

A New Species of *Sphenia* (Bivalvia: Myidae) from the Gulf of Maine

by

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Abstract. A new species of the genus *Sphenia* Turton, 1822, is described from the Gulf of Maine. Also, a lectotype for *Sphenia binghami* Turton, 1822, type species for the genus, is designated. *Sphenia sincera* Hanks & Packer, spec. nov., is easily distinguished from other members of the genus. It is the first *Sphenia* reported from the northeast coast of the United States, and, unlike other *Sphenia*, *S. sincera* is not found in a nestling habitat. The unique, undistorted shell of *S. sincera* reflects this habitat difference. The new species remained undetected until now because it had been confused with juveniles of the well-known *Mya arenaria* and *M. truncata*. *Sphenia sincera* differs from species of *Mya* in the shape of the chondrophore, small adult size, short life span, and completely subtidal occurrence. The species is found in greatest abundance at depths from 30 to 63 m. Unlike species of *Mya*, *S. sincera* prefers soft silt-clay sediments where it may be a deposit-feeder as well as a filter-feeder. It appears to be a major food item for bottom-feeding fish.

INTRODUCTION

THE GENUS *Sphenia* Turton, 1822, is one of the lesser known taxa in the bivalve family Myidae. Small size, nestling habit, and rarity in collections have restricted scientific interest in the group to taxonomic and faunistic studies. On the other hand, the genus *Mya* Linné, 1758, owing to commercial importance, wide distribution, and great abundance, has been studied intensively. Species of *Mya* are found on parts of all coastlines of the Northern Hemisphere; species of *Sphenia* have been reported from the Atlantic and Pacific coasts of North and South America, from Japan and Korea, from Puerto Rico, from the

Atlantic coast of Europe, and from the Mediterranean Sea (HABE, 1951; WARMKE & ABBOTT, 1961; KEEN, 1971; ODE, 1971; RIOS, 1975; ROSEWATER, 1975; TEBBLE, 1976; BERNARD, 1983). Some *Sphenia* are said to occur on the South African, Indian, and Malay coasts (LAMBY, 1919), but documentation is poor. *Sphenia binghami* Turton, 1822, the type species of the genus by subsequent designation of GRAY (1847), has been recorded along the shores of the Eastern Atlantic from Morocco north to the British Isles and into the Mediterranean (TEBBLE, 1976).

Several specimens of *Sphenia* were dredged from the Sheepscot River estuary in 1956, during studies of the benthic fauna of the midcoast region in the Gulf of Maine (HANKS, 1961, 1964). In subsequent years, large numbers of this small bivalve were collected from deep waters of the estuary, from coastal regions, and from fish stomachs. *Mya arenaria* Linné, 1758, is abundant in this region, and *M. truncata* Linné, 1758, has been reported. Although the

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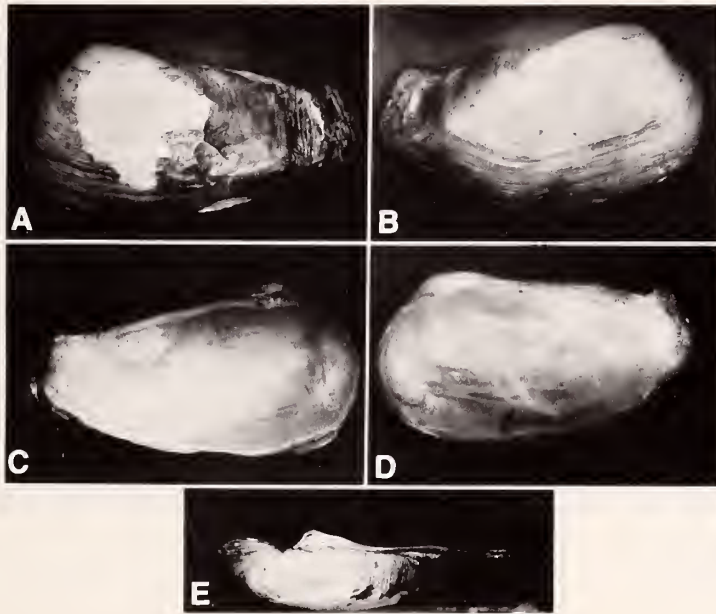


Figure 1

Lectotype herein of *Sphenia binghami* Turton, 1822, USNM 171240. $\times 4.7$. A and B, outer surface of left and right valves. C & D, inner surface of left and right valves. E, chondrophore of left valve.

two species of *Mya* are easily separated as adults, juvenile *Mya* and any stage of *Sphenia* might easily be confused. Great abundance and a few previously unidentified museum specimens indicate that this new species of *Sphenia* has long been an inhabitant of the Maine coast, but it has remained unknown because of its small size and similarity to *Mya*, in combination with a habitat entirely different from that of other *Sphenia*. The presence of a new species of *Sphenia* in the northwestern Atlantic represents a significant addition to the known range of the genus.

Family MYIDAE Lamarck, 1809

Subfamily Spheniinae Bernard, 1983

Sphenia Turton, 1822

Type species: *Sphenia binghami* TURTON, 1822:36, pl. III, figs. 4, 5; by subsequent designation GRAY, 1847:190.

To the best of our knowledge, no type specimen has previously been identified. Turton's original material appears to have passed to the Jeffreys collection and thence into the U.S. National Museum of Natural History, where specimens labeled "*Mya binghami* Turton, ex. mus. Turton. Jeffreys Coll. #75" (USNM 171240) were found. The allocation to *Mya* can be ascribed to Jeffreys, who did not feel that Turton was justified in erecting a new genus (JEFFREYS, 1862-1869:vol. 3, p. 72). The specimens found were two, separated but matched, pairs of valves, one unseparated pair, several unmatched right valves, and

what appears to be a piece of old oyster shell bored by *Cliona* in which are several minute *Sphenia*. Although none of these specimens matches TURTON's (1822) figure, it is believed that this material was part of his original collection. Therefore, one of the matched pairs (remaining in USNM 171240) that was most similar to that of Turton's original description is here designated as lectotype (Figures 1, 2). The remainder of this material is designated as paralectotypes (USNM 679166). The designation of the lectotype parallels the action of DAVIS (1964) in identifying type specimens of other Turton species, where there is sufficient evidence that the original material is now in the U.S. National Museum of Natural History.

TURTON's original description (1822) was brief and somewhat ambiguous, and it led to descriptive errors by later authors. For example, Turton said (p. 36), "From the *Mya* it [*Sphenia*] differs, in having the valve which contains the tooth smaller, and received within the opposite one; in being closed at the hinder extremity; and in being furnished with a concave tooth in the larger valve, behind which is a small denticle." In reality, the left valve in both *Mya* and *Sphenia* is the smaller and bears the relatively large chondrophore. NICOL (1958) commented on this point as follows: "A few of the related Myidae are also inequivalve, having in all such cases larger right than left valves." In young *Mya* and undistorted *Sphenia* the posterior end is closed and the two valves fit tightly together. Also, the concavity in the right valve occurs in both genera.

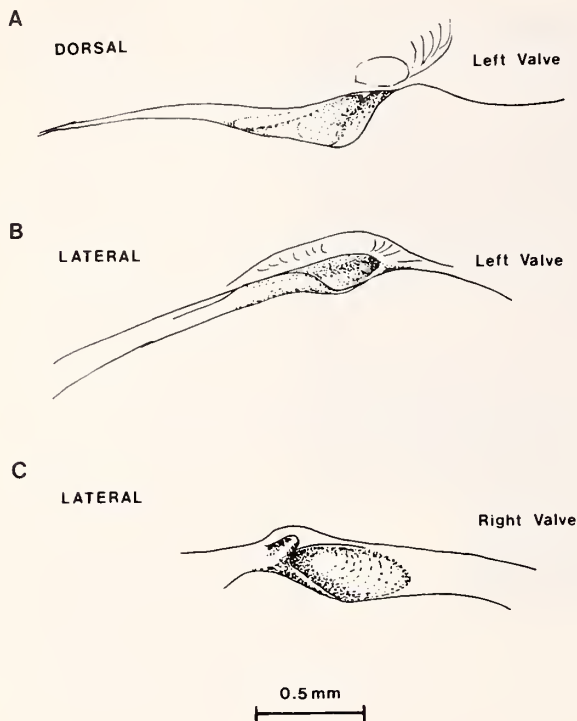


Figure 2

Hinge structure of *Sphenia binghami* Turton, 1822, lectotype USNM 171240. A, dorsal view of chondrophore of left valve. B, lateral view of chondrophore of left valve. C, lateral view of resilifer of right valve.

Turton's description of the species *Sphenia binghami* was, fortunately, accurate. FISCHER (1887) and LAMY (1919) correctly described the *Sphenia* hinge.

Although *Sphenia binghami* is the best known species of the genus, most accounts deal superficially with the shell morphology, and only two descriptions of the entire animal have been published (FORBES & HANLEY, 1853; YONGE, 1951); the latter description is by far the more complete. Accounts of other species of *Sphenia* consist primarily of records of new species or distributions, and emphasize shell morphology (e.g., CARPENTER, 1864; SMITH, 1893; DALL & SIMPSON, 1901; etc.).

Sphenia sincera Hanks & Packer, spec. nov.

(Figures 3–5)

Description—External: Shell elongate; strongly inequivalve, right valve larger and more deeply cupped. Posterior gape small; siphons completely withdrawable into shell. Umbones prominent, often eroded; one-third the length from anterior end; prosogyrate; umbo of right valve larger than left. Anterior end inflated, generally rounded;

dorsal margin somewhat straighter than ventral, sloping gradually and evenly to posterior end, which may be slightly rounded or vertical. Color chalky white; rarely with a narrow, dark orange-brown color along margins. Thin, yellowish periostracum sometimes present, but generally eroded from valves, covering only paired siphons. Surface with fine, irregular concentric growth lines. A distinct ridge running from umbo to posteroventral angle, more acute on left valve.

Internal: Shell smooth, dull white. Adductor scars and pallial line usually obscure. Anterior scar long; tear shaped; extending to, or slightly past horizontal midline of shell. Posterior scar oval; higher than wide (width two-thirds of height); one-half distance between umbo and posterior. Pallial line well back from edge of shell and complete between anterior and posterior adductor scars, joining ventral margin of pallial sinus in an acute angle at a point directly below posterior adductor scar. Pallial sinus small, "U" shaped; extending anteriorly two-thirds distance between posterior and umbo; dorsal margin attached to adductor scar at a slight angle.

Hinge: Nomenclature for the myid hinge follows BERNARD (1979a) based on FUJIE (1957) and MACNEIL (1965) (Figure 4).

Left valve: Chondrophore narrow, strongly arched, resulting in ligamental pit being directed in an oblique anterior angle. Ligamental pit small; anterior ridge prominent, its junction with ventral or outer margin directly opposite or posterior to umbo. Radial groove large as a consequence of posterior ridge being directed in an oblique posterior angle. Posterior ridge expanded and flattened, not projecting sharply beyond outer margin; median groove shallow and open, often represented by a median undulation. Anterior buttress vestigial; posterior buttress much reduced laterally, generally extended posteriorly. Deep pit under umbo for tooth of right valve.

Right valve: Resilifer concave, ovate-triangular, dominated by a projecting blunt tooth on anterior end that articulates with anterior surface of anterior ridge in left valve. Lateral end of tooth fitting into concavity under umbo of left valve, as in a ball and socket joint, possibly providing movement about dorsoventral axis (see TRUEMAN, 1954).

Type locality: Mouth of the Sheepscot River, Lincoln County, Maine (69°42'W, 43°47'N); depth 33.6 m; soft mud, primarily silt and clay. Full description of associated fauna and environment can be found in HANKS (1964) and LARSEN (1979).

Holotype: U.S. National Museum of Natural History, USNM 679164.

Dimensions of the holotype: Length 5.6 mm, height 4.0 mm, width 2.5 mm, umbo to anterior 2.2 mm, umbo to posterior 3.4 mm, chondrophore length 1.43 mm, chondrophore width 0.34 mm.

Paratypes: USNM 679165. The balance of our collection remains in our possession at the National Marine Fish-

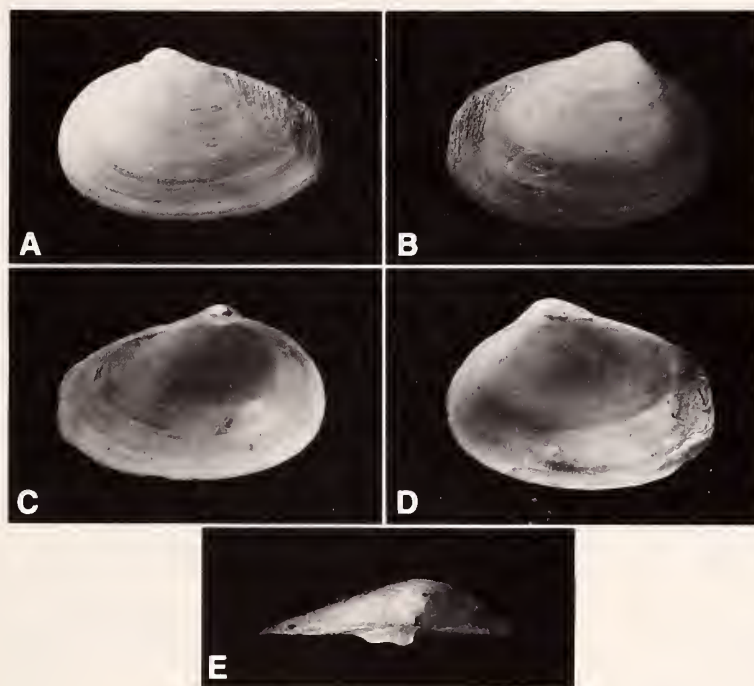


Figure 3

Holotype of *Sphenia sincera* Hanks & Packer, spec. nov., USNM 679164. $\times 6.3$. A and B, outer surface of left and right valves. C and D, inner surface of left and right valves. E, chondrophore of left valve.

eries Service, Oxford, Maryland 21654, and the Marine Systems Laboratory of the Smithsonian Institution in Washington, D.C. 20560. In addition, the following is a list of previously unidentified material in the U.S. National Museum of Natural History now assigned to *Sphenia sincera*: 1 specimen from Casco Bay (Portland), Maine, USNM 150763; 6 specimens from off Mt. Desert Island, Maine, 16.5 m, USNM 173122; 7 specimens from Bar Harbor (Mt. Desert Island), Maine, USNM 199189; 1 specimen from off Gotts Island (Mt. Desert region), Maine, USNM 451224; 2 specimens from off Gotts Island, Maine, USNM 451230; 75+ specimens from Frenchman Bay, Maine, USNM 451334; 1 specimen from Winter Harbor (Mt. Desert region), Maine, USNM 451368; 4 specimens from Frenchman Bay, Maine, USNM 462652.

Total number of specimens collected was about 977, of which about 350 have been closely examined. The average length of 70 *Sphenia sincera* shells, collected in June of 1962, was 5.4 mm, with a range of 3.4 to 8.9 mm. The average height of these shells was 3.6 mm, with a range of 2.4 to 5.3 mm. The largest shell collected from the Sheepscot region was 9.9 mm in length.

Etymology: The specific epithet *sincera*, derived from the Latin *sincerus*, which is defined as "clean, natural, without

mutilation," refers to the undistorted shape of the valves, a feature rarely found in the genus *Sphenia*, as well as to their clean, brilliant whiteness.

Distribution: Known populations of *Sphenia sincera* are centered around the mid-coast region of Maine, near Boothbay Harbor and the mouth of the Sheepscot River in the south and Gouldsboro Bay in the north. It is likely that *S. sincera* has a continuous distribution from about Casco Bay in the south (sandy sediments become prominent farther southward), to perhaps the coast of Nova Scotia in the North (Figure 6).

Comparisons: Nearly all previous records, with the exception of those for *Sphenia antillensis* Dall & Simpson, 1901 (DALL & SIMPSON, 1901; WARMKE & ABBOTT, 1961; RIOS, 1975), have reported species of *Sphenia* to be nestlers living in the burrows constructed by other invertebrates. On the coast of England, *S. binghami* is frequently found living in the vacant burrows of *Hiatella* (YONGE, 1951). Every account of European *S. binghami* emphasizes the shell distortion caused by conformity to crevices and burrows formed by other animals (FORBES & HANLEY, 1853; JEFFREYS, 1865; TEBBLE, 1976; see also BALUK & RADWAŃSKI, 1979, for a comparison of *S. binghami* with its presumed Neogene ancestor, *Sphenia anatina* Basterot,

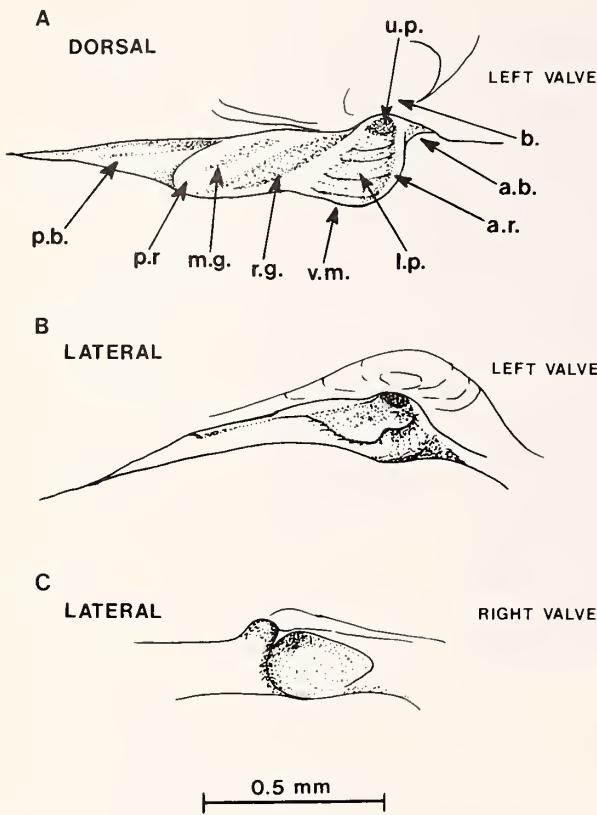


Figure 4

Hinge structure of *Sphenia sincera* Hanks & Packer, spec. nov., holotype USNM 679164. A, dorsal view of chondrophore of left valve. B, lateral view of chondrophore of left valve. C, lateral view of resifier of right valve. Key: b, beak or umbo; u.p., umbonal pit; a.b., anterior buttress; a.r., anterior ridge; l.p., ligamental pit; v.m., ventral or outer margin; r.g., radial groove; m.g., median groove; p.r., posterior ridge; p.b., posterior buttress.

1825). Generally, the shell posterior is truncate or rostrate and is usually distorted by the confines of its habitat (STANLEY, 1970; BALUK & RADWAŃSKI, 1979). Often, the posterior region of the shell is weakly calcified, which gives flexibility to the shell, and apparently this feature has selective value for the nestling species. Additionally, YONGE (1951) stated that lack of mobility and the nature of the habitat is further indicated by the presence of encrusting growths on the shell and periostracum of the siphons.

In contrast, *Sphenia sincera* has none of the characteristics of the typical nestling form, and has not been observed in a nestling habit, although *Hiatella* is common on the rocky New England coastline (THEROUX & WIGLEY, 1983), and extensive collections were made throughout the lower Sheepscot estuary in the dense *Hiatella* populations adjacent to deep-water populations of *S.*

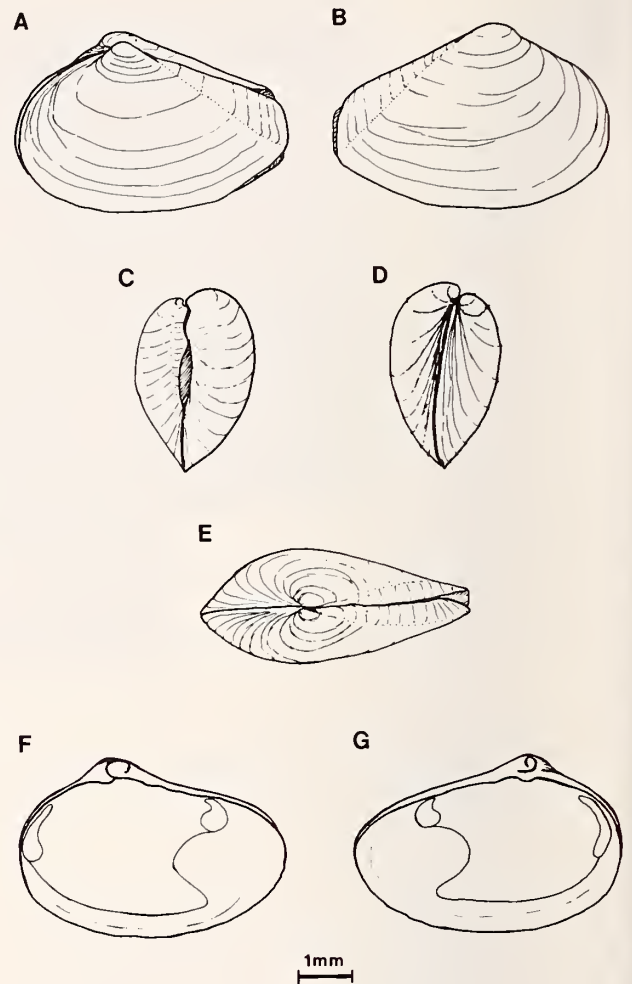


Figure 5

Sphenia sincera Hanks & Packer, spec. nov. Camera lucida drawing of holotype USNM 679164. A, left valve. B, right valve. C, posterior. D, anterior. E, dorsal view. F, inner surface of right valve. G, inner surface of left valve. Pallial complex usually obscure, but has been highlighted in this drawing.

sincera. The burrows and tubes of other organisms were also examined closely. *Sphenia sincera* is always found living on or near the surface of the soft, clay-silt mud found along the Maine coast. The shells are never distorted, and the periostracum is quite thin. In most respects they resemble the juveniles of *Mya arenaria* and *Mya truncata*, but *S. sincera* differs from *Mya* in having a chondrophore that is more strongly arched, a reduced ligamental pit, an expanded radial groove, and an anterior ridge that joins with the outer margin directly opposite or posterior to the umbo (never anterior as in *Mya*). Also, the pallial sinus is shallower and does not extend to the middle of the shell.

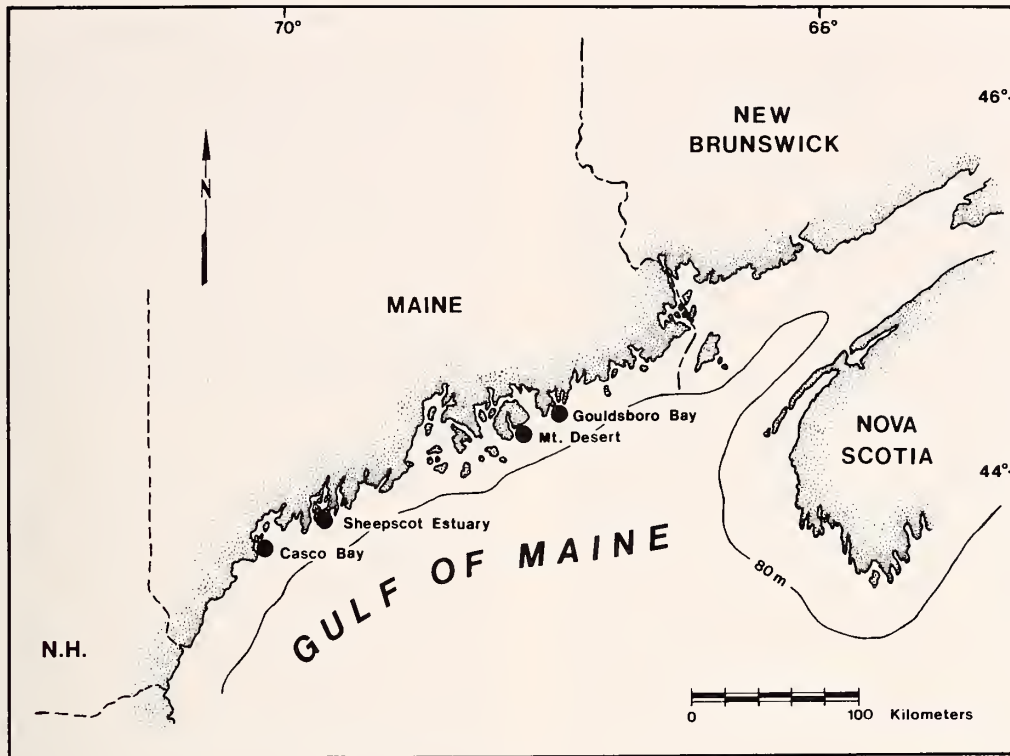


Figure 6

Distribution of *Sphenia sincera* Hanks & Packer, spec. nov., in the Gulf of Maine. Dots are points of actual collection; the 80-m contour bounds the inferred range (from Casco Bay to perhaps northeastern Nova Scotia) based on known habitat requirements.

The unique characteristics of *Sphenia sincera*—bright, clean, undistorted shell of distinct shape, solid calcification, and geographic remoteness from other species of *Sphenia*—are probably sufficient to prevent confusion with any other species in the genus. However, specific comparisons help to establish the precise differences between species and to define the new taxon.

Sphenia antillensis Dall & Simpson, 1901, appears to be the closest living species to *S. sincera* both in geographic location and its generally non-nestling existence. It has been reported from Puerto Rico (DALL & SIMPSON, 1901; WARMKE & ABBOTT, 1961), Brazil (RIOS, 1975), Surinam (RIOS, 1975), the Atlantic coast of Panama (ROSEWATER, 1975), and South Padre Island, Texas (ODE, 1971). Recent additions of *S. antillensis* to the collections of the U.S. National Museum of Natural History have extended its range northward. Specimens were found at Sebastian Inlet, Florida, in 1978 (USNM 836238), and at Cumberland Island, Georgia, in 1982 (USNM 819628). Even though *S. antillensis* is the only member reported to be living in sandy bottoms and having undistorted shells (DALL & SIMPSON, 1901; WARMKE & ABBOTT, 1961; RIOS,

1975), ODE (1976) mentions it as being a deformed species found in a nestling habitat. In addition, specimens in the U.S. National Museum of Natural History from worm reefs in Sebastian Inlet, Florida (USNM 836238), had the characteristic convoluted, distorted shells of a nestler. In any case, the shell of *S. antillensis* is quite distinct from *S. sincera* in having more acute umbones, a distinctly flattened anterior margin not curving regularly as in *S. sincera*, a broader posterior end, and an unusual concavity on the posteroventral portion of the shell, giving the shell a keeled shape. *Sphenia antillensis* has a yellow periostracum but, apparently, this is often missing.

LEWIS (1968) has recently described *Sphenia tumida* from the Pleistocene of Flagler County, Florida. Three other fossil species recorded from this region are *Sphenia dubia* (Lea, 1845), *S. attenuata* Dall, 1898, and *S. senterfeiti* Gardner, 1936. The first is from the Miocene of Virginia and North Carolina, the latter two from the Pliocene and Miocene of Florida respectively. *Sphenia sincera* differs in being larger and more regular in shape than *S. dubia* or *S. senterfeiti* and in being neither attenuated, tumid, nor rostrate as are *S. attenuata* and *S. tumida*. Of course, *S.*

sincera differs in being a living species, although ODE (1971, 1976) has reported a single valve of *S. tumida* found in Freeport, Texas, that might be recent.

Two species of *Sphenia* are found in the Eastern Pacific. They are *Sphenia luticola* (Valenciennes, 1846) and *Sphenia ovoidea* Carpenter, 1864. *Sphenia luticola* is apparently the most ubiquitous member of the genus on the Pacific coast, having been reported from Oregon to Peru (see KEEN, 1971; ABBOTT, 1974; REHDER, 1981; under the synonym *fragilis* H. & A. Adams, 1854). The shell is elongate and opaque, but not solid. The periostracum is dull yellowish-gray to brown and adherent, but the surface of the shell is somewhat nacreous and almost smooth, with indistinct annuli. The posterior is attenuated, truncate, and commonly twisted. Internally, the shell is white; the pallial sinus is slightly oblique and not large. The anterior adductor scar appears to be more ventrally displaced than in most other *Sphenia*. Although there is considerable variation in shell shape as a result of the nestling habit (KEEN, 1971; REHDER, 1981), this species can be separated from *S. sincera* by the yellowish-gray to brown periostracum, the attenuated posterior end, and the size and position of the adductor scars. *Sphenia ovoidea* has a small shell and occurs from the Aleutian Islands to Panama. The anterior end of this shell is ovally rounded and the shell bears a yellow, somewhat rugose periostracum. The posterior end is truncate and somewhat attenuated. The pallial sinus is large and deep, often reaching to the middle of the shell. The pallial line is quite pronounced, and this would appear to be a good distinguishing feature in separating the shell from *S. sincera*. ABBOTT (1974) lists *S. ovoidea* as a possible ecologic form of *Sphenia luticola*.

Sphenia sincera differs from the type species, *S. binghami*, in having a thin, deciduous periostracum rather than a heavy, thick, brown periostracum, and in having the posterior end undistorted, with the dorsal and ventral margins converging rather than nearly parallel as in *S. binghami*. This latter characteristic appears to be an excellent diagnostic feature, and nearly all *S. binghami* that have been examined or figured have a square posterior end. Juvenile shells exhibit this characteristic at the smallest sizes. Of course, some larger *S. binghami* become so distorted posteriorly that the square shape is masked, but it is still evident even in very twisted shells. *Sphenia binghami* has a thinly calcified posterior end, whereas the entire shell is evenly calcified in *S. sincera*. The umbones are usually situated less than one-third of the distance between the anterior and posterior ends—the umbones of *S. sincera* are located about one-third of the distance. The anterior end of *S. binghami* is obliquely truncate, whereas in *S. sincera* it is generally rounded. The adductor scars are larger in *S. binghami*; the posterior adductor scar is wider (height two-thirds of width), as compared to that in *S. sincera* (width two-thirds of height). YONGE (1951) reported that the siphons of *S. binghami* are short, whereas the siphons of *S. sincera* are comparatively long.

Sphenia coreanica Habe, 1951, described from the coasts

of Korea and Japan, is very truncate posteriorly, has a somewhat crenulated anterior and ventral margin, and has a discontinuous pallial line. This shell is so different from *S. sincera* that there is no possibility of confusing the two.

Identification of the species of *Sphenia* can be difficult because of their small size and often extreme distortion resulting from the nestling habit. The taxonomic status of some specimens remains uncertain, and the genus is in need of a thorough review in regard to taxonomy and distribution. However, each species has distinctive morphological features, and *Sphenia sincera* presents an idealized morphological ground plan that, by its perfection, separates the shell from other members of the genus.

Growth and age: Measurements of the increments between successive external shell annuli were used to determine growth rates. Although growth rings have been used to determine age and growth in mollusks, this method has several sources of error, because annuli can be caused by any source of arrested growth in addition to that resulting from low water temperature, including unusual environmental conditions, spawning, poor feeding conditions, predation, and changes in sediment structure (NEWCOMBE, 1935, 1936a; BROUSSEAU, 1979; MACDONALD & THOMAS, 1980). However, small, fast growing, short-lived mollusks appear to produce more discrete and predictable rings than others (PETERSEN, 1978; BROUSSEAU, 1979).

Specimens of *Sphenia sincera* collected in June of 1962 were held in laboratory trays, with flowing seawater at ambient local temperature, until February of 1963. Measurements of each annulus, and overall shell length, were made on 147 shells using the right, or largest, valve. Generally, three annuli were apparent, and can be interpreted from smallest to largest as (1) first winter check (1961–62), (2) check caused by collection and handling in June, and (3) second winter (1962–63) check. Usually, the final (second winter) check coincided with total length, but in some specimens new growth of about 0.1 to 0.2 mm width was noted. The mean length at the first winter check was 3.0 mm (range 1.1 to 4.6 mm), at the collection check 4.0 mm (range 2.4 to 6.1 mm), and at the final check 5.1 mm (range 4.1 to 7.1 mm). Since this mean ultimate size is similar to the mean size of natural populations, it is assumed that laboratory growth rates were comparable to growth in wild populations. Mean growth in one year, under the conditions described, was a little more than 2 mm in length. The fastest growth recorded for the period was 4.7 mm, and the slowest 0.6 mm. Slow growth was characteristic of clams that were small at the first winter check. Growth of *Sphenia sincera* is considerably less than that reported for *Mya arenaria* by various authors (BELDING, 1907, 1916; PACKARD, 1918; NEWCOMBE, 1935, 1936b; DOW & WALLACE, 1951; MERRILL, 1959; STICKNEY, 1964a, b; HANKS, 1968, 1969; ARBUCKLE, 1982). *Mya truncata* also grows at a relatively slow rate, but even in the cold waters of coastal Greenland, the growth

rate appears to be twice as rapid as that of *Sphenia sincera* from Maine (PETERSEN, 1978).

The maximum length of *Sphenia sincera* appears to be about 1 cm; the largest specimen was taken in the Sheepscot region, had a total length of 9.9 mm, and had four shell annuli. Most individuals, however, apparently live only two to three years, and the mean size of all specimens measured was 5.4 mm.

DISCUSSION

Sphenia sincera has been collected from depths of 10 to 80 m in the Sheepscot region. Ninety percent of the dried sediment samples from this area consists of silt and clay. Specimens collected from the lower third of Gouldsboro Bay at 15 m depths were found in sediments consisting of 12% clay, 12% silt, and 76% sand, whereas collections taken 1.5 nautical miles (2.8 km) west of Petit Manan Island near the mouth of Gouldsboro Bay at depths ranging from 37 to 44 m were found in sediments that consisted on the average of 27% clay, 28% silt, and 45% sand (Packer, unpublished data). In both Gouldsboro Bay and the Sheepscot estuary, water temperatures near the bottom range from 1°C in the winter to 14°C in the summer. Salinities at the bottom are nearly uniform throughout the year at about 32‰. Mean tidal range for both areas is about 3 m. This presumably has little effect on populations of animals living at the depths *Sphenia* inhabits. Since the Gouldsboro populations seem to center outside the bay in offshore waters with depths to 63 m, the tidal effects are negligible as compared to those within the bay (ADEY, 1982). Most of the Sheepscot population centers in the mouth of the "lower estuary" (STICKNEY, 1959), where the major effect of tide is on current flow, both velocity and direction, and mixing (GARSIDE *et al.*, 1978; LARSEN *et al.*, 1980).

Most faunal associates of *Sphenia sincera* in the Sheepscot are members of a general *Nucula-Nephtys* dominated community described by HANKS (1964) and LARSEN (1979). Particularly abundant in these deeper waters are the bivalves *Nucula proxima* Say, 1822, *Nucula annulata* Hampson, 1971, *Thyasira gouldii* (Philippi, 1845), juvenile *Arctica islandica* (Linné, 1767), *Cerastoderma pinnulatum* (Conrad, 1830), *Yoldia limatula* (Say, 1831), and such polychaetes as *Sternaspis scutata* (Renier, 1807), *Nephtys incisa* Malgrem, 1865, and *Nephtys ciliata* (O. F. Müller, 1789). Tube-building amphipods, such as *Corophium* and *Ampelisca*, often produce thick mats of old tubes that lace the surface sediments in which the scale-worm *Hartmania moorei* Pettibone, 1955, may live as a commensal. In Gouldsboro Bay, the community is dominated by *Nucula* and the cumaceans *Diastylis sculpta* Sars, 1871, *Diastylis polita* (S. I. Smith, 1879), and *Eudorella pusilla* Sars, 1871, as well as such polychaetes as *Scoloplos acutus* (Verrill, 1873a) and *Prionospio steenstrupi* Malmgren, 1867. Outside the bay, *S. sincera* may reach a density of as much as 250/m², and is one of the dominant

soft-bottom invertebrates, along with *Nucula* and the polychaetes *Prionospio steenstrupi*, *Ninoe nigripes* Verrill, 1873a, and *Capitella capitata* (Fabricius, 1780) (Packer, unpublished data).

Major predators of these *Sphenia* populations are bottom-feeding cod, haddock, and flounder. Stomach contents of small cod and haddock, captured near the mouth of the Sheepscot River in June 1962, revealed that they were feeding almost exclusively on *Sphenia*. One small haddock (total length about 46 cm) contained over 400 specimens of *Sphenia*, with only a few other small mollusks (*Arctica* and *Clinocardium*). If the range of *Sphenia sincera* extends along the Maine coast, and if its abundance is as great as in the Sheepscot and Gouldsboro regions, it must be an important food for inshore groundfish populations. In addition to the extensive use as food for fish, *Sphenia sincera* is undoubtedly prey for many other animals. Three shells collected near Mt. Desert Island (USNM 172122) and several from Gouldsboro Bay were drilled by a gastropod. From the tapered edges of the small hole, it is believed that they were drilled by a naticid (CARRIKER, 1981), common predatory gastropods found in these waters.

Sphenia sincera has the morphological characteristics of a filter-feeding mollusk (YONGE, 1951) and could feed on materials similar to those utilized by *Mya arenaria*, such as phytoplankton (NEWCOMBE, 1935; STICKNEY, 1964a, b; ARBUCKLE, 1982). Specimens of *Sphenia sincera* collected in Maine were held in artificial seawater aquaria in the laboratory at Oxford, Maryland, from July to November 1967. During these 4 to 5 months the clams were offered weak suspensions of *Phaeodactylum* and *Chlorella*. Since mortalities were less than 10% during this period, it is assumed that the clams did feed, but we could not confirm that the algae were used. It is entirely possible that other microorganisms may have been nutritionally significant—there is some evidence that *M. arenaria* may be a deposit-feeder as well as a suspension-feeder (RASMUSSEN, 1973) as is true in such other bivalves as *Macoma balthica* (Linné, 1758) (BRAFIELD & NEWELL, 1961). This may also be the case for *Sphenia sincera*, since it appears that many benthic species are generalist feeders (MAURER *et al.*, 1979). *Sphenia sincera* may be more of a deposit than a suspension-feeder because it is found in high silt-clay sediments along with very large numbers of such other deposit-feeders as *Nucula proxima*. Deposit-feeders tend to be dominant in bottoms of these types because they destabilize the soft sediments and suffocate suspension-feeding organisms (SANDERS, 1958; RHOADS & YOUNG, 1970; LEVINTON, 1977). Also, selective deposit-feeders are most sensitive to the abundance of the clay-sized particles, a reflection of the availability of organic detritus in the fine-grained sediment. Greater amounts of organic matter permit larger bacterial populations that are a food source for deposit-feeders (SANDERS, 1958; DRISCOLL & BRANDON, 1973; LEVINTON & BAMBACH, 1975). In the Sheepscot and Gouldsboro regions abundant detritus is available from such macroalgae as *Ulva*, *Fucus*,

and especially *Ascophyllum* (ADEY, 1982) along with the seagrass *Zostera marina* Linné, 1753.

The habitats of *Mya arenaria* and *Sphenia sincera* are separated by difference in bathymetric preference; the former species rarely extends much below the low-tide level (THEROUX & WIGLEY, 1983), and the latter inhabits much deeper water, deeper than 10 m with greatest abundance below 30 m. Although it is difficult to retain the natural relation with the bottom surface in deep-water samples, individuals of *S. sincera* appear to have a similar orientation to juvenile *M. arenaria* of the same size; that is, the anterior end directed down and the posterior end with the siphons directed toward the surface. The burrows do not appear to be lined with mucus or other supportive material. Clams held in our aquaria rarely dug into sediments, or buried themselves partially, but this could be unusual behavior induced by the sediments (generally sandy) used, as it was extremely difficult to reproduce the typical sediment structure of the Sheepscot region in the laboratory. As a possible filter-feeder in such soft sediments, *Sphenia sincera* is restricted to the top 25 mm of sediment due to its short siphons, also evidenced by the prevalence of clams of this species in the stomachs of bottom-feeding fish. *Mya arenaria*, on the other hand, is a deep burrower, and in order to maintain an open tube through which its long siphons can be withdrawn and re-extended, it prefers to live in a more cohesive, stable substrate, such as muddy sand. STANLEY (1970) notes that young *Mya arenaria* living in soft mud are unable to maintain permanent tubes for their siphons.

Mya truncata is also found in the deeper waters of the Gulf of Maine (VERRILL, 1873) but not in dense populations. Specimens have not been taken in samples for this study or in other surveys (HANKS, 1961, 1964; LARSEN, 1979; THEROUX & WIGLEY, 1983). Scattered reports of *M. truncata* along the Maine, New Brunswick, Nova Scotia, and Gaspé coasts indicate that inshore populations are widely distributed and low in density. Adult *M. truncata*, obtained from the Maine coast and Canada, were all true *M. truncata* and not *Mya pseudoarenaria* Schlesch, 1931, which resembles *M. arenaria* (LAURSEN, 1966; BERNARD, 1979a, b; LUBINSKY, 1980; SIMONARSON, 1981). Extreme phenotypes of *M. truncata* have a superficial resemblance to *Sphenia sincera* (FOSTER, 1946), but this species of *Mya* has a smaller anterior tooth in the right valve (this tooth is not found in *M. arenaria*) and the anterior adductor scar extends farther ventrally than it does in *S. sincera*. Although *M. truncata* is generally subtidal in deep water along the southern part of the Gulf of Maine, it also occurs in shallow water and can be found intertidally on the northern part of the Maine coast and on Canadian shores (LUBINSKY, 1980) in all types of sediments, although it frequently prefers firm clay bottoms. René Lavoie (personal communication) of the Faculty of Science, Laval University, Quebec, P.Q., said that he found adult *M. truncata* valves still joined by the ligament—indicating fairly recent mortality—on the Gaspé shores of the St.

Lawrence. SMITH (1953) demonstrated that adult *Mya arenaria* decayed slowly after death, and that some remains of meat and adductor muscle were still evident after three months in summer and four months in winter. We can infer that the ligamentally joined *M. truncata* shells from the St. Lawrence had been dead for at least one year, and possibly much longer.

The evidence, therefore, indicates that *Sphenia sincera* occupies a habitat different from that of adult *Mya arenaria* and *Mya truncata*, that it does not compete for space with juvenile *Mya arenaria* which live mostly in shallow waters and intertidal regions, and that little competition can occur with juvenile *Mya truncata*, which are not common in offshore Maine waters near the southern limit of their distribution.

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LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells. The marine molluscs of the Atlantic and Pacific coasts of North America. Van Nostrand Reinhold: New York. 663 pp.
- ADAMS, H. & A. ADAMS. 1854. The genera of recent Mollusca; arranged according to their organization. John van Voorst: London. Vol. 2, 661 pp.
- ADEY, W. H. 1982. A resource assessment of Gouldsboro Bay, Maine. Unpublished report to the National Oceanic and Atmospheric Administration Marine Sanctuary Program, Grant No. NA81AA-D-C2076. 47 pp.
- ARBUCKLE, J. 1982. The soft-shelled clam and its environment: a study in Jonesboro, Maine. Maine Sea Grant Program Report No. NA81AA-D-0035, Univ. Maine, Orono. 35 pp.
- BALUK, W. & A. RADWAŃSKI. 1979. Shell adaptation and ecological variability in the pelecypod species *Sphenia anatina* (Basterot) from the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland). Acta Geol. Polonica 29: 269-286.
- BASTEROT, M. B. DE. 1825. Memoire geologique sur les environs de Bordeaux. Premiere partie, comprenant les observations generales sur les mollusques fossiles, et la description particuliere de ceux qu'on rencontre dans ce bassin . . . Paris. Vol. 1.
- BELDING, D. L. 1907. A report on the shellfisheries of Massachusetts. Pp. 46-53. In: Commonwealth of Mass., Public Doc. No. 25, Report of the Commissioners on Fisheries and Game for the year ending December 31, 1906. Wright and Potter Printing Co.: Boston, Mass.
- BELDING, D. L. 1916. A report upon the clam fishery. Pp. 93-

234. In: Commonwealth of Mass., Public Doc. No. 25, Fiftieth Annual Report of the Commissioners on Fisheries and Game for the year 1915. Wright and Potter Printing Co.: Boston, Mass.
- BERNARD, F. R. 1979a. Identification of the living *Mya* (Bivalvia: Myoida). *Venus* 38(3):185-204.
- BERNARD, F. R. 1979b. Bivalve mollusks of the western Beaufort Sea. *Contrib. Sci. Natur. Hist. Mus. Los Angeles County* 313:1-80.
- BERNARD, F. R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. *Can. Spec. Publ. Fish. Aquatic Sci.* 61:1-102.
- BRAFIELD, A. E. & G. E. NEWELL. 1961. The behavior of *Macoma balthica* (L.). *J. Mar. Biol. Assoc. U.K.* 41:81-87.
- BROUSSEAU, D. J. 1979. Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Mar. Biol.* 51: 221-227.
- CARPENTER, P. R. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. *British Assoc. Adv. Sci. Rep.* 33 (for 1863):517-686.
- CARRIKER, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* 20(2):403-422.
- CONRAD, T. A. 1830. Description of fifteen new species of recent, and three fossil shells, chiefly from the coast of the United States. *J. Acad. Natur. Sci. Phila.* 6:256-268.
- DALL, W. H. 1898. Contribution to the Tertiary fauna of Florida, with especial reference to the Silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part IV: Prionodesmacea, *Nucula* to *Julia*; Teleodesmacea, *Teredo* to *Ervilha*. *Trans. Wagner Free Inst. Sci. Phila.* 3, pt. 4:571-947.
- DALL, W. H. & C. T. SIMPSON. 1901. The mollusca of Porto Rico. *Bull. U.S. Fish Comm.* 20:351-524.
- DAVIS, J. D. 1964. *Mesodesma deauratum*: synonymy, holotype, and type locality. *Nautilus* 78(1):96-100.
- DOW, R. L. & D. E. WALLACE. 1951. Soft-shell clam growth rates in Maine. Unpublished mimeo report available from authors. Maine Dept. Sea and Shore Fish., Augusta, Maine. 10 pp.
- DRISCOLL, E. G. & D. E. BRANDON. 1973. Mollusc-sediment relationships in northwestern Buzzards Bay, Massachusetts, U.S.A. *Malacologia* 12(1):13-46.
- FISCHER, P. H. [1880]-1887. Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles suivi d'un appendice sur les brachiopodes par D. P. Oehlert. Paris. 1369 pp.
- FORBES, E. & S. HANLEY. 1853. A history of British Mollusca and their shells. John van Voorst: London. Vol. 1, 486 pp.
- FOSTER, R. W. 1946. The genus *Mya* in the western Atlantic. *Johnsonia* 2(20):29-35.
- FUJIE, T. 1957. On the myarian pelecypods of Japan. Part 1. Summary of the study of the genus *Mya* from Hokkaido. *J. Hokkaido Univ. Fac. Sci.* (4th ser.) 9(4):381-413.
- GARDNER, J. 1936. Additions to the molluscan fauna of the Alum Bluff Group of Florida. *Florida Geol. Surv., Bull.* 14:7-82.
- GARSDALE, C., G. HULL & C. S. YENTSCH. 1978. Coastal source waters and their role as a nitrogen source for primary production in an estuary in Maine. Pp. 565-575. In: M. L. Wiley (ed.), *Estuarine interactions*. Academic Press: New York.
- GRAY, J. E. 1847. A list of the genera of Recent Mollusca, their synonymy and types. *Proc. Zool. Soc. Lond.* 15(15): 129-219.
- HABE, T. 1951. Donacidae and Myidae in Japan. Pp. 71-78. In: T. Kuroda (ed.), *Illustrated catalogue of Japanese shells, 1949-1953*. Vol. 1. Kyoto, Japan.
- HAMPSON, G. R. 1971. A species pair of the genus *Nucula* (Bivalvia) from the eastern coast of the United States. *Proc. Malacol. Soc. Lond.* 39:333-342.
- HANKS, R. W. 1961. A study of the macroscopic benthic fauna of an estuary on the coast of Maine. Master's Thesis, Univ. New Hampshire, Durham. 99 pp.
- HANKS, R. W. 1964. A benthic community in the Sheepscot River estuary, Maine. U.S. Fish Wild. Serv., Fish. Bull. 63(2):343-353.
- HANKS, R. W. 1968. Benthic community formation in a "new" marine environment. *Chesapeake Sci.* 9(3):163-172.
- HANKS, R. W. 1969. The soft-shell clam industry. Pp. 112-119. In: F. R. Firth (ed.), *Encyclopedia of marine resources*. Van Nostrand-Reinhold Co.: New York.
- JEFFREYS, J. G. 1865. British conchology, or an accounting of the Mollusca which now inhabit the British Isles and the surrounding seas. John Van Voorst: London. Vol. 3., 393 pp.
- KEEN, A. M. 1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press: Stanford, Calif. 1064 pp.
- LAMARCK, J. B. DE. 1809. Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux, la diversité de leur organisation et des facultés qu'ils en obtiennent, aux causes physiques qui maintiennent en eux la vie, et donnent lieu aux mouvements qu'ils exécutent; enfin, à celles qui produisent les unes les sentiments, et les autres l'intelligence de ceux qui en sont doués. Paris. Vols. 1 & 2, pp. 1-422, 1-473.
- LAMY, E. 1919. Revision des Myidae vivants du Museum National d'Histoire Naturelle de Paris. *J. Conchyl.* 70:151-185.
- LARSEN, P. F. 1979. The shallow-water macrobenthos of a northern New England estuary. *Mar. Biol.* 55:69-78.
- LARSEN, P. F., L. DOGGETT, C. GARSIDE, J. TOPINKA, T. MAGUE, T. GARFIELD, R. GERBER, S. FEFER, P. SHETTIG & L. THORNTON. 1980. The estuarine system. Pp. 5-1-5-148. In: S. I. Fefer & P. A. Schettig (eds.), *An ecological characterization of coastal Maine*. Vol. 2. U.S. Fish and Wild. Serv., Biol. Serv. Prog., Northeast Region, Massachusetts.
- LAURSEN, D. 1966. The genus *Mya* in the Arctic region. *Malacologia* 3(3):399-418.
- LEA, H. C. 1845. Description of some new fossil shells, from the Tertiary of Petersburg, Virginia. *Trans. Amer. Philo. Soc., ser. II*, 9:229-274.
- LEVINTON, J. S. 1977. Ecology of shallow water deposit-feeding communities Quisset Harbor, Massachusetts. Pp. 191-227. In: B. C. Coull (ed.), *Ecology of marine benthos*. Univ. South Carolina Press: Columbia, South Carolina.
- LEVINGTON, J. S. & R. K. BAMBACH. 1975. A comparative study of Silurian and recent deposit-feeding bivalve communities. *Paleobiology* 1:97-124.
- LEWIS, J. E. 1968. Taxonomy and paleoecology of a new species of *Sphenia* (Bivalvia; Myidae) from the Pleistocene of Florida. *Tulane Stud. Geol.* 6(1):23-32.
- LINNÉ, C. VON. 1758. *Systema naturae per regna tria naturae* Edit. decima, reformata. Vol. 1. Regnum Animale. Laurentii Salvii: Stockholm. 824 pp.
- LINNÉ, C. VON. 1767. *Systema naturae per regna tria naturae* Edit. duodecima, reformata. Vol. 1. Regnum Animale. Laurentii Salvii: Stockholm. Pt. 2:533-1327.

- LUBINSKY, I. 1980. Marine bivalve molluscs of the Canadian Central and Eastern Arctic: faunal composition and zoogeography. *Can. Bull. Fish. Aquat. Sci.* 207:1-111.
- MACDONALD, B. H. & M. L. H. THOMAS. 1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. *Mar. Biol.* 58:105-109.
- MACNEIL, F. S. 1965. Evolution and distribution of the genus *Mya*, and Tertiary migrations of Mollusca. U.S. Geol. Surv. Prof. Pap. 483-G:1-51.
- MAURER, D., L. WATLING, W. LEATHEM & P. KINNER. 1979. Seasonal changes in feeding types of estuarine benthic invertebrates from Delaware Bay. *J. Exp. Mar. Biol. Ecol.* 36:125-155.
- MERRILL, A. S. 1959. An unusual occurrence of *Mya arenaria* L. and notes on other marine mollusks. *Nautilus* 73(2):39-43.
- NEWCOMBE, C. L. 1935. Growth of *Mya arenaria* L. in the Bay of Fundy region. *Can. J. Res.* 13:97-137.
- NEWCOMBE, C. L. 1936a. Validity of concentric rings of *Mya arenaria* L. for determining age. *Nature* 137:36.
- NEWCOMBE, C. L. 1936b. A comparative study of the abundance and the rate of growth of *Mya arenaria* in the Gulf of St. Lawrence and Bay of Fundy regions. *Ecology* 17(3):418-428.
- NICOL, D. 1958. A survey of inequivalve pelecypods. *J. Wash. Acad. Sci.* 48(2):56-62.
- ODE, H. 1971. *Sphenia tumida* Lewis, 1968 from Bryan Beach, Freeport, Texas. *Texas Conchologist* 7(7):79-80.
- ODE, H. 1976. Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). *Texas Conchologist* 13(1):16-32.
- PACKARD, E. L. 1918. A quantitative analysis of the molluscan fauna of San Francisco Bay. *Univ. Calif. Publ. Zool.* 18(13):299-336.
- PETERSEN, G. H. 1978. Life cycles and population dynamics of marine benthic bivalves from the Disko Bugt area of West Greenland. *Ophelia* 17(1):95-120.
- PHILIPPI, R. A. 1845. Bemerkungen über die Mollusken fauna von Massachusetts. *Z. Malakozool.* 2:68-79.
- RASMUSSEN, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11:1-495.
- REHDER, H. A. 1981. The Audubon Society field guide to North American seashells. Alfred A. Knopf: New York. 894 pp.
- RHOADS, D. C. & D. K. YOUNG. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* 28:150-178.
- RIOS, E. C. 1975. Brazilian marine mollusks iconography. Fundação Universidade do Rio Grande Centro de Ciências do Mar Museu Oceanográfico, Rio Grande. 331 pp.
- ROSEWATER, J. 1975. Mollusks of Gatun Locks, Panama Canal. *Bull. Amer. Malacol. Union* 1974:42-43.
- SANDERS, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.* 3:245-258.
- SAY, T. 1822. An account of some of the marine shells of the United States. *J. Acad. Natur. Sci. Phila.* 2:221-248, 257-276, 302-325.
- SAY, T. 1831. American conchology; or, descriptions of the shells of North America. Illustrated by colored figures from original drawings executed from nature. New Harmony, Indiana. Pt. 2, pp. 151-170.
- SCHLESCH, H. 1931. Beitrag zur Kenntnis der marinen Mollusken-Fauna Islands. 2 Studien über *Mya*-Arten. *Arch. Molluskenkd.* 63:133-155.
- SIMONARSON, L. A. 1981. Upper Pleistocene and Holocene marine deposits and faunas on the north coast of Nügssuaq, West Greenland. *Grønlands Geologiske Undersøgelse* 140:1-107.
- SMITH, E. A. 1893. Observations on the genus *Sphenia*, with descriptions of new species. *Ann. Mag. Natur. Hist.* 12(6):277-281.
- SMITH, O. R. 1953. Observations on the rate of decay of soft-shell-clams (*Mya arenaria*). *Ecology* 34(3):640-641.
- STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Mem. Geol. Soc. Amer.* 125:296 pp.
- STICKNEY, A. P. 1959. Ecology of the Sheepscot River estuary. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fish. 309:1-21.
- STICKNEY, A. P. 1964a. Salinity, temperature, and food requirements of soft-shell clam larvae in laboratory culture. *Ecology* 45(2):283-291.
- STICKNEY, A. P. 1964b. Feeding and growth of juvenile soft-shell clams, *Mya arenaria*. U.S. Fish Wild. Ser., Fish. Bull. 63(3):635-642.
- TEBBLE, N. 1976. British bivalve seashells, a handbook for identification. British Museum (Natur. Hist.): London. 212 pp.
- THEROUX, R. B. & R. L. WIGLEY. 1983. Distribution and abundance of east coast bivalve mollusks based on specimens in the National Marine Fisheries Service Woods Hole collection. *Natl. Mar. Fish. Ser., Spec. Sci. Rep., Fish.* 768:1-172.
- TRUEMAN, E. R. 1954. Observations on the mechanism of the openings of the valves of a burrowing lamellibranch, *Mya arenaria*. *J. Exp. Biol.* 31(2):291-305.
- TURTON, W. 1822. *Conchylia dithyra Insularum Britannicarum*, the bivalve shells of the British Isles, systematically arranged. Quarto, London (1848). 279 pp. [Reprinted verbatim from the original (1822) edition entitled: "Conchylia Insularum Britannicarum, the shells of the British Islands systematically arranged."]
- VALENCIENNES, A. 1846. Mollusques. Pl. 24 (no text). In: Abel du Petit-Thouars (ed.), Voyage autour du monde sur la frégate *La Venus*, pendant . . . 1836-1839. Atlas de Zoologie, Mollusques. Paris.
- VERRILL, A. E. 1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters with an account of the physical characters of the region. Rep. U.S. Fish Comm. for 1871-1872, 1:295-778.
- WARMKE, G. L. & R. T. ABBOTT. 1961. Caribbean seashells, a guide to the marine mollusks of Puerto Rico and other West Indian Islands, Bermuda and the lower Florida Keys. Livingston Publ. Co.: Narberth, Pa. 346 pp.
- YONGE, C. M. 1951. Observations on *Sphenia binghami* Turton. *J. Mar. Biol. Assoc. U.K.* 30(2):387-392.