSE ORGANS are present and asymmetrical.

Glycymeridids are SUSPENSION-FEEDING, shallow INFAUNAL burrowers just below the surface of coarse sand. Some species show intolerance of silt and turbid water. Atlantic species are slow, inefficient burrowers that are believed to be active exclusively at night.

The family Glycymerididae is known since the Cretaceous, is represented by 4 living genera and at least 50 species, and is distributed worldwide except in polar and deep seas. *Glycymeris* is commercially fished in parts of Europe and the Mediterranean; the common name "bittersweet clam" undoubtedly refers to their taste.

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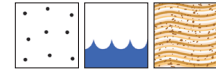
66 ~ GLYCYMERIDIDAE

Glycymeris americana (DeFrance, 1826) – Giant American Bittersweet



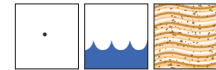
Circular, mottled tan to brown, with numerous radial ribs bearing fine riblets, periostracum velvety, umbones orthogyrate; interior white. North Carolina to Florida, Bermuda, Gulf of Mexico. Length 25 mm (juvenile; to 98 mm).

Glycymeris decussata (Linnaeus, 1758) – Decussate Bittersweet



Circular, posterior end slightly produced, mottled brown and white with velvety brown periostracum, with fine radial riblets, umbones opisthogyrate; interior white, often stained with brown, cardinal area in front of umbones. Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (Colombia, Brazil). Length 40 mm (to 55 mm). Compare *Glycymeris undata*, which is orange mottled and less posteriorly rostrate.

Glycymeris spectralis Nicol, 1952 – Spectral Bittersweet



Circular, but ventrally flattened, uniformly light brown to white with velvety brown periostracum, with numerous radial ribs bearing fine riblets, umbones slightly opisthogyrate; interior white with brown stain. North Carolina to Florida, Gulf of Mexico, Caribbean Central America. Length 25 mm.

Glycymeris undata (Linnaeus, 1758) – Atlantic Bittersweet



Circular, posterior end slightly produced in some individuals, cream to white with bold orange-brown mottlings and velvety brown periostracum, near-smooth with fine radial ribs bearing fine riblets, umbones orthogyrate; interior white stained with brown. North Carolina to Florida, Bahamas, West Indies, Caribbean Central America, South America (to Uruguay). Length 12 mm (to 50 mm). Compare *Glycymeris decussata*, which is brown mottled and more posteriorly rostrate. Note: Also known as Wavy Bittersweet.

Tucetona subtilis Nicol, 1956 – Bermudan Bittersweet



Circular, ventrally rounded, white with orange-brown mottlings, with ca. 50 coarse subequal rounded radial ribs crossed by fine commarginal striae, periostracum inconspicuous, umbones orthogyrate or slightly opisthogyrate; interior white. Florida Keys, Bermuda. Length 6 mm (to 12 mm). Formerly in *Glycymeris*. Compare *Tucetona pectinata*, which is ventrally flattened and has fewer radial ribs. Note: The left valve of this specimen has been drilled by a predatory gastropod.

Tucetona pectinata lives epibenthically on seagrass- and sand-covered hard bottoms in the Florida Keys, such as this site (with an adult Queen Conch, *Strombus gigas* Linnaeus, 1758) at Looe Key back reef.



Glycymeris americana



Glycymeris decussata



Glycymeris spectralis



Glycymeris undata



Tucetona subtilis



Family Limopsidae – Limops Clams

Classification

AUTOLAMELLIBRANCHIATA Grobben, 1894

Pteriomorphia Beurlen, 1944

Arcoidea Stoliczka, 1870

Limopsoidea Dall, 1895

Limopsidae Dall, 1895

Featured species

Limopsis cristata Jeffreys, 1876 – Crested Limops



with periostracum

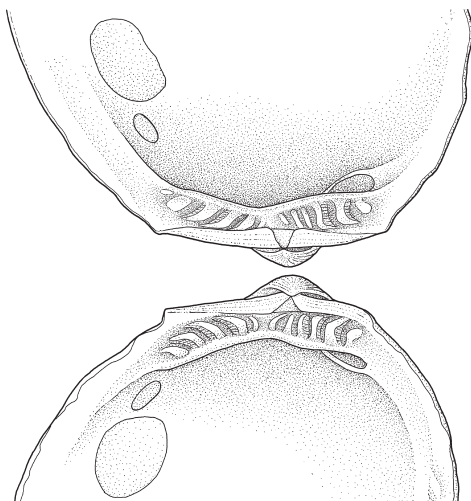


dorsal

Circular to obliquely oval, white with light yellowish periostracum in radial rows, with radial ribs more prominent than commarginal ridges; interior white, margin denticulate. Massachusetts to Florida, West Indies, Gulf of Mexico, also western Europe. Length 4 mm.

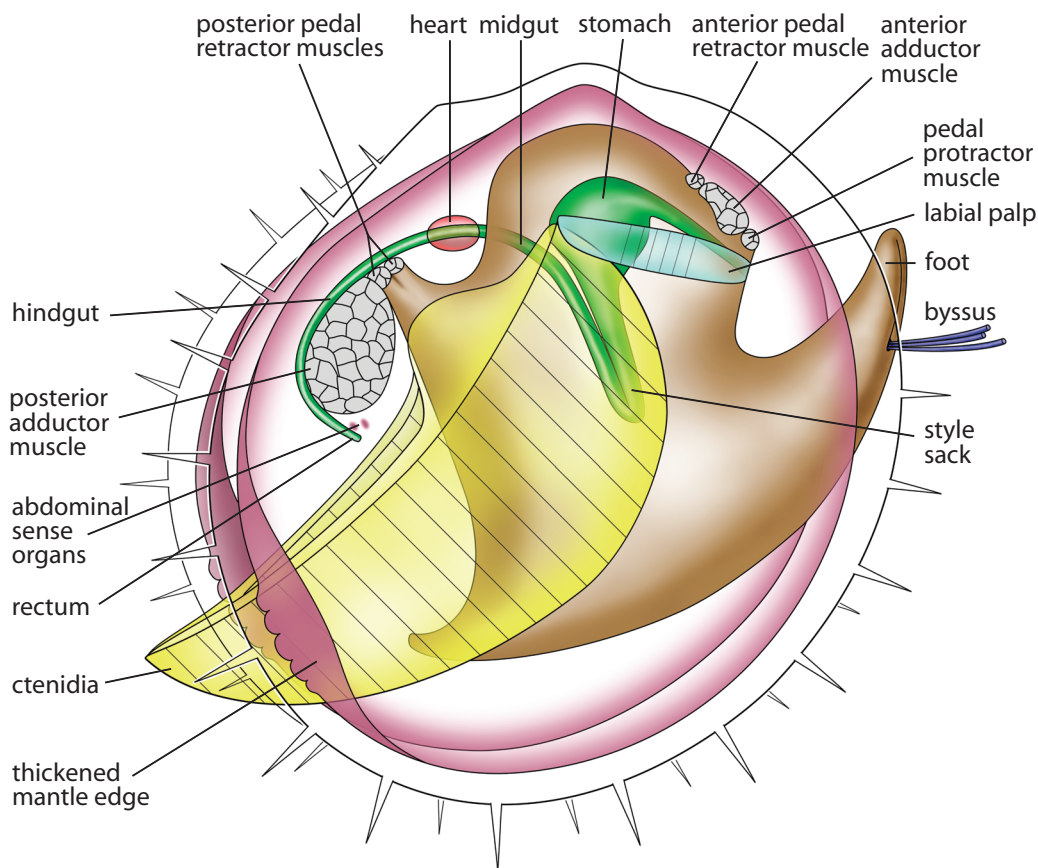
Family description

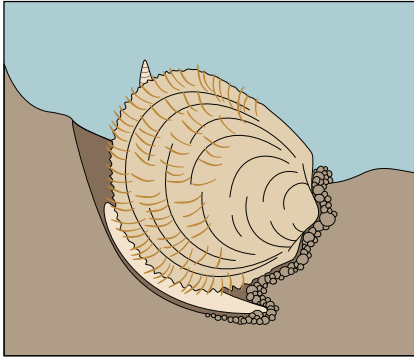
The limopsid shell is small to medium-sized (to 70 mm), obliquely oval to orbicular to rounded trigonal, and thin-walled to solid. It is EQUIVALVE, compressed to moderately in-



flated, and not gaping. The shell is EQUILATERAL or INEQUILATERAL (umbones anterior), with ORTHO- or PROSO- GYRATE UMBONES separated by a narrow CARDINAL AREA. Shell microstructure is ARAGONITIC and three-layered, with a PRISMATIC outer layer (restricted to the cardinal area), a CROSSED LAMELLAR middle layer, and COMPLEX CROSSED LAMELLAR inner layer. TUBULES have been reported for some species through all shell layers except the outermost (PERIOSTRACUM). Exteriorly limopsids are usually uniformly light-colored, and are covered by a thick, velvety, tufted periostracum that can extend beyond the shell margin. Interlocking periostracal tufts presumably help stabilize the clam in the sediment (analogous to shell spines) and prevent intrusion of sediment into the mantle while the animal is active. Sculpture is smooth or finely radial or commarginal. LUNULE and ESCUTCHEON are absent. Interiorly

tracal tufts presumably help stabilize the clam in the sediment (analogous to shell spines) and prevent intrusion of sediment into the mantle while the animal is active. Sculpture is smooth or finely radial or commarginal. LUNULE and ESCUTCHEON are absent. Interiorly





the shell is non-NACREOUS. A radial ridge of varying strength extends from the UMBONAL CAVITY along the posterior edge of the anterior adductor muscle. The PALLIAL LINE is ENTIRE. The inner shell margins are smooth or denticulate. The HINGE PLATE is strong and weakly arched, TAXODONT, with numerous radially arranged teeth that are diminished in size or absent below the umbones. The LIGAMENT is SIMPLE, ALIVINCULAR (interpreted as modified or reduced DUPLIVINCULAR), and AMPHIDETIC; an internal portion (RESILIUM) sits on a deep RESILIFER (especially differing from Glycymerididae by the presence of this feature).

The animal is HETEROMYARIAN (anterior ADDUCTOR MUSCLE smaller and more dorsal); the pedal retractor and protractor muscles are well developed. Pedal elevator muscles have not been reported. The MANTLE margins are not fused ventrally, and in some species have a thickened edge near the termini of the gills; SIPHONS are absent. Temporary EXCURRENT and INCURRENT APERTURES can be formed by appression of the mantle edges and positioning of the gill tips. HYPOBRANCHIAL GLANDS have not been reported. The MANTLE margins are usually nontentaculate, but the outer folds can have a few tentacles and simple PALLIAL EYES (cup-shaped, without lens). The FOOT is elongated, narrow, arcuate, heeled, and has a BYSSAL GROOVE; the adult is byssate in most species. The byssal threads do not have terminal disks and have small sediment particles attached along their lengths.

The LABIAL PALPS are small with few ridges restricted to midpalp. The CTENIDIA are FILIBRANCH (ELEUTHERORHABDIC), HOMORHABDIC, and not inserted into (or fused with) the distal oral groove of the palps (CATEGORY III association). In some species the ascending lamella of the outer demibranchs are absent; the gill axis has been reported as muscular in some species. Incurrent and excurrent water flows are posterior; incurrent flow is also anterior. The STOMACH is TYPE III. The MIDGUT is not coiled. The HINDGUT passes through the ventricle of the heart, and leads to a freely hanging rectum. Limopsids are usually GONOCHORISTIC and produce planktonic VELIGER larvae; deepwater species often are LECITHOTROPHIC. The nervous system is not concentrated. STATOCYSTS and ABDOMINAL SENSE ORGANS are present.

Limopsids are marine SUSPENSION FEEDERS, living epi- or endobyssally in soft sedi-

Limopsis minuta (Philippi, 1836) – Minute Limops



Obliquely oval, flattened posteriorly, white with light yellow-brown periostracum in radial rows, surface cancellate with slightly stronger radial ribs; interior chalky white, margin denticulate. North Atlantic, eastern Canada to Florida, West Indies, Gulf of Mexico, Caribbean Central America, South America (Brazil), also western Europe. Length 13 mm.

ments in deep, cold waters. Living individuals typically plough vertically through the surface of soft sediments, using the byssal surface as a flattened “sole.” Inefficient burrowing and the weak byssus make dislodgement from the sediment frequent.

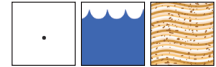
The family Limopsidae is known since the Triassic, is represented by 5 living genera and 25–50 species, and is distributed worldwide mainly in deep, cold, and temperate waters.

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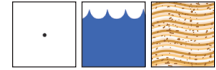
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Limopsis aurita (Brocchi, 1814) – Eared Limops



Obliquely oval, slightly flattened posteriorly, white with light yellow-brown periostracum in radial rows, surface weakly cancellate; interior white, margin denticulate. Florida, Bermuda, Gulf of Mexico, South America (Brazil). Length 9 mm. Note: This species was described as a European fossil; some authors consider the name *L. aurita* a senior synonym of the Recent western Atlantic species *Limopsis paucidentata* Dall, 1886, whereas others (including the present authors) recognize both as valid and extant. The left valve of this specimen has been drilled by a predatory gastropod.



Limopsis sulcata Verrill & Bush, 1898 – Sulcate Limops

Obliquely oval, flattened posteriorly, somewhat produced posteroventrally, white with light yellow periostracum in radial rows, with coarse, rounded commarginal ridges notched dorsally by radials; interior white, margin smooth. Eastern Canada to Florida, West Indies, Gulf of Mexico. Length 8 mm.

Seemingly lifeless deepwater sediments (here at 427 m in the Florida Straits) are home to limopsids and the Blackfin Goosefish.

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