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# THE GENUS SPHENIA (PELECYPODA, MOLLUSCA) IN THE WESTERN NORTH ATLANTIC, WITH OBSERVATIONS ON OTHER MYIDAE

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University of New Hampshire, Ph.D., 1969
Zoology

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WESTERN NORTH ATLANTIC, WITH OBSERVATIONS ON

OTHER MYIDAE

by

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ABSTRACT

THE GENUS <u>SPHENIA</u> (PELECYPODA, MOLLUSCA) IN THE

WESTERN NORTH ATLANTIC, WITH OBSERVATIONS ON

OTHER MYIDAE

by

ROBERT W. HANKS

A new species of the genus <u>Sphenia</u> is described.
It is the first living species of the genus reported from
the Atlantic Coast of North America.  The taxonomy of
<u>Sphenia</u> is discussed, and a type specimen is designated
for the genus.  The distribution for two species of <u>Mya</u>
and for all living species of <u>Sphenia</u> is listed with
comments on the zoogeography of the Myidae.  In addition
to a general taxonomic description, some aspects of the
biology of the new species are described, with emphasis
on reproduction, growth, and ecology.  Significant biolog-
ical factors are compared between the new species and the
two species of <u>Mya</u> found in the same coastal regions.

x.

# SECTION I

## INTRODUCTION

The genus _Sphenia_ Turton 1822 is one of the lesser known pelecypod taxa in the molluscan family Myidae. Small size, nestling habit, and sporadic collections have restricted scientific interest in the group to taxonomic and faunistic studies. On the other hand, the genus _Mya_ Linne 1758, owing to commercial importance, wide distribution, and great abundance has been studied intensively; although, paradoxically, much of its evolution, occurrence, and biology is still obscure. Species of _Mya_ are found on parts of all coastlines of the Northern Hemisphere; species of _Sphenia_ have been reported from the Pacific Coast of North and South America, from Japan and Korea, from Puerto Rico and the extreme south Atlantic coast of South America, from the Atlantic coast of Europe, and from the Mediterranean Sea. Some _Sphenia_ are said to occur on the South African, Indian, and Malay coasts, but documentation is poor. That _Sphenia_ have a much broader distribution than presently recorded is, I believe, a safe assumption.

Sphenia binghami Turton 1822 is the type species
(by subsequent designation of Gray 1847) for the genus,
and has been recorded along the shores of the United King-
dom and France. No living species of Sphenia had ever
been reported from the Atlantic coast of North America,
although Dall and Simpson (1901) recorded Sphenia
antillensis from Puerto Rico.

In 1956, while studying the benthic fauna of the
mid-coast region in the Gulf of Maine (Hanks 1961, 1964),
I dredged several specimens of Sphenia from the Sheepscot
River estuary. In subsequent years, I collected large
numbers of this small pelecypod from deep waters of the
estuary, from coastal regions, and from fish stomachs.
Mya arenaria Linne 1758 is abundant in this region, and
M. truncata Linne 1758 has been reported. Although the
two Mya are easily separated as adults, juvenile Mya and
any stage of Sphenia are easily confused. In fact, sur-
prisingly little has been written on the juveniles of
either Mya arenaria or M. truncata, and our knowledge of
Sphenia binghami (the best known species of this genus) is
restricted to several short accounts of shell morphology
and only two descriptions of the living animal (Forbes and
Hanley 1853, Yonge 1951). Great abundance and a few pre-
viously unidentified museum specimens indicate that a

species of _Sphenia_, first described in this dissertation, has been an inhabitant of our coast for some time, but its small size and similarity to known Myidae, in combination with an entirely different habitat from the European species, have obscured its identity.

MacNeil (1964) observed: "The genus _Mya_, by virtue of both its morphological peculiarities and its heavy commercial harvest, should be one of the best understood mollusks. Instead, its comparatively few species, comparitively simple evolution, and comparatively restricted geographical occurrence involve subtleties that evade and confuse paleontologists and malacologists alike."

Discussion of the genus _Mya_ in this paper is restricted to the locally occurring _Mya arenaria_ and _Mya truncata_. Readers who desire more information on other species, both recent and fossil, should refer to MacNeil (1964).

The genus _Sphenia_ has been suggested as being ancestral to _Mya_, and it follows that understanding of the distribution and biology of _Sphenia_ should be beneficial to our understanding of the geologic and phylogenetic history of the family Myidae. A major extension of the range of the genus _Sphenia_, and the establishment of a new species in North America may shed considerable light on these long standing problems.

# SECTION II

## TAXONOMY OF THE GENUS SPHENIA

### A. Turton's Original Description

Since the wording of Turton's paper is critical to the material presented here, all pertinent sections of Turton's report are quoted for the convenience and information of the reader:

The genus Sphenia Turton 1822

"SPHENIA testa transversa, inaequivalvis, inaequilateralis, latere antico hiante. Cardo valvae sinistrae dente elevato transversim dilatato, dextrae dente concavo cum denticulo postico: lateralibus nullis. Ligamentum internum.

"Shell tranverse, inequivalve, inequilateral, open at the anterior end. Hinge of the left valve with an elevated transversly dilated tooth, of the right valve with a concave tooth and a small denticle behind it: lateral teeth none. Ligament internal.

"This new and interesting genus, which in the Linnean arrangement would rank with the Myae, is sufficiently defined by its own fixed and peculiar characters.

"From the Mya it 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. The valves are also very unequal.

"And from the Corbula, in having the tooth of the left valve flat and transversely extended, with the anterior extremity a little open.

"The outline is subject to some variation; but all of them have a flattish or wedge-shaped form; and inhabit the interior of rocks, and the inside of dead bivalves.

"SPHENIA Binghami testa cuneata, dente concavo oblique inflexo.

"Shell wedge-shaped, with the concave tooth oblique and inflected. Tab. nost. 3, fig. 4 and 5, and fig. 19, fig. 3.

"Mus. nost. Rocks in Torbay.

"Shell a quarter of an inch long, and half an inch broad, covered with a brown wrinkled skin which extends beyond the anterior end, wedge-form, truncate at the hinge, with the upper margin often a little contracted about the middle, gradually tapering to the anterior end which is slightly open; beaks rather prominent, with the points not quite opposite but divaricating from each other; inside glossy white with a purplish tint, the margin sharp and plain; the elevated tooth running in a gradually narrower and wedge-shaped manner nearly half way along the back margin.

"Except for the very distinct and visible teeth, we should be much inclined to think that this is the Mytilus praecisus of Montague, p. 165, tab.4, fig. 2. He speaks of his shell as not being uncommon among rocks, subject to much variety of shape; and some of our specimens much resemble his figure.

"Named from General Bingham, our diligent fellow-laborer among the rocks in Torbay."

Errors in Turton's original description (i.e., the left-valve bears the chondrophore or resiliophore, and the left valve is smaller than the right in both Mya and Sphenia) have been perpetuated by later workers although Fischer (1887) and Lamy (1919) correctly describe the hinge. 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, furthermore, when the valves of an inequivalve myid are closed the umbo of the right is higher than that of the left."

Most accounts of <u>Sphenia</u> <u>binghami</u> deal superficially with shell morphology, and only two descriptions of the entire animal have been published (Forbes and Hanley 1853, Yonge 1951). Yonge's paper is by far the more complete. Accounts of other species of <u>Sphenia</u> are equally scanty; primarily records of new species or distributions, and based on shell morphology.

Turton (1822) included in his original publication the description of two species which were later determined to belong to other genera. <u>Sphenia</u> <u>swainsoni</u> was identified by Jeffreys (1865) as a juvenile <u>Mya</u> <u>truncata</u> and <u>Sphenia</u> <u>decussata</u> was a shell that Turton had not examined. The latter had been described by Montague as <u>Mya</u> <u>decussata</u> and Jeffreys (1863) identified it as <u>Petricola</u> <u>lithophaga</u>.

B.  Designation of Type Specimen

for Sphenia binghami Turton 1822

To the best of my knowledge, no type specimen
exists.  Gray (1847) established S. binghami as the type
species by subsequent designation of Turton's (1822)
description.  Turton's original material appears to have
passed to the Jeffreys collection and thence into the
holdings of the U. S. National Museum.  While studying the
latter institution's collections, I found a vial labelled
"Mya binghami Turton, ex. mus. Turton.  Jeffreys Coll. #75,
U. S. Nat. Mus. No. 171240".  The generic designation "Mya"
can be ascribed to Jeffreys, who did not feel that Turton
was justified in erecting a new genus (Jeffreys 1862-69,
vol. III, pg. 72).  The vial contains two, separated but
matched, pairs of valves, one intact shell, several un-
matched right valves, and what appears to be a piece of
old oyster shell bored by Cliona in which are several
minute Sphenia shells.  Although none of the shells in this
vial match Turton's (1822) figure, I believe that this
material could be part of his original collection.  I have,
therefore, selected one of these shells (now deposited as
USNM # 171240) as most similar to that of Turton's original
description and designate it as a modern lectotype for
Sphenia binghami Turton 1822, and designate the remainder

of this material as paralectotypes (USNM #679166).  This
action follows the precedent set by Davis (1964) in speci-
fying type specimens of other species described by Turton,
where there is sufficient evidence that the original
material is now held by the U. S. National Museum.  The
material elevated to type by Davis was labelled similarly
to the <u>Sphenia</u> material examined.


### C.   Synonomy of <u>Sphenia binghami</u> Turton

| 1822 | SPHENIA Binghami | Turton |
|------|------------------|--------|
| 1825 | Sphoenia Binghami | Blainville |
| 1827 | Sphenia binghami Turton | Brown |
| 1842-56 | Corbula binghami | Hanley |
| 1856 | Sphenia binghami Turton | H. and A. Adams |
| 1862-69 | Mya binghami Turton | Jeffreys |
| 1869 | Sphenia binghami | Petit de la Saussaye |
| 1881 | Mya binghami Turton | Jeffreys |
| 1887 | Sphenia binghami Turton | P. Fisher |
| 1919 | Sphenia binghami Turton | Lamy |
| 1951 | "        "        " | Yonge |

SECTION III

GEOGRAPHIC DISTRIBUTION OF <u>MYA</u> AND <u>SPHENIA</u>

A. Distribution of the Genus <u>Mya</u>

Geographic distribution of <u>Mya</u> <u>arenaria</u> (Circum-
boreal) and <u>Mya</u> <u>truncata</u> (Circumpolar or Circumarctic) has
been fully reviewed in Slodkewitsch (1938), Foster (1946),
MacNeil (1964), and Laursen (1966). Briefly, the ranges
of these species are as follows:

<u>Mya</u> <u>arenaria</u>

> <u>Eastern Atlantic</u>: West coast of Norway, Baltic
> Sea and coast of Sweden to Arcachon, France
> and the Bay of Biscay.
>
> <u>Western Atlantic</u>: Labrador to Chesapeake Bay;
> some reports of dead valves from Beaufort,
> North Carolina.
>
> <u>Eastern Pacific</u>: Akutan Island, Alaska south
> to Monterey, California.
>
> <u>Western Pacific</u>: Southern Kamchatka Peninsula
> south to Nagasaki, Japan, and east coast of
> China (Yellow Sea).

<u>Mya</u> <u>truncata</u> (all forms)

> Most arctic shores (i.e., Greenland, Iceland,
>
> Novaya Zemlya, Franz Josef Land and Spitzbergen,
>
> Kara Sea, Bering Sea, etc.) south to:
>
> <u>Western Atlantic</u>: Massachusetts, Nantucket
>
> Island, U. S.
>
> <u>Eastern Atlantic</u>: La Rochelle, France
>
> <u>Eastern Pacific</u>: Puget Sound, Washington, U. S.
>
> <u>Western Pacific</u>: Hokkaido, Japan.

There has been some confusion in the past about the arctic distribution of <u>Mya</u> <u>arenaria</u>. Jensen (1900) demonstrated that all records of arctic <u>Mya</u> <u>arenaria</u> (a boreal species) were in fact a form of <u>Mya</u> <u>truncata</u> which he named <u>ovata</u>. Unfortunately his paper, in Danish, was not widely circulated, and was actually misquoted by some later workers. Laursen (1966) has translated Jensen's paper, restated the original thesis, and demonstrated its correctness by offering supplementary information from the intervening 65 years.

## B. Distribution of the Genus _Sphenia_

Known ranges of _Sphenia binghami_

A detailed review of the distribution of this species has not been offered for nearly 100 years (see Forbes and Hanley 1853, and Jeffreys 1865). During this period only two new records have been added to the range: the observations of Bruce, Coleman and Jones (1963) for the Isle of Man and the observations of Lucas (1953) for Den Helder in the Netherlands.

Eastern Atlantic: British Isles north to Scarborough on the east coast and Isle of Skye on the west coast; Coast of Ireland; Atlantic coast of the Netherlands north to Den Helder; Atlantic coast of France and Spain.

Mediterranean: Italian coast at Naples and Spezzia; Tunis, Tunisia, North Africa.

Other living species of the genus _Sphenia_

_Sphenia fragilis_ Carpenter 1857 - Oregon to Mazatlan (Pacific coast U. S. and Mexico) [possibly to Peru]

_S. ovoidea_ Carpenter 1864 - Aleutian Islands to Puget Sound and San Diego, California [possibly to Panama]

S. <u>trunculus</u> Dall 1916 - San Diego to Panama

S. <u>pholadidea</u> Dall 1916 - Bolinas Bay to Imperial

Beach, California [may be same as S. <u>globula</u>

Dall 1919, and S. <u>nana</u> Oldroyd].

S. <u>coreanica</u> Habe 1951 - Ulsan, South Korea and

Coast of Japan

S. <u>antillensis</u> Dall & Simpson 1901 - West and

South coast of Puerto Rico

Other living species have been reported from South America,
South Africa, India, and the Malay Peninsula (Lamy 1919).

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, unless
existing records are grossly inaccurate, <u>Sphenia</u>'s global
distribution is more extensive than <u>Mya</u>, crossing the
Equator and both Tropics (figure 1).

Figure 1.  Approximate world distribution of Mya and

Sphenia.  Note that Mya truncata is generally

north of the Arctic circle, that M. arenaria

is generally north of the Tropic of Cancer,

but that Sphenia crosses the Equator and is

found in both hemispheres.  The range is

generally continuous between symbols; Sphenia

in the southern hemisphere are individual

collections.
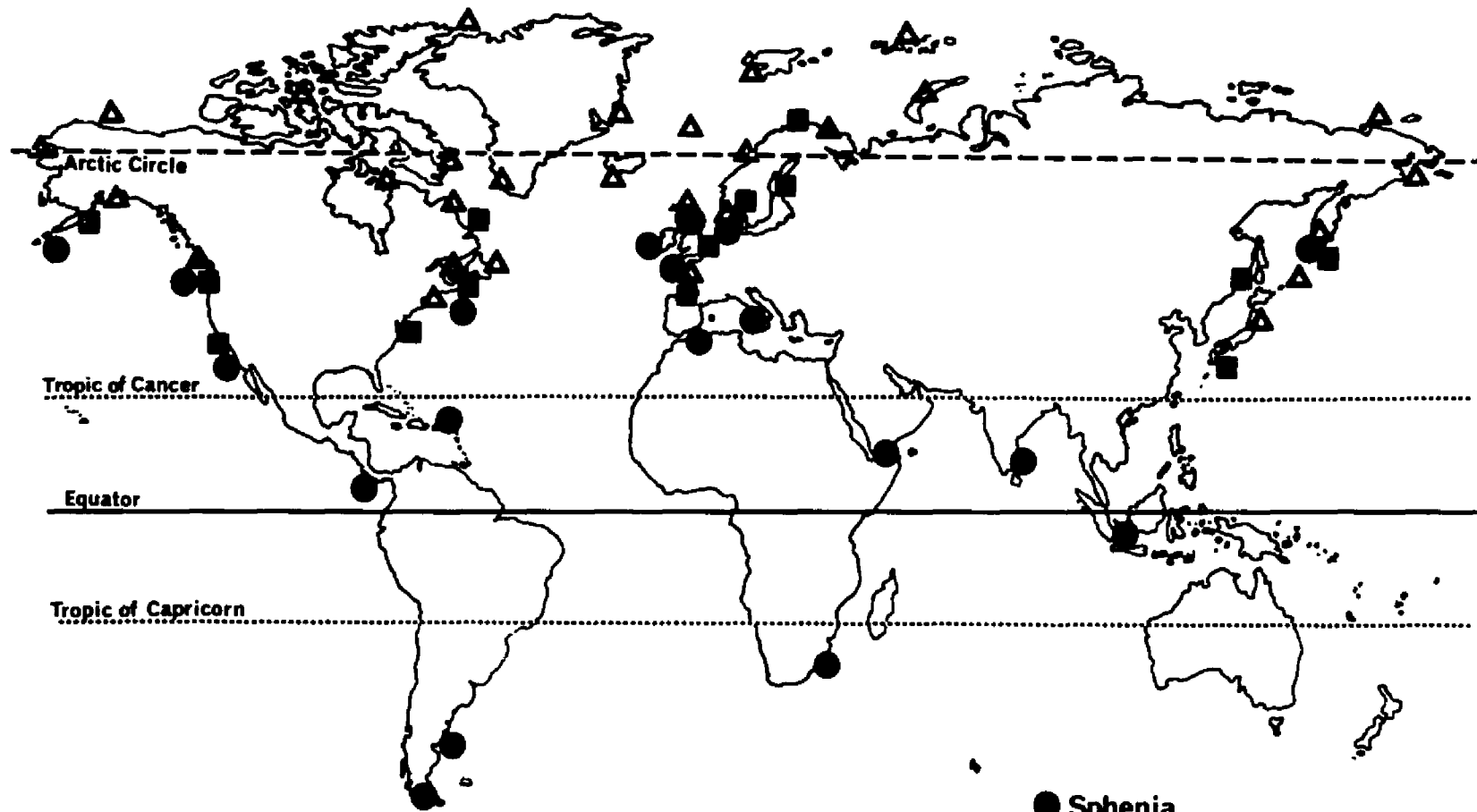
| ● | Sphenia |
| ■ | Mya arenaria |
| △ | Mya truncata |

In a recent paper, Lewis (1968) has described a new fossil species, _Sphenia tumida_, from the Pleistocene of Florida. Lewis points out that no living _Sphenia_ have ever been reported from eastern North America, and that only three fossil species had been recorded from this region. He lists them as _Sphenia dubia_ Lea 1845, _S. attenuata_ Dall 1898, and _S. senterfeiti_ Gardner 1936. The first was from the Miocene of Virginia, and the latter from the Pliocene and Miocene of Florida. As more extensive faunal studies are undertaken on our east coast, perhaps other living species of _Sphenia_ will be revealed, and certainly the range of _Sphenia sincera_, first described here, will be extended and defined. One can also predict that other fossil species of _Sphenia_ will be uncovered.

If these predictions come true, and even in light of our present knowledge, the extensive range of the genus _Sphenia_ in tropical as well as boreal waters lends further support to the implication of _Sphenia_ as the ancestral genus of the family Myidae. Whether the ancestral genus originated in East Asia from a presently unknown form, or from a non-Asian source is speculative. MacNeil (1964) suggested _Sphenia_ ? _minor_ from the British early Eocene.

SECTION IV

DESCRIPTION OF <u>SPHENIA</u> <u>SINCERA</u> sp. nov.

A. Classification and Description

Phylum MOLLUSCA

Class BIVALVIA  Linne, 1758

Subclass HETERODONTA  Neumayr, 1884

Order MYOIDA  Stoliczka, 1870

Suborder MYINIA  Newell, 1965

Superfamily MYACEA  Lamark, 1818

Family MYIDAE  Lamark, 1818

Genus <u>SPHENIA</u> Turton, 1822

<u>Genotype</u>.  By subsequent designation, Gray 1847;

<u>Sphenia</u> <u>binghami</u> Turton 1822

<u>Generic Description</u>.  see page 4 of this dissertation

<u>Type Specimen</u>.  see page 7 of this dissertation. USNM #171240

<u>Sphenia</u> <u>sincera</u> Hanks, sp. nov.

Type specimen: U. S. Nat. Mus. #679164

Figure 2

Plates III and IV

<u>Holotype</u>.  Deposited in the U. S. National Museum as lot

no. 679164 collected by Robert W. Hanks.

<u>Repository of other type material</u>.  Paratypes are

deposited in the U. S. National Museum, lot no. 679165.

The balance of the collection remains in the author's

possession at the Bureau of Commercial Fisheries Biological

Laboratory, Oxford, Md. 21654.

Total number of specimens collected as of August,

1968 was about 900, of which about 350 have been examined

critically.

<u>Type Locality</u>.  Mouth of the Sheepscot River, Coast of

Maine, U.S.A.  Longitude 69° 42'W, Latitude 43° 47'N.

Depth from 30 to 265 feet.  Sediments: soft mud, primarily

of silt and clay.  Full description of associated fauna and

environment can be found in Hanks (1963).

Figure 2.   Camera lucida drawing of a <u>Sphenia sincera</u>

specimen from the mid-coast region of Maine.

Total length about 6 mm.


A. Left valve             B. Right valve

C. Dorsal view            D. Posterior

E. Anterior

A

B

C

D

E
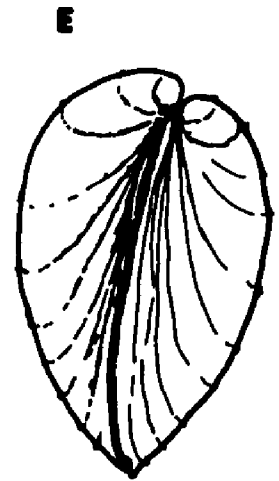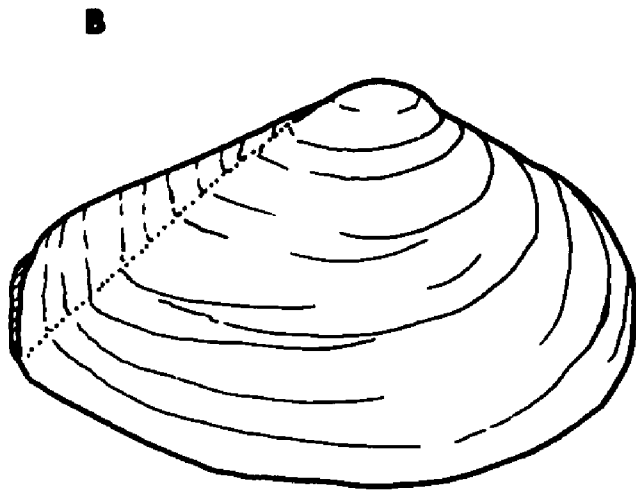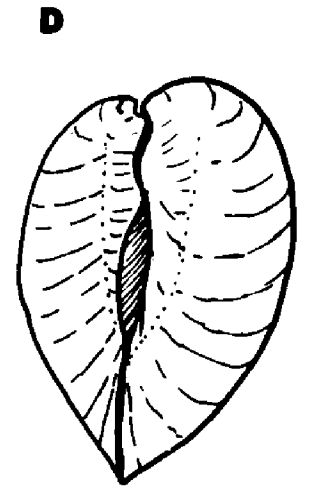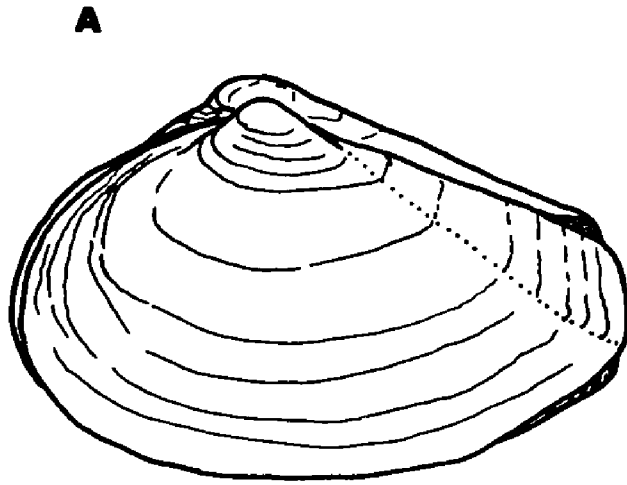
1mm
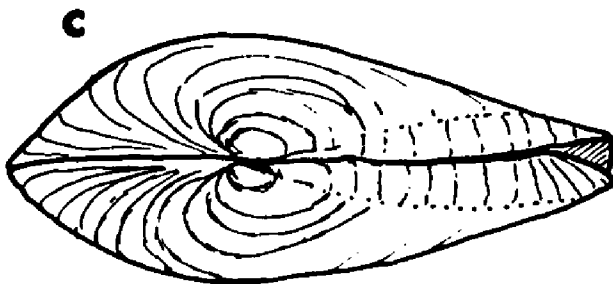
**Sphenia sincera**

Distribution. The center of the known populations of Sphenia sincera is in the mid-coast region of Maine, near Booth Bay and the mouth of the Sheepscot River. Table 1 lists the previously unidentified material held in the collection of the U. S. National Museum, which I have assigned to Sphenia sincera. It appears likely that Sphenia sincera has a continuous distribution from about Portland, Maine in the south (sandy sediments become prominent further southward), to perhaps the coast of Nova Scotia in the north (fig. 3).

Remarks. The specific epithet sincera is derived from the Latin word for sound, clean, natural, without mutilation and refers to the undistorted shape of the valves, a feature rarely found in the genus Sphenia, as well as to the clean, brilliant whiteness of the shell.

Sphenia differs from Mya in three important characteristics: the shape of the chondrophore, the relatively small ultimate size that corresponds to a comparatively short life span, and the early reproductive maturity.

TABLE 1: Specimens from the miscellaneous section, family Myidae, U. S. Nat. Museum collection now assigned as _Sphenia sincera_ Hanks.

| USNM No. | Previous Designation | Area Collected | Number of Specimens | Remarks |
|---|---|---|---|---|
| 150763 | _Sphenia_ ? | Casco Bay (Portland, Maine) | 1 | -- |
| 173122 | _Sphenia_ ? | Off Mt. Desert Island, Maine   8-10 fathoms | 6 | H. S. Colton (collector; 3 drilled by Lunatia.) |
| 199189 | _Sphenia_ ? | Bar Harbor (Mt. Desert Island) | 7 | Henderson collection |
| 451230 | -- | Off Gotts Island, Maine (Mt. Desert region) | 2 | Henderson collection |
| 451334 | -- | Frenchmans Bay | 75 + | Henderson collection (poor hinges) |
| 451368 | -- | Winter Harbor, Maine (Mt. Desert Island) | 1 | -- |
| 451244 | -- | Off Gotts Island, Maine (Mt. Desert Island region) | 1 | Henderson collection |
| 462652 | -- | Frenchmans Bay, Maine | 4 | Henderson collection |

Figure 3. Distribution of _Sphenia_ _sincera_ in the Gulf

of Maine. Dots are points of actual collection;

the 80-meter contour bounds the inferred range

(from Casco Bay to perhaps northeastern Nova

Scotia) based on known habitat requirements.

NEW BRUNSWICK

NOVA SCOTIA

MAINE

● Mt Desert

● Booth Bay

● Casco Bay

80 meters

Distribution of
Sphenia sincera
in the Gulf of Maine
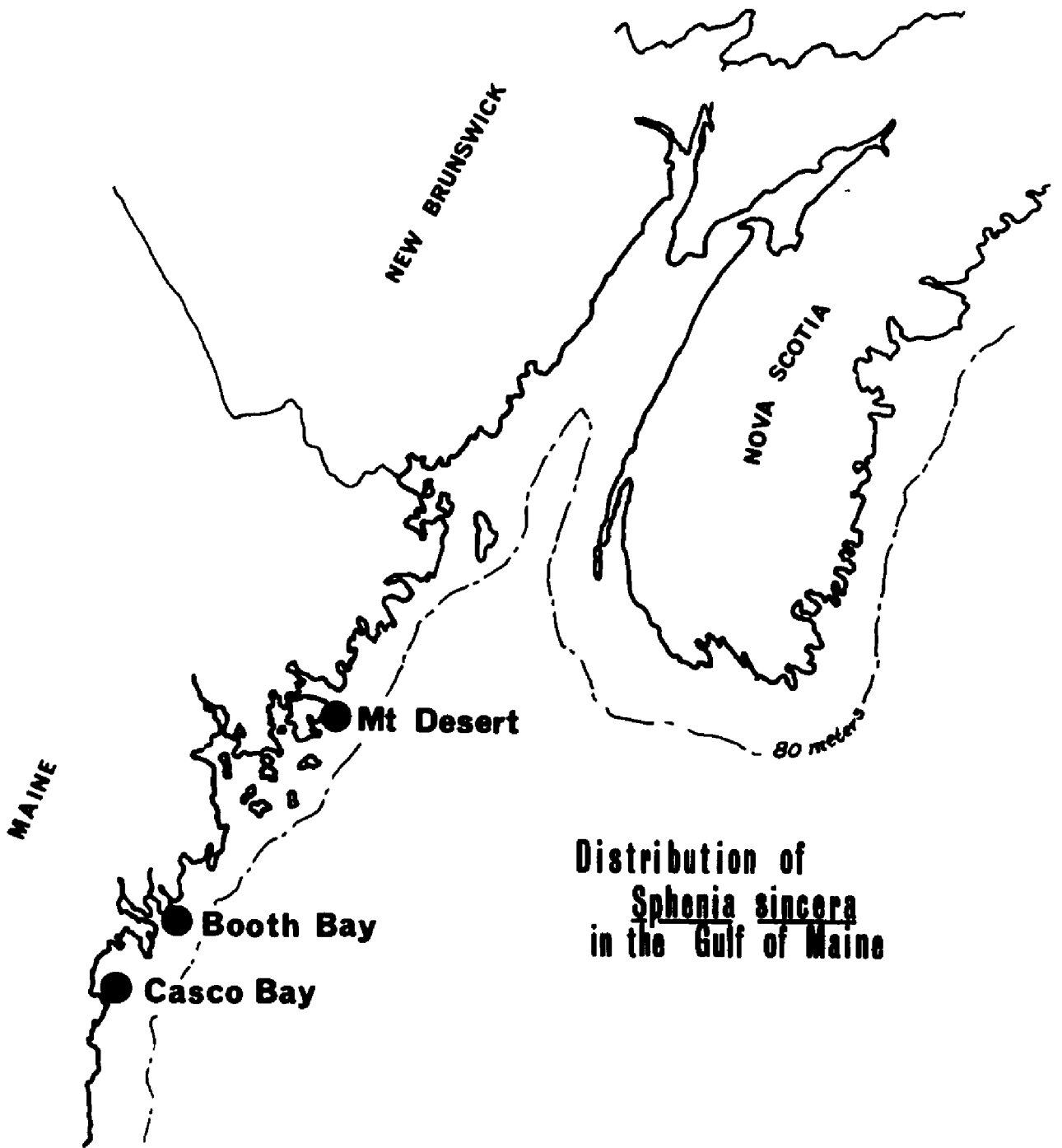
## B. Shell and Hinge Morphology

External. Shell small and wedge-shaped. Valves tightly closed, not gaping in front, but with a slight posterior gape. Color chalky white, rarely with a narrow, dark orange-brown, distal border. A thin periostracum may coat the shell giving a yellowish cast, but is generally absent, covering only the paired siphons. Umbones located about one-third of the length from the anterior end, inclined toward the anterior and often eroded. Umbones prominent, that of the right valve larger than the left. Strongly inequivalve, with the right valve larger and more deeply cupped. Anterior outline generally rounded; not obliquely truncated as in Sphenia binghami; dorsal margin somewhat straighter than ventral margin. Dorsal outline slopes gradually and evenly to posterior, which may be slightly rounded or vertical. External sculpture of fine concentric growth lines; some more prominent than others. A distinct ridge runs from the umbo to the posterior ventral angle, more acute on left valve than on right. Shell strongly calcified throughout.

Internal. Smooth, dull white: adductor scars and pallial sinus usually obscure, but complete. Anterior adductor scar long and tear shaped; posterior adductor scar oval. Adductor scars small, about half the area of Sphenia binghami. Posterior adductor scar higher than wide (width 2/3 of height), as compared to S. binghami (height 2/3 of width). Anterior adductor scar extends to, or slightly past, horizontal mid-line of shell, but not as far ventrally as in Mya truncata. Posterior adductor scar 1/2 to 2/3 distance between umbo and posterior. Pallial line joins ventral leg of pallial sinus in an acute angle. Pallial line well back from edge of shell and complete between anterior and posterior adductor scars. Pallial sinus "U" shaped, deeply indented, but not to middle of shell as in Mya.

Hinge. The hinge nomenclature used in this dissertation follows that established by MacNeil (1964). Figure 4 shows MacNeil's diagrammatic myid hinge with the specific areas indicated. MacNeil defined the hinge regions as follows:

"The extraligamental parts of the spoon are:
2. The anterior leg - a line or ridge, often
   undercut marking the edge of the live mantle.
   The periostracum-elasticum connection between
   the two valves attaches to it.

Figure 4. Diagrammatic hinge structure of the Myidae (after MacNeil 1964).
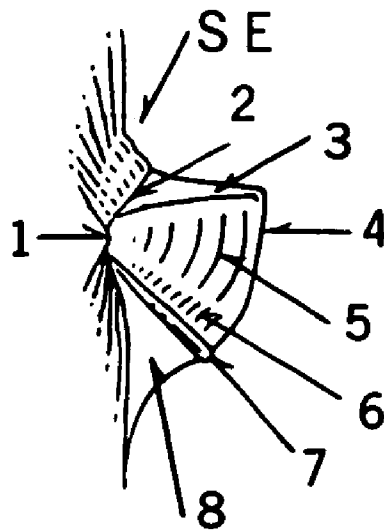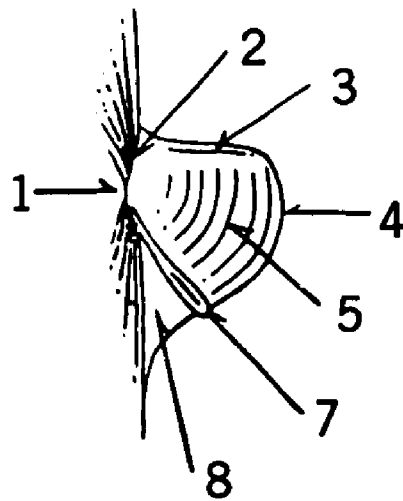
FIGURE 2.—Diagram showing terminology of parts of spoon. Upper figure is *Mya* (*Arenomya*), and the lower figure is *Mya* (*Mya*). From Fujie (1957).

| *This report* | *Fujie* |
|---|---|
| 1. Beak or umbo | Beak. |
| 2. Anterior leg | Leg. |
| 3. Anterior ridge | Anterior ridge. |
| 4. Ventral margin | Outer margin. |
| 5. Fibrum receptacle | Sculpture. |
| 6. Laminum attachment | Undulated part. |
| 7. Posterior ridge | Posterior ridge. |
| 8. Posterior furrow | Furrow. |
| SE. Anterior subumbonal groove | Subumbonal excavation. |

3. The anterior ridge - the anterior confining
   wall of the ligament receptacle. It may be
   narrow and overturned, or broad and flat.
   The dorsal part ranges from narrow to very
   wide.

7. The posterior ridge - the posterior confining
   wall of the ligament. In adults its point of
   contact with a buttress in the right valve
   forms an articulation or rocking point for the
   valves along a dorsoventral axis. In juveniles
   it is the attachment or concealing fold for the
   outermost of the two non-calcareous or conch-
   iolin elements of the ligament.

8. The posterior furrow - an excavated area occu-
   pied by mantle. The outermost border reaches
   the edge of the live mantle; the innermost
   border is the posterior ridge.

S.E. The anterior subumbonal groove - a grooved area
     radiating from the beak and marking the outer
     edge of the intervalve periostracum - elasticum
     connection and thus properly a part of the
     exterior of the shell; this is found only in
     the Mya truncata group. The ligamental parts
     of the spoon are as follows:

6. The laminum attachment - the attachment or
   insertion of the laminated and innermost of the
   two noncalcareous or conchiolin elements of the
   ligament.

5. The fibrum receptacle - the receptacle or attach-
   ment of the calcareous element of the ligament".

Left valve: The entire hinge (fig. 5) is strongly

arched in lateral view, more than Mya arenaria or

M. truncata, resulting in the fibrum receptacle facing

obliquely anterior. Viewed dorsally, the chondrophore is

very narrow; the anterior ridge is pronounced and prominent.

The junction of the anterior ridge and the ventral or outer

margin is directly opposite or posterior to the umbo - never

anterior as in Mya. The fibrum receptacle is generally

Figure 5. Hinge structure of _Sphenia_ _sincera_ sp. nov. from the Maine coast.

LEFT VALVE

DORSAL

LATERAL

RIGHT VALVE
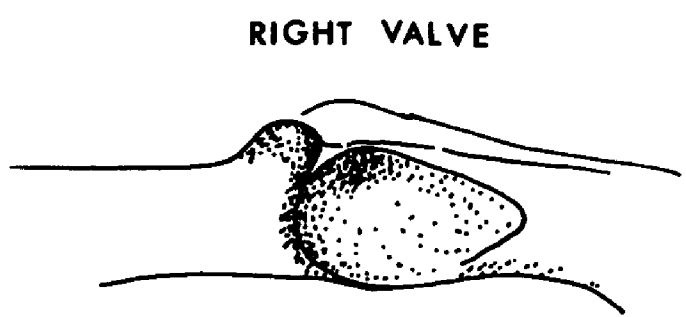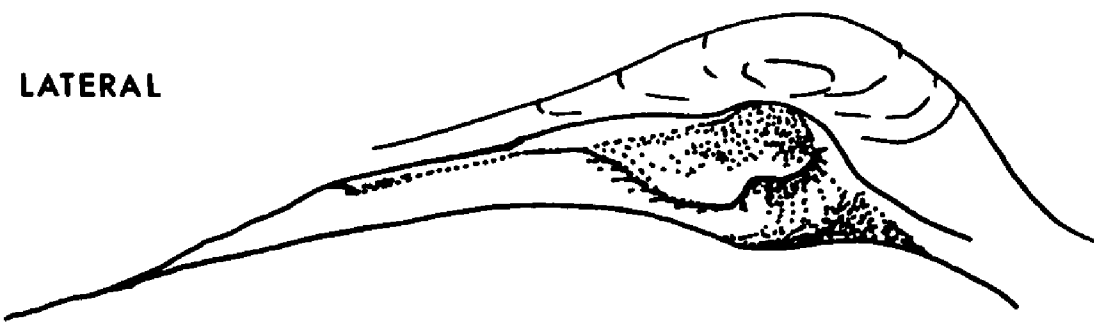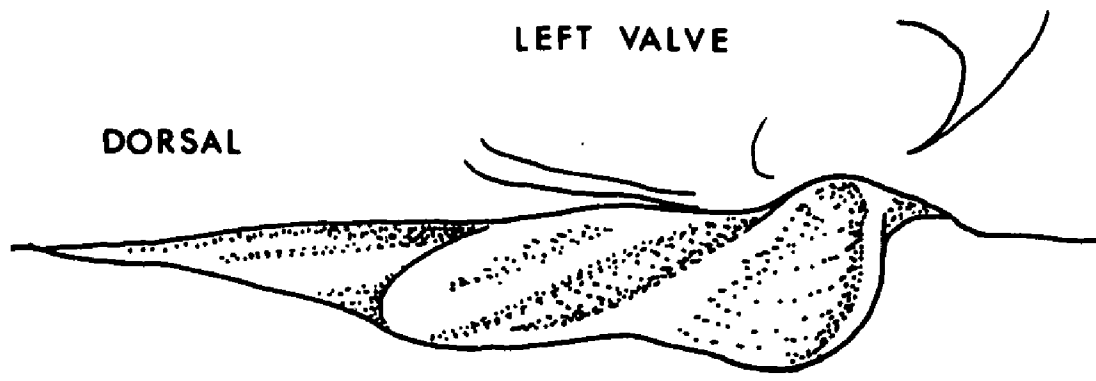
**Sphenia sincera**

reduced in area, as compared to Mya, and the laminum attachment is much expanded as a consequence of the posterior ridge being directed much more obliquely posterior. The posterior ridge is expanded and flattened, does not project sharply beyond the outer margin, and the median groove, chink-like in Mya, is shallow and open; often represented by a median undulation. The posterior furrow is much reduced laterally, but generally extended posteriorily. There is a deep pit under the umbo, in which an unusual tooth of the right valve articulates.

Right valve: Chondrophore concave and roundly triangular in outline. Dominated by a projecting blunt tooth on the anterior side that would apparently articulate with the anterior surface of the anterior ridge in the left valve; perhaps allowing for a rocking motion about the lateral axis. The lateral end of this tooth fits into the concavity under the umbo of the left valve, as in a ball and socket joint, and may provide for a movement about the dorso-ventral axis (see also Trueman 1954). This tooth is not found in Mya arenaria, but is found in M. truncata. No posterior denticle, as described by Turton (1822) for Sphenia binghami, is evident, but this has rarely been found in S. binghami by other authors. Since there appears to be some confusion in Turton's description between right and

left valves, there could also be a reversal of anterior and posterior.

The hinge of Sphenia sincera is more robust than that of S. binghami (fig. 6), but is definitely similar in structure. The differences are those that might be expected to arise from natural selection in relation to habitat adaptations. Mya truncata (fig. 7; see also Foster 1946), at extreme phenotypical expressions, may appear to have a superficial resemblance to S. sincera, but close inspection will reveal definitive character- istics (i.e.; larger fibrum receptacle facing dorsally in Mya, flatter chondorphore in lateral view, and smaller anterior tooth in right valve, etc.). No confusion can arise between any of the above and Mya arenaria (see Foster 1946).

Shell length to height ratios, and the hinge length to width ratios are compared in figure 8. The ratios were calculated from measurements of 50 Sphenia sincera and 25 of each species of Mya. Lines were fitted by the method of least squares.

Figure 6.  Hinge structure of <u>Sphenia binghami</u> Turton
(Type specimen USNM No. 171240).
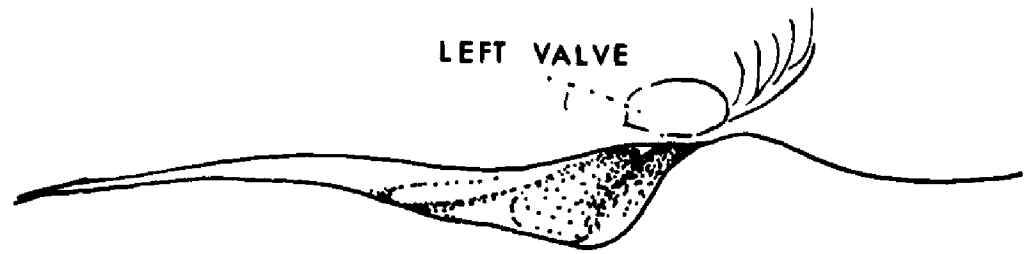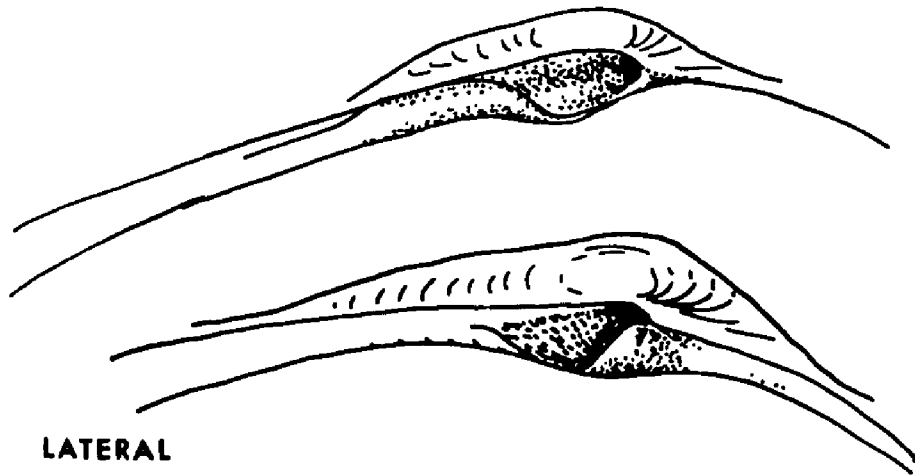
LEFT VALVE

DORSAL

LATERAL
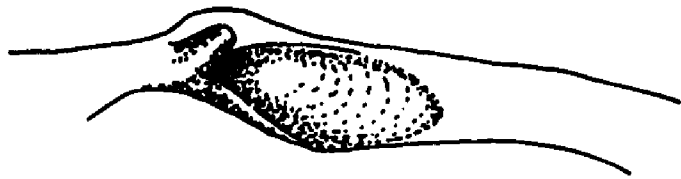
RIGHT VALVE

**Sphenia binghami**

Figure 7. Hinge structure of <u>Mya</u> <u>truncata</u> (juvenile) from the Greenland coast.

LEFT VALVE
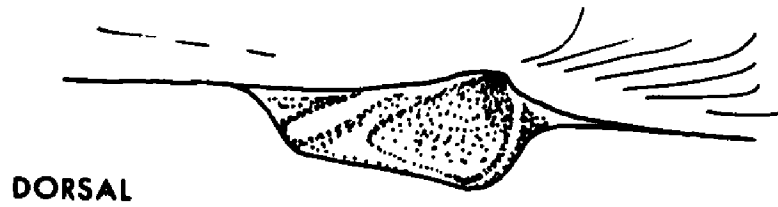
DORSAL

DORSAL
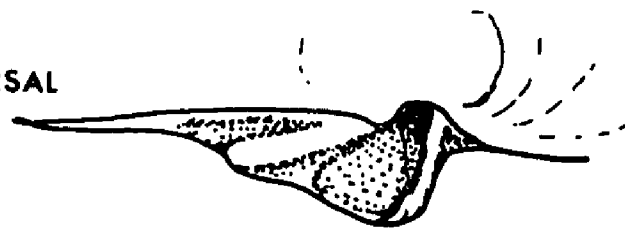
LATERAL

RIGHT VALVE

**Mya truncata**

Figure 8.  Comparisons of shell length to height ratios,
and hinge length to width ratios.  Although
shell ratios are similar, hinge ratios easily
separate _Mya_ and _Sphenia_.

## Shell

Height (mm)

Length (mm)

Sphenia sincera

Mya arenaria

Mya truncata

## Hinge

Width (mm)

Length (mm)

Mya truncata

Mya arenaria
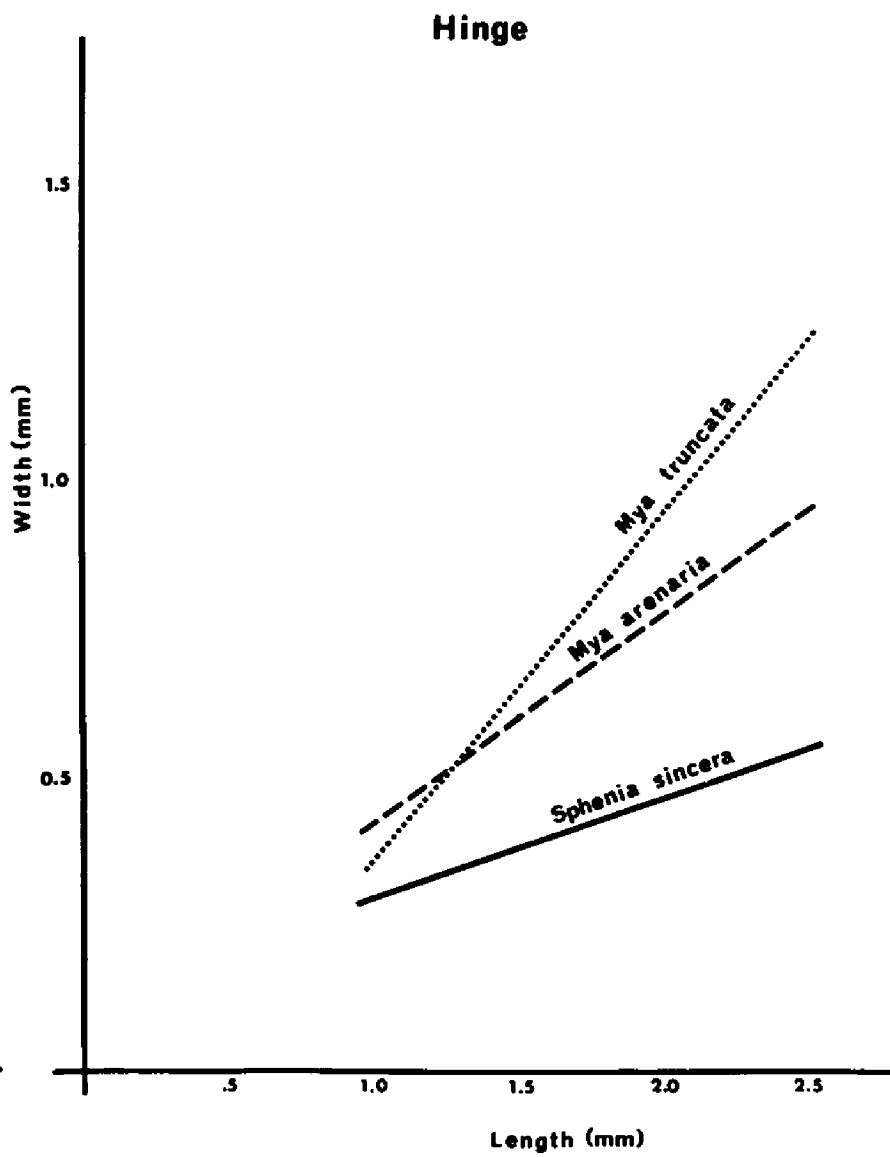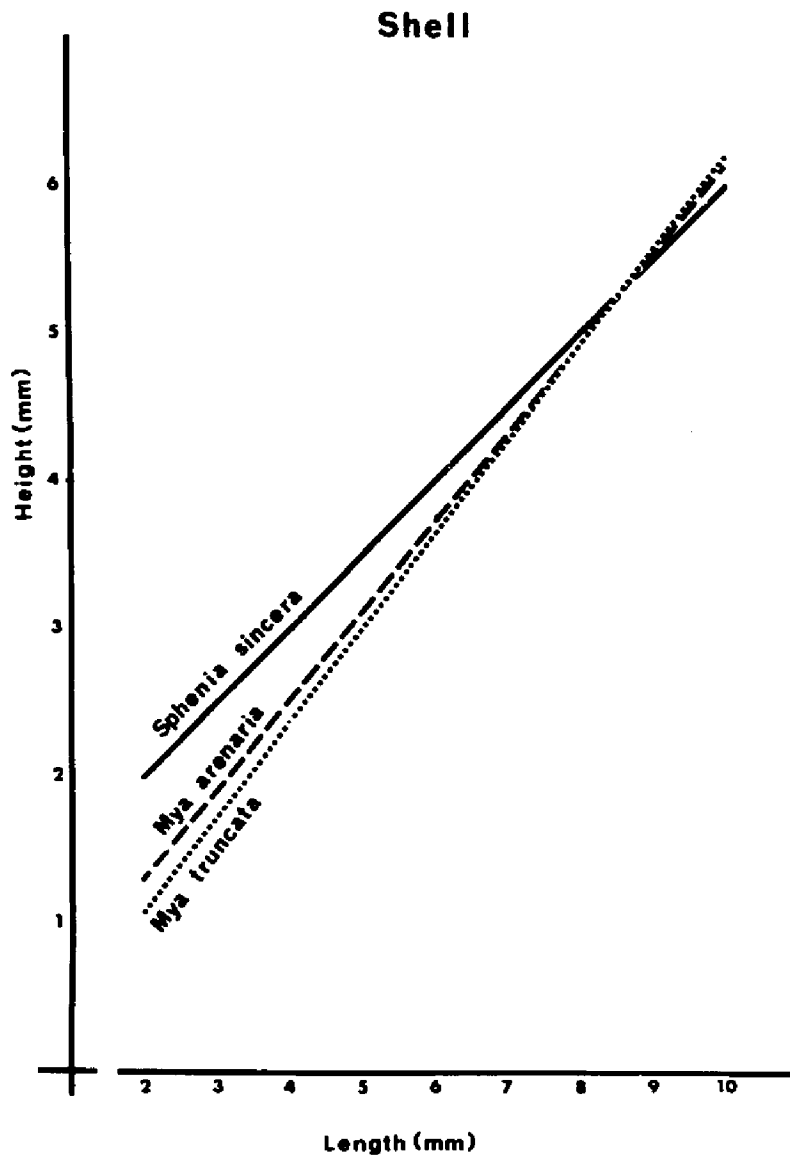
Sphenia sincera

## C. Anatomy

The anatomy of Sphenia sincera is similar to that described in other general accounts of the Myidae (Vlès 1909), and Yonge's (1951) description of Sphenia binghami. There are few differences in anatomical details. The digestive systems appear identical, as do the nervous systems. The reproductive system is similar to that of mature Mya arenaria, as described by Stickney (1963). The muscular system is similar, but differs from both Mya and from Sphenia binghami in the size, shape, and positions of the anterior and posterior adductors.

The body is oval, as in other Myidae, and inclosed within the mantle which is fused along the entire periphery except for the pedal gape and the openings of the paired siphons. The pedal gape extends from about the ventral margin of the anterior adductor to a point just below the posterior base of the foot.

The siphons are united and surrounded by periostracum. An outer row of 12 to 15 tentacles protects the inhalent and exhalent openings; the former is fringed by a circlet of 8 to 10 tentacles acting as strainers, and the latter appends a transparent, tubular, mobile membrane that serves to conduct water away from the inhalent opening.

The extended siphons are as long as those of juvenile
*Mya arenaria* of equal shell length; that is, at maximum
extension nearly the length of the shell.

The gills are large; the inner demibranch is larger
than the outer. The two lamina of the inner demibranch are
about equal in size, but the outer demibranch is unequal
with the external leaflet much larger than the internal.
The supra-axial extension of the outer demibranch joins the
mantle dorsally and separates the suprabranchial chamber
from the branchial chamber.

Structurally, the foot of juvenile *Mya arenaria*,
*M. truncata*, and adult *Sphenia sincera* is similar, and the
description of *M. arenaria* by Barrois (1885) generally
applies to all three. The foot is large and muscular,
laterally compressed, and bluntly rounded. In adult *Mya*
the byssal gland becomes inactive and often atrophies or
disappears completely. The byssal gland in *Sphenia* remains
active and functional throughout life. The foot is cili-
ated, heavily on the ventral surface but diminishing
toward the dorsal surface, where ciliation disappears near
the body mass. A prominent byssal groove is evident along
the ventral surface of the foot and the passage from the
byssal gland to this groove is generally found in the

posterior angle of the foot. The foot contains a sinus
(perhaps more than one) which, with the anterior and
posterior pedal retractors, controls movement of the foot.
Yonge (1962) and Purchon (1968) have discussed the evolu-
tionary significance of the retention or loss of byssal
activity. They point out that the byssal gland appears
with the foot at the close of planktonic life during the
veliger or late veliger stage and usually becomes function-
ally inoperative in the juvenile. In some bivalves, a
functional byssus is retained in the adult animal.
Extension of byssal activity into adult life was possibly
a result of paedomorphosis, enabling some lines of bivalves
to colonize hard, rocky substrates and to become members of
the attached epifauna. The small size of Sphenia and the
presence of an active byssal gland at sexual maturity may
be evidence for neotony.

Yonge (1951) points out three important character-
istics of the Sphenia binghami specimens he examined. He
states, "Unlike the other members of the Myidae, Sphenia
is heteromyarian". This statement is not valid for most
members of the genus. Close examination of Turton's shells
show that these specimens are isomyarian (as much as Mya
truncata and M. arenaria), and Sphenia sincera also is
isomyarian. I have not observed a single instance in any

Sphenia shell where the adductors would be termed heter-
omyarian. It appears that Yonge's material was unusual
in this respect and therefore not typical of the genus,
nor even of Sphenia binghami.

Yonge calls attention to the fact that the poste-
rior region of the shell is weakly calcified, and from my
observations this is confirmed for most nestling Sphenia.
Sphenia sincera and Sphenia antillensis (both freeliving)
are strongly calcified in the posterior shell region and
this would apparently be an excellent shell characteristic
on which to separate habitat preferences.

Finally Yonge draws attention to the short siphons
in his S. binghami specimens, and concludes that the reduc-
tion in siphon length is an adaptation or selection for the
possibly cleaner environment of the nestling habitat. The
description of Forbes and Hanley (1853) also calls atten-
tion to the short siphons. The siphons of Sphenia sincera
are not short but are as long as those of Mya of the same
shell length. It would be of interest to compare the
siphonal length of Sphenia antillensis to see if this
anatomical feature is also related to habitat.

### D. Size, Growth, and Age

Dimensions. The average length of 70 <u>Sphenia</u> 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 same shells was 3.6 mm, with a range of 2.4 to 5.3 mm.

The type specimen has the following dimensions:

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

The largest shell collected was 9.9 mm in length.

Growth and Age. Measurements of the increments between successive shell annuli were used to determine growth rates. With the difficulties of collecting large numbers of <u>Sphenia</u> <u>sincera</u>, this appears to be the only practical method to assess growth. Interpretation of growth rings has been used extensively to determine age and growth in mollusks (Mossop 1922, Orton 1926, Stevenson and Dickie 1954, Kristensen 1957). The method has several sources of error, since annuli can be caused by any source

of arrested growth, in addition to that which results from low water temperature. Such factors as unusual environmental conditions, spawning, poor feeding conditions, predation, and changes in sediment structure are known to produce annuli in many bivalves. Small, fast growing, short-lived mollusks appear to produce more discrete and predictable rings than others.

Sphenia sincera collected in June of 1962 were held in laboratory trays, with flowing sea water at ambient local temperature, until February of 1963. Measurement of each annulus, greatest anterior-posterior dimension (i.e., length), were made on 147 shells with a Wild M-5·microscope, using a calibrated ocular grid at 6 diameters magnification. Only the right, or largest, valve was used in all measurements. 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 (2nd 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).

Therefore, 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 large at the first winter check, while fast growth was typical of clams that were small at the first winter check. Assuming that growth curves are probably sigmoid as in many other bivalves (Weymouth and McMullin 1931, Weymouth and Thompson 1931, Yancey and Welch 1968), time of spawning will be one of the most critical factors in observations of annual growth rates for short-lived animals. Clams spawned early in the first year will have attained most of their growth before the first winter and therefore will grow slowly during the second year. Clams spawned at mid-year will have about equal growth in both years, and clams spawned late in the year will have relatively little growth the first year, and attain most of their adult size in the second year.

The maximum size (length) of _Sphenia_ _sincera_ appears to be about 1 cm; the largest I have taken in the Sheepscot region had a total length of 9.9 mm and had 4 shell annuli. Most _Sphenia_, however, apparently live only 2 to 3 years and the mean size of all specimens collected was 5.4 mm.

In contrast to the slow growth of <u>Sphenia sincera</u>, <u>Mya arenaria</u> grow much more rapidly. Packard (1918) gives the following growth rates for <u>M</u>. <u>arenaria</u> on the Atlantic coast:   3.5 mm in 3½ months, 25 mm at 6 months, 70 mm at 1½ years, 82 mm at 2½ years, and 91 mm at 3½ years. This is more rapid growth than that reported by others studying <u>Mya</u> in the New England region. Belding (1907) stated that clams set in Massachusetts waters by late August had attained an average size of 12.9 mm by mid-November when growth stopped for the winter. Belding also stated that it took an average of two years to produce a 2 to 2½ inch clam. Belding (1916) reported the following rates of growth: Spawned summer 1906, 12.9 mm at 4 mos., 15.5 at 9 mos., 20.3 at 11 mos., 26.4 at 12 mos., and 45.9 at 23 mos. Merrill (1959) found that <u>Mya arenaria</u> living in the stabilizer tubes of oceanic bouys grew exceptionally fast, reaching a length of over 1 inch in the first winter, and over 2 inches by the second winter.

Dow and Wallace (1951) gave the following growth

rates for <u>Mya</u> <u>arenaria</u> from two Maine coastal regions where

<u>Sphenia</u> is abundant:

| Mean age (years) | Mean Size (mm) | |
| | Port Clyde to Pemaquid | Pemaquid to Small Point |
| --- | --- | --- |
| 1 | 16.02 | 10.85 |
| 2 | 22.49 | 21.7 |
| 3 | 28.65 | 32.62 |
| 4 | 35.47 | 43.9 |
| 5 | 42.44 | 50.6 |

Stickney (1964) concluded from laboratory and field data

that the first summer's growth of young clams in most

northern New England areas would average about 5 mm and

seldom exceed 10 mm.

Hanks (1968) reported that wild clams (<u>Mya</u> <u>arenaria</u>)

reached a total length of about 40 mm in 1 year in natural

brackish waters of Chesapeake Bay, whereas larvae that met-

amorphosed in man-made ponds grew only half as fast and

reached an average total length of 20 mm in the same period

(Figure 9). The warm waters and other environmental factors

of Chesapeake Bay probably provide for the fastest growth

in this species of nearly any region, although isolated

sections of New England coast may match these growth rates

in some years, and Edmondson (1922) implied that Oregon

clams could grow 25 mm in 4 months.

Figure 9.   Growth of young <u>Mya</u> <u>arenaria</u> in wild popula-

tions and in man-made pond populations in the

Chesapeake Bay region (from Hanks 1968).

MYA GROWTH RATES
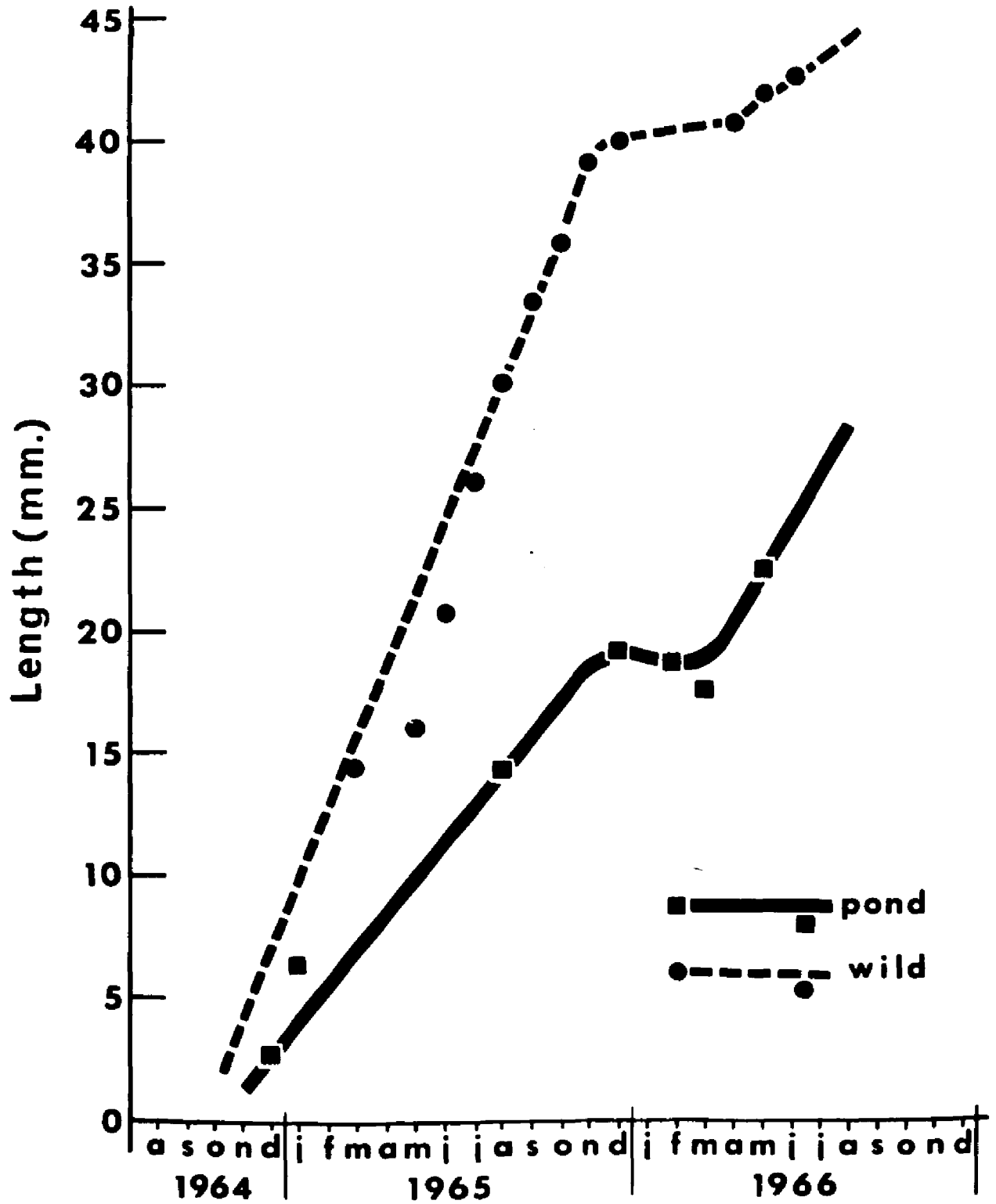
References to the growth of *Mya truncata* are few. In Danish waters, *M. truncata* larvae are most abundant in the winter period, November to January (Jorgensen 1946), whereas in northeast Greenland the peak of spawning occurs in July (Thorson 1936). Veligers of *M. truncata* are most abundant in Danish and Greenland waters when water temperature (surface) is about 5°C (Spärck 1933). Assuming a mid-summer spawning period for the 18 Greenland shells I obtained from the Danish museum, and that shell annuli are winter checks, I found the mean length at first annulus to be 6.0 mm, and mean total length (summer collection, or about 1 year old) to be 7.8 mm. Thorson (1936) observed that *Mya truncata* from the coast of Greenland grew between 3 to 6 mm in one year, but his size-frequency diagrams indicate a one year modal length of about 6 mm. Therefore, from the little material available, the growth of *Mya truncata* appears to be twice as rapid as that of *Sphenia sincera*, even in the cold waters off the eastern Greenland coast.

E.  Reproduction

Development and Spawning in Mya arenaria.  The
reproductive cycle of Mya arenaria was studied histo-
logically by Battle (1932) and by Coe and Turner (1938).
Recently, the cycle was analyzed by Ropes and Stickney
(1965) for northern populations and by Shaw (1964, 1965)
and Pfitzenmeyer (1965) for populations in the mid-
Atlantic coast region and Chesapeake Bay.  In these
studies monthly samples of clam gonads, examined histo-
logically, were used to define the developmental process
of eggs and sperm up to and through the period of spawn-
ing.  The cycle has been arbitrarily split into 5 phases
(nomenclature of Coe and Turner as modified by Ropes and
Stickney); inactive, active, ripe, partially spawned,
and spent.

The general sequence of egg development is as
follows:

Inactive Phase - gonadal activity is lowest; period
    of nutritive build-up.

Active Phase - ovocytes enlarge and grow between
    follicle cells toward center of alveoli, producing
    large, rounded ovocytes with constricted cyto-
    plasmic bases.  The free ends of the ovocytes
    project into the lumina of the alveoli.

Ripe Phase - ovocysts are connected only by a very

thin stalk or may be free in the lumina. Nuclei

contain amphinucleoli.

Partially Spawned Phase - final meiotic division

takes place in the oviduct and later. This phase

is marked by general absence of ripe ovocytes in

many alveoli and the cessation of ovogenesis in

all alveoli.

Spent Phase - follicle cells are prominent with some

unspent ovocytes in early stages of cytolysis;

lipoid droplets are prominent. This stage inter-

grades with the inactive stage.

Development of sperm in the male is judged by the

following criteria:

Inactive Phase - aberrant meiotic activity; pycnotic

cells and multinucleated, nonpycnotic cysts appear

in the follicle cells; the latter fill the alveoli.

Active Phase - entire process of spermatogenesis;

primary spermotocytes are found at the basal mem-

brane of the alveoli; early stages of meiosis occur

near the basal membrane and later spermatids at

centers of alveoli.

Ripe Phase - masses of spermatozoa, arranged in radial

columns with tails toward center of alveoli.

Partially Spawned Phase - few spermatogonia at basal

   membrane; follicle cells appear between basal

   membrane and groups of cells undergoing spermato-

   genesis; some pycnotic cells are present.

Spent Phase - few or no spermatozoa in center of

   alveoli, no cells in active spermatogenesis;

   numerous follicle cells with non-pycnotic cysts and

   pycnotic cells.

   Size and Age of Reproductive Maturity in Sphenia

and Mya. Virtually no observations have been made on the

reproductive cycle of any species of Sphenia, nor of the

gonadal histology. The following descriptions are based

on Sphenia sincera from the mid-coast regions of Maine,

collected over a period of several years and in all seasons.

   Sphenia sincera from Maine do not exceed 10 mm in

length and, based on shell annuli, it is doubtful if it

exceeds 4 years in age. Fully viable sperm and eggs,

appearing normal and producing motile larvae, have been

obtained from Sphenia as small as 6.3 mm, and histological

sections of Sphenia as small as 3 mm have shown mature

gonads with apparently fully developed sperm and eggs.

Mya have never been reported to be mature at this size.

Belding (1916) observed that most soft shell clams in

Massachusetts waters became sexually mature at the end

of one year and a size of 1½ inches. Belding implied that rate of growth and adequate size were more important to the onset of sexual maturity than age. Coe and Turner (1938) found the gonad of Mya arenaria to be established (but not functional) as early as 6 mm, yet sexual differentiation rarely occurred before a length of 20 mm. These observations are compatible with Belding's generalization. Some dwarfed or slow growing individuals appeared capable of spawning at 10 mm, but histological preparations showed that the number of gametes was very low. Pfitzenmeyer (1965) found male Mya arenaria from Chesapeake Bay as small as 25 mm with fully mature sperm. In many years of personal observations on clam populations of the mid-coast region of Maine, specifically in areas adjacent or contiguous with those where Sphenia were commonly collected, I have never found a sexually mature Mya less than 18 mm in length.

Figure 10 compares gonad sections from Mya arenaria population and from a Sphenia sincera population, held under identical conditions for one year. The Mya arenaria were spawned and set entirely within the laboratory, from known parental stock. The Sphenia were dredged from the bottom of the Sheepscot River estuary in about 120 feet of water on a soft mud bottom in June of 1962. Both of these

Figure 10.   Sections of _Sphenia sincera_ (A. male,

B. female), _Mya arenaria_ (C), and

_Mya truncata_ (D).  _Mya arenaria_ and

_Sphenia_ were held for one year under

identical conditions; _Mya truncata_ from

the coast of Greenland.  All about 6 mm

total length.  Gonads of male and female

_Sphenia_ are mature, while no development

is evident in _Mya_.

populations were held in running sea water, at ambient
Boothbay Harbor water temperature, for the same period of
time. <u>Mya</u> <u>truncata</u> sections were obtained from museum
specimens, collected on the east coast of Greenland, of
comparable size to the other species examined. It was
obvious that there was a complete lack of gonad develop-
ment in the <u>Mya</u> group , while both males and females of
the <u>Sphenia</u> group were fully mature. <u>Sphenia</u> are probably
capable of reproduction, at least within the first year of
life, whenever environmental conditions are adequate. One
can suspect that, since recovery to full spawning potential
is short, <u>Sphenia</u> may reproduce more than once a year, and
further that perhaps multiple generations may be possible
in the same year.

<u>Comparisons of Gamete Morphology and Reproductive</u>
<u>Cycle in Mya and Sphenia</u>. Although no reproductive studies
similar to those of Ropes and Stickney (1965) or Shaw(1964,
1965) have been made with <u>Sphenia</u>, histological sections of
a small number of specimens have been prepared. Also,
observations of captive <u>Sphenia</u> have given additional data
on the reproductive cycle.

Nearly all samples of _Sphenia_, taken from the Sheepscot River, were induced to spawn immediately by simple thermal stimulation. Males and, particularly, females taken in the months of June through November invariably spawned within 4 to 24 hours when water temperatures were raised to between $24°$ to $26°$C. _Sphenia_, held in running sea water in laboratory trays, also spawned in February when the temperature of tray water was near $0°$C. Records of the Bureau of Commercial Fisheries Biological Laboratory at Boothbay Harbor, Maine, show that water temperatures near the bottom of the Sheepscot River estuary never attain temperatures higher than $15°$C. Therefore, natural spawning temperatures must be somewhat lower than those found to induce spawning. This is not unexpected, since the rate at which the water is heated, about $1°$C per 15 minutes in the experiments, results in higher observable spawning temperatures than would be found in natural waters with gradual temperature increase.

From these observations, that _Sphenia sincera_ can be spawned at any time, we can deduce that the periods of inactive and active phases are shortened in _Sphenia_ as compared to _Mya_, and that the ripe phase is much more extensive. Admittedly, the gametes produced from thermal

stimulation have often resulted in aberrant larvae and none have been carried through to metamorphosis. High water temperatures, low oxygen levels, polyspermy, and other factors may be implicated as agents detrimental to normal development.

In contrast to the ease with which spawning can be induced in Sphenia sincera, most biologists who have worked with Mya arenaria will attest to the extreme difficulties in stimulating spawning at any time of year outside its normal spawning period (Stickney 1964, Loosanoff and Davis 1963). Indeed, no completely reliable procedure has yet been found. Stickney (1964) induced spawning in Mya from New England and Chesapeake Bay by providing cyclic warming and cooling periods (basic 6 hour period) over extended time periods. He found that a temperature elevation of $5°$ to $10°C$ above normal seasonal temperatures was required. He was also able to induce spawning by injection of 0.1 N ammonium hydroxide into the gonad through the mantle strap. However, chemical stimulation killed the adult, and produced only a small fraction of the eggs produced by thermal stimulation. In all cases, only ripe clams were used. Loosanoff and Davis (1963) also found it difficult to spawn Mya even when fully ripe. They used gradual changes in water temperature, changes in pH,

salinity, hydrostatic pressure, light intensities, and addition of sex products with little or no success. Their most successful method was to subject ripe clams to relatively high temperatures of $26^{\circ}$ to $28^{\circ}C$, for periods of 6 to 8 hours, with the addition of sex products. Many clams were stimulated to spawn by this method, but a high percentage of eggs developed into abnormal larvae.

A common practice, with bivalves that are difficult to spawn, is to strip the gametes from ripe males and females. Stripping involves the removal of the outer membrane of the gonad and then washing the exposed tissues which frees eggs and sperm without serious injury. The entire procedure is outlined in Loosanoff and Davis (1963). Belding (1931) showed that eggs stripped from Mya arenaria could be fertilized, but that they failed to develop normally. Stickney (1963) indicated that Mya and Mercenaria shed their eggs with the nuclear membrane dissolved and with the eggs in the initial stages of meiosis, and contrasted this with other bivalves studied (i.e., Spisula, Crassostrea, and most other lamellibranchs) in which the eggs are released with nucleus intact. Meiosis in these latter species is induced by sperm penetration. Stickney believes that the eggs of Mya and Mercenaria are "activated" by special secretory cells lining the terminal

portion of the oviducts in these species. Stripped eggs are therefore not "activated" and viable larvae are rarely produced.

Thus, where great difficulty is encountered with the spawning of Mya even during its natural spawning period and when fully ripe, Sphenia can be induced to spawn by simple thermal stimulation during the greater part of the year. Therefore, no attempts were made to "strip" gametes from Sphenia. I have obtained active sperm by simply inserting a pipette into the gonad tissue, but have not used these gametes in fertilization experiments because natural products are easily obtained.

Ropes and Stickney (1965) demonstrated a single reproductive cycle in M. arenaria north of Cape Cod. Maine clams spawned from June through August, and Massachusetts clams spawned from July to late September. Clams south of Cape Cod, and particularly in the Chesapeake Bay region, apparently have a biannual cycle. Shaw (1964, 1965) demonstrated that there was a biannual cycle in Chesapeake Bay Mya, with a definite fall spawning from September to November, but that the spring spawning in April was not consistent, and was often aborted with gametes retained until fall. Pfitzenmeyer (1962, 1965) found the spring spawning occurred more frequently in the lower, western

portion of the Bay. European M. arenaria appear to have a summer spawning season similar to M. arenaria on our New England Coast.

Mya truncata has been reported to be a winter breeder (Jørgenson 1946) in Danish waters, with larvae occurring during the period October to March, but with maximum larval abundance during November to January. In contrast, Thorson (1936) found M. truncata spawning from June to September in northeast Greenland; the most intense activity was in July. The surface water temperatures were similar (5°C) at the peak of spawning and larval abundance in both areas (Laursen 1966).

The eggs of Mya arenaria and Sphenia sincera are about the same diameter. Loosanoff, Davis and Chanley (1966) reported the average diameter of spawned eggs of Mya arenaria to be 70.5μ. Pfitzenmeyer (1965) stated that a "morphologically mature" length of M. arenaria oocytes, in histological section, was 76 to 81μ. Shaw (1964) observed that mature ova of clams from the middle region of the Chesapeake Bay measured 60μ in diameter. Measurements of over 100 Sphenia sincera eggs, in histological sections from 12 different specimens, gave a mean diameter of 70μ with a range of 65 to 75μ.

## F.  Chromosome Complement

The *Sphenia* egg begins mitotic division shortly after fertilization. The first two divisions are longitudinal and at right angles to each other, while the third division is somewhat latitudinal and results in the spiral division characteristic of the mollusks (Raven 1958, Hyman 1967). Chromosome smears were prepared from gametes obtained by induced spawning. After fertilization, the eggs were incubated at 5.5°C, and chromosome smears were prepared at regular intervals of 30 minutes and stained with aceto-orcein. Selected clear smears were examined under the microscope, and chromosomes counted and photographed for subsequent detailed study.

There are no records of chromosome numbers in the family Myidae. Longwell, Stiles, and Smith (1967) demonstrated that the American oyster <u>Crassostrea</u> <u>virginica</u> has a diploid number of 20 (n=10), and supported Rosenfield's observation (cited in Ahmed and Sparks 1967) that the chromosome number was uniform in several oyster species. Ahmed and Sparks (1967) reported a 2n of 20 for <u>Ostrea</u> <u>lurida</u> and <u>Crassostrea</u> <u>gigas</u>, two species of oysters under commercial cultivation on the Pacific coast. Menzel and Menzel (1965) recorded a 2n of 38 for the hard clams

Mercenaria mercenaria and M. campechiensis, and their hybrids. The chromosome numbers of only a few other pelecypod species were recorded by Makino (1951): Cumingia (n=18; 2n=36) and Mactra (n=12; 2n=24)[*]. Menzel (1968) has published a list of chromosome counts for 23 species of mollusks in 9 families: Mytilidae 2n=24, Ostreidae 2n=20, Cardiidae 2n=38, Mactridae 2n=36, and Pholodaiedae 2n=34. Within the four families, in which more than one species were examined, counts for all species and genera were identical. Menzel correctly indicates that this apparent constancy of chromosome number within families could be a useful systematic tool.

About 25 clear preparations of Sphenia material were obtained, and in each preparation the haploid (n) number was 17 and the diploid (2n) number 34 (fig. 11). As in other Myidae, meiotic divisions occur after the eggs are released (Raven 1958, Stickney 1963, Longwell and Stiles 1968). All of the clear preparations were of meiotic figures, generally tetrads, some perhaps in anaphase I and others in diplonema or diakinesis. These figures were obtained about 1½ to 2 hours after gametes were brought together (not necessarily fertilization).

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[*] Note that Menzel (1968) has corrected the number for the Mactridae.

Figure 11.  Aceto-orcein stained chromosomes of

Sphenia sincera.

*Sphenia* *sincera* chromosome smears

Mya arenaria could not be induced to spawn, so eggs
and sperm were stripped from obviously mature and ripe in-
dividuals. These gametes were mixed, with sperm in dilute
concentrations to avoid polyspermy, and the material incu-
bated as before. Although egg squashes were prepared at the
same period previously used (i.e., 30 minutes), no usable
figures were obtained until three hours after initial mix-
ing, and good preparations were obtained for the next three
hours, after which cells were too small and numerous to
provide good smears. All division figures were obviously
mitotic during this period. Once again the chromosomes
were counted and photographed (fig. 12). Although chromo-
some counts were not as consistent as in the Sphenia mater-
ial, the modal number was again n=17 and 2n=34. Most of
the clearest figures were found in late anaphase or early
telophase.

Unfortunately, only a few chromosomes in the photo-
graphs are adequately defined for karyological study. The
sophisticated techniques developed by Longwell, Stiles,
and Smith (1967) and Longwell and Stiles (1968) could be
applied to Sphenia gametes with excellent results.

Figure 12.  Aceto-orcein stained chromosomes of

Mya arenaria.
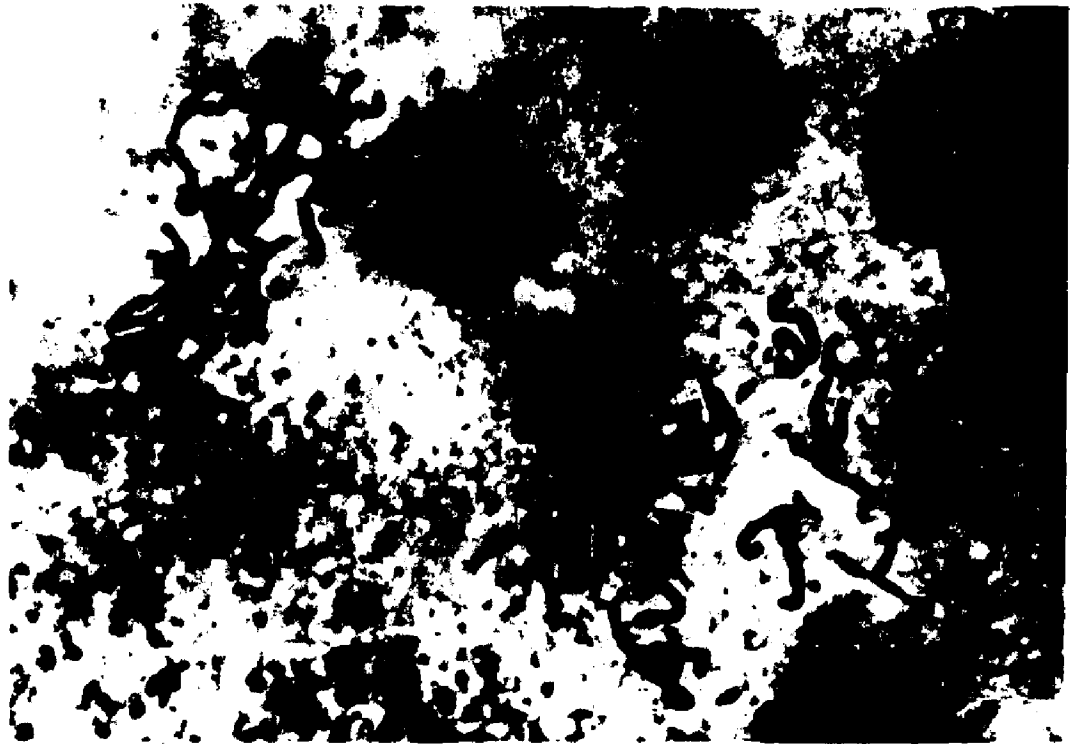
**Mya arenaria** chromosome smears

Nevertheless, there is sound evidence for a chromosome number of n=17 and 2n=34 for the Myidae. This is a definite advance in our knowledge of pelecypod cytology, and appears to correlate nicely with the consistence in chromosome numbers found in the other molluscan families.

## G. Ecology

Nearly all previous records, with the exception of those for _Sphenia antillensis_ (Dall and Simpson 1901, Warmke and Abbott 1961), have reported _Sphenia_ to be nestlers living in the burrows provided by other invertebrates. On the coast of England _S_. _binghami_ are frequently found living in the vacant burrows of _Hiatella_ (Yonge 1951). Jeffreys (1862-69) records the habitat of _S_. _binghami_ as "the cavities of limestone rocks and old oyster-shells perforated by _Saxicava_ [=_Hiatella_] _rugosa_ and _Cliona_ _celata_, as well as among the roots or bases of _Laminaria_ _saccharina_", "in the deserted cases of _Serpula_ _triguetra_"; and "other places of shelter and concealment". Forbes and Hanley (1853) stated "very solid and aged single valves of the common oyster seem its favorite burrowing places". Every account of European _S_. _binghami_ emphasizes the shell distortion caused by conformity to crevices and burrows formed by other animals. _Sphenia_ apparently have no boring capacity. Additionally, Yonge (1951) stated that lack of mobility and the nature of the habitat was further indicated by the presence of encrusting growths on the shell and periostracum of the siphons.

In contrast, _Sphenia sincera_ have not been found in a nestling habitat, and although _Hiatella_ is a common bivalve on the rocky New England coastline, especially boring into the calcareous encrustations of coraline algae, _Sphenia sincera_ was never found in _Hiatella_ burrows, nor in any other burrowing situation. Extensive collections were made throughout the lower Sheepscot estuary in dense _Hiatella_ populations adjacent to deep-water populations of _Sphenia sincera_. The burrows and tubes of other organisms were also examined closely. Not one _Sphenia_ was found in these ideal situations for a nestling animal. They are always free-living on or near the surface of the soft, clay-silt mud found in this region. The shells are never distorted, the periostracum is quite thin, and in most respects they resemble the juveniles of _Mya arenaria_ and _Mya truncata_. It should be noted that _Sphenia antillensis_ from Fuerto Rico is the only other known non-nestling species of _Sphenia_.

_Sphenia sincera_ have been collected from depths of 10 to 81 meters in the Sheepscot region. Ninety percent of dried sediment samples pass through U. S. standard screen with openings of 62$\mu$. They are usually found within the top 25 mm of the surface, forming siphonal connections with the surface as do most other Myidae. Water

temperatures, near the bottom, range from 1°C in the winter to 14°C in the summer. Salinities are relatively high, and at the bottom nearly uniform throughout the year at about 32 ‰ . The mean tidal range in this section of the river is about 3 meters. This, presumably, has little effect on populations of animals living at the depths Sphenia inhabit. Since most of the population centers in the mouth of the "lower estuary" (see Stickney 1959), the major effect of tide is on current flow, both velocity and direction, and mixing.

Most faunal associates of the Sphenia sincera populations are members of the Nucula-Nephtys community as described by Hanks (1963). Particularly abundant in these deeper waters are the bivalve mollusks Nucula proxima, Thyasira gouldi, juveniles of Artica islandica, Cerastoderma pinulatum, Yoldia limutula, such polychaete annelids as Sternaspis scutata and Nephtys incisa, and the sea star Ctenodiscus crispatus. Tube-building amphipods of such genera as Corophium and Ampelisca often produce thick mats of old tubes that lace the surface sediments. Major predators of these Sphenia populations are the bottom-feeding fish (cod, haddock, and flounder). Stomach contents of small cod and haddock, captured near the mouth of the Sheepscot River in June of 1962, revealed that they were

feeding almost exclusively on Sphenia. One small haddock (total length about 16 inches) contained over 400 Sphenia with only a few other small mollusks (Arctica and (Clinocardium). The implication is that some ground-fish prefer Sphenia to other forms of food items and actively select it. If the range of this Sphenia extends along the Maine coast, and if its abundance is as great as in the Sheepscot region, it must be an important food item for inshore ground-fish populations.

Relatively little positive information is available concerning the food of bivalve mollusks. Sphenia have the morphological characteristics of a filter-feeding mollusk . (Yonge 1951) and probably feed on materials similar to those utilized by other Myidae. Stickney (1964) demonstrated that juvenile Mya arenaria could grow at rates nearly double that of clams in natural waters, when fed diets of certain unicellular algae under laboratory conditions. He found that Dicrateria sp.; a diatom, Cyclotella nana; and a flagellate, Monochrysis lutheri were all reasonably good foods. Phaeodactylum and Olithodiscus were satisfactory in promoting growth, and Chlorella and Tetraselmis were poor Non-living food materials produced no growth. Blegvad (1914) and Coe (1948) considered detritus to be an important factor in the nutrition of many marine organisms.

and in the Sheepscot, abundant detritus is available from such sources as <u>Ulva</u>, <u>Zostera</u> and <u>Fucus</u>. <u>Sphenia</u> <u>sincera</u> collected in Maine were held in artificial sea water 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 <u>Phaeodactylum</u> and <u>Chlorella</u>. Since mortalities were less than 10% during this period, I assume that <u>Sphenia</u> did feed but could not confirm that the algae were used. It is entirely possible that other microorganisms may have been nutritionally significant.

The habitats of <u>Mya</u> <u>arenaria</u> and <u>Sphenia</u> <u>sincera</u> are separated by differences in preference for location; the former rarely extend much below the low-tide level, and the latter inhabit much deeper water; deeper than 30 feet, with greatest abundance below 100 feet. <u>Mya</u> <u>truncata</u> is also found at depths in the Gulf of Maine (Verrill, 1873) but are not found in dense populations, and have never been taken in samples for this study or previous surveys (Hanks 1961, 1964). Scattered reports of <u>M</u>. <u>truncata</u> along the Maine, New Brunswick, Nova Scotia and Gaspe coasts indicate that inshore populations are widely distributed and low in density. In an effort to secure juvenile <u>M</u>. <u>truncata</u> for this study, I contacted every coastal laboratory in the above areas, and additionally requested assistance from the

Canadian Arctic Research Unit, and laboratories in Iceland, Greenland, and Denmark. In not a single instance were there known available populations of juvenile M. truncata. The most recent specimens obtainable were from collections made in 1933 on the coast of Greenland. Adult M. truncata from the Maine coast and Canada were all true M. truncata and not M. truncata ovata, whose external morphology is so similar to M. arenaria. Although M. truncata is generally sub-tidal in deep water along the southern part of the Gulf of Maine, it comes into shallow water and can be found intertidally on the northern part of the Maine coast and on Canadian shores. In a personal communication, Mr. René Lavoie of the Faculty of Science, Laval University, Quebec, P.Q., told me that he had found adult M. truncata valves still joined by the ligament -- indicating fairly recent mortality. These shells were found along 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 3 months in summer and 4 months in winter. We can infer that the ligamentally-joined M. truncata shells from the St. Lawrence have been dead for at least one year, and possibly much longer.

The evidence indicates that _Sphenia_ _sincera_ occupies a habitat different from that of adult _Mya_ _arenaria_ and _M_. _truncata_; that it does not compete for space with juvenile _Mya_ _arenaria_ which live mostly in the shallower waters and intertidal regions; and that little competition can occur with juvenile _Mya_ _truncata_, which have not been found abundant in the off-shore Maine waters, where they approach the southern limit for the species.

_Mya_ _arenaria_ generally reach highest densities in sandy-mud sediments, where salinities are somewhat brackish. _Mya_ _truncata_ is more often found in waters of oceanic salinity, and frequently selects firm clay sediments. The latter may account for the difficulty in obtaining living specimens. Even when found in the intertidal regions of the north, this preference for clay seems to hold, although _M_. _truncata_ can be found in other sediments.

Although it is difficult to retain the natural relation with the bottom surface in deep water samples, _Sphenia_ appear to be in similar orientation to juvenile _Mya_ of the same size; that is, the anterior directed down and the posterior (siphon) directed toward the surface.

The clams are restricted by the small siphons and gener-
ally are found in the top 25 mm of sediment. The burrows
do not appear to be lined with mucus or other supportive
material. Clams held in laboratory aquaria rarely dug
into the sediments, or only buried themselves partially,
but this could be unusual behavior induced by the sediments
(generally sandy) used. It should be noted that it is
extremely difficult to reproduce the typical sediment
structure of the Sheepscot region in the laboratory, for
it consists of a surface layer of rich organic detritus
(very light, fluffy and easily displaced by slight currents)
overlying fine silt and clay, which blends at deeper levels
into stiff mud-clay. Usually the detrial layer is quite
thin, and I presume that the <u>Sphenia</u> live in the silt-clay
sediments with the siphons projecting through the detrial
layer. The prevalence of <u>Sphenia</u> in the stomachs of
bottom-feeding fish also rules against their being deeply
imbedded in the substratum.

Parasites. The Myidae are relatively free from parasites (Clay 1962, Vlès 1909, Hanks 1963) and Sphenia sincera appears to be no exception. In one clam, of the many studied, a portion of an arthropod was found in the digestive diverticula. The animal's appendages terminate in hooked dactyls, similar to those exhibited by other parasitic arthropods, but other specimens would be needed to identify the animal and to establish its relationship with Sphenia.

Predators. In addition to the extensive use as food for fish, mentioned earlier, Sphenia sincera are undoubtedly prey for many other animals. Three shells collected near Mt. Desert Island, Maine (USNM #173122) were drilled by a gastropod. From the tapered edges of the small hole, I believe that they were drilled by one of the moon shells. The most common moon snail in these waters (Abbott 1954), at the depth of collection (10 fathoms), is Lunatia triseriata.

## H. Separation of <u>Sphenia sincera</u> and <u>Mya arenaria</u>

## by Electrophoresis

The development of electrophoretic and immuno-
electrophoretic techniques in recent years and their appli-
cation to taxonomic studies (Leone 1964) has opened new
approaches to the characterization of species. Not all
scientists believe that the methods are without pitfalls;
"Electrophoretic techniques are limited in their use as
taxonomic criteria. ...Attempts to elucidate taxonomic
relationships by measurement of electrophoretic ...
properties alone may easily be misleading." (Wilson and
Kaplan 1964). Dessaures and Fox (1964) however, point out
that "Starch-gel electrophoresis is useful in studies at
the interspecific and specific taxonomic levels, where the
probability is high that proteins of identical mobility
are of identical structure."

The staff of the U. S. Bureau of Commercial
Fisheries, Biological Laboratory at Oxford, Maryland have
been conducting electrophoretic separations of total
proteins of several species of oysters. The objective of
the study was to determine if the system could detect
protein differences at the species and racial levels.

With the availability of equipment and refined techniques I felt that a comparison of the total proteins of _Sphenia sincera_ and _Mya arenaria_ might provide additional evidence on their taxonomic affinities.

Both vertical and horizontal starch-gel techniques were used. The principles are well known (see Smithies 1955 for detail), but in general involve the separation, by molecular size and electrical charge, of proteins in liquid solution subjected to an electrical field causing differential migration through a buffered plate of starch jelly.

Total protein preparations were made from homogenized and sonically blended tissues of juvenile _Mya arenaria_ and _Sphenia sincera_. Both populations had been held for nearly one year under as close to identical environmental conditions as possible to maintain in the laboratory in order to cancel the effect of environmental factors on the observations.

Starch-gel plates were prepared with 10 sample slots and innoculated as follows: Slot 1 contained human serum as a control, slot 2 was blank, slots 3, 4, and 5 contained juvenile _Mya arenaria_ preparations, slot 6 was blank, slots 7 and 8 contained _Sphenia sincera_ preparations.

Separations of proteins tested with acid phosphatase, α-naphthyl acetate (showing esterase activity), and α-naphthyl proprionate are shown in figure 13.

In every instance a differential separation is evident between the protein preparations of Mya arenaria and Sphenia sincera. These protein separations are considered to be a further indication of differences between Sphenia and Mya. They are not conclusive in themselves. Too much remains to be done in refinement of electrophoretic techniques. However, when used with morphological, anatomical, and other criteria, electrophoresis might prove valuable in separating specimens.

Figure 13.  Diagrams of electrophoretic separations

for the proteins of Sphenia sincera (right)

and Mya arenaria (middle).  Human serum is

used as a control (left).  The slots are

numbered beginning with 1 on the left and

ending with 8 on the right.

ACID PHOSPHATASE

ALPHA-NAPHTHYL ACETATE

ALPHA-NAPHTHYL PROPRIONATE
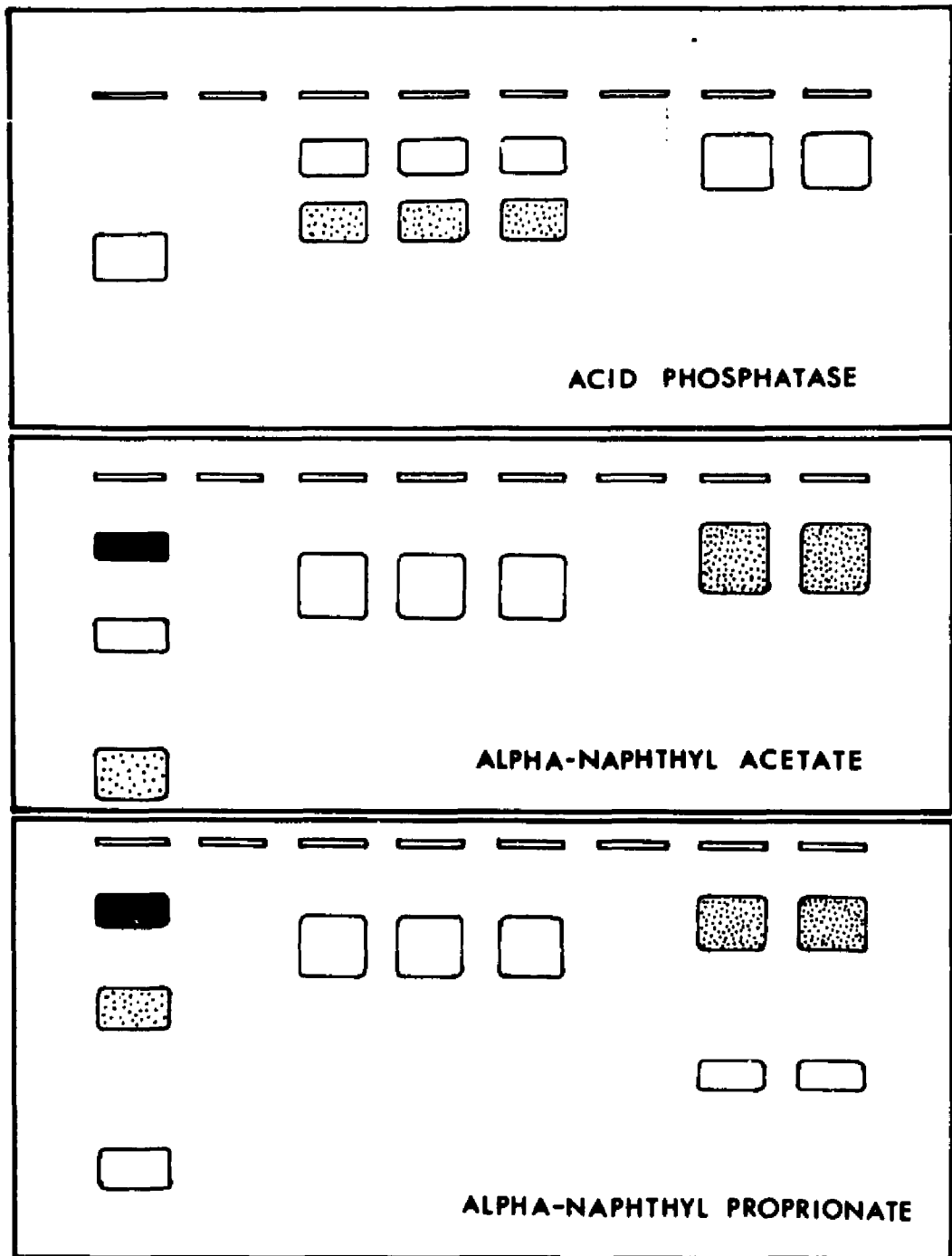
**Electrophoretic comparison of human control (left), Mya arenaria (middle), and Sphenia sincera (right) serum proteins**

## I.  Separation of Sphenia sincera from

## other species of Sphenia

The unique characteristics of Sphenia sincera
(bright, clean, undistorted shell of distinct shape, solid
calcification, free-living existence, and geographic remote-
ness from other living Sphenia) are probably sufficient to
prevent confusion with any other species in the genus.
However, specific comparisons help to establish the precise
difference between shells and define the new species.

From the fossil species Sphenia dubia Lea 1845,
S. attenuata Dall 1898, S. senterfeiti Gardner 1936, and
S. tumida Lewis 1968 it differs in being larger and more
regular in shape than S. dubia or S. senterfeiti and in
being neither attenuated, tumid, or rostrate as S. attenuata
and S. tumida.  Of course S. sincera also differs in being
a living animal and its geographic range is much further
north than recorded for any fossil species -- fossil
specimens are reported only to Virginia on our Atlantic
Coast.

Of all the living species, only S. sincera and
S. antillensis are not nestlers.  The others live in the
burrows of worms or the cavities established by many other
marine organisms.  Generally, the shell posterior is

truncate or rostrate and is usually distorted by the pressures exerted on the shell by the confines of the appropriated habitat. Often, the posterior region of the shell is weakly calcified, which gives flexibility to the shell, and apparently this feature has selective survival value for the nestling species. Sphenia sincera has none of these characteristics of the typical nestling forms.

Sphenia sincera is the only living member of the genus found on the Atlantic Coast of North America. It differs from the type species, S. binghami, from the coast of Europe, in having a thin deciduous periostracum, rather than a heavy thick brown periostracum, and in having the posterior undistorted with the dorsal and ventral margins converging rather than nearly parallel as in S. binghami. This appears to be an excellent diagnostic feature and nearly all S. binghami that I have examined, or seen figured, demonstrate the "square" appearance of the posterior. Juvenile shells exhibit this characteristic at the smallest sizes. Of course, some of the larger S. binghami become so distorted in the posterior that the "square" shape is secondarily masked, but it is still evident even in badly twisted shells (Appendix Plates I and II). S. binghami has a weakly calcified posterior, and the umbones are usually situated less than 1/3 of the distance

between the anterior and posterior ends -- the umbones of

S. sincera are located about 1/3 of the distance. Yonge

(1951) reported that the siphons of S. binghami were short,

whereas the siphons of S. sincera are comparatively long.

Sphenia coreanica was described from the coasts of

Korea and Japan by Habe (1951). S. coreanica is very

truncated in the posterior, has a somewhat crenulated ante-

rior and ventral margin, and the pallial line is disconti-

nuious. This shell is so different from S. sincera that

there is no possibility of confusion the two species.

Six species of Sphenia have been described from the

Pacific Coast of the United States. Two of these, S. globula

Dall 1916 and S. nana Oldroyd 1924, are represented by few

shells and their generic designation is doubtful. In any

case, the shells are so distinctively shaped (Oldroyd 1924)

that they are easily separated from the other species of

Sphenia. The remaining four species are S. fragilis

Carpenter 1857, S. ovoidea Carpenter 1865, S. trunculus

Dall 1916, and S. pholadidea Dall 1916. S. pholadidea is

known only from the type locality at Santa Barbara, Cali-

fornia. It has a dark, blackish periostracum which tends

to be conspicuously laminate on the posterior shell surface;

it is very inequalateral and the umbones are much reduced.

The posterior is truncate and somewhat attenuated. The external prosopon (sculpture or surface appearance) is more rugose than S. sincera. Sphenia trunculus is a short whitish shell with a dirty ash-colored periostracum, rugose on the exterior and abruptly truncate. The arterior is considerably swollen and the posterior is attenuated. The shell is almost equilateral. The latter feature, and the swollen anterior easily distinguish S. trunculus from S. sincera. S. trunculus ranges from San Diego, California to Panama on the Pacific Coast. Sphenia ovoidea is a small shell from the northern regions of our Pacific Coast ranging from the Aleutian Islands to Puget Sound. The anterior of this shell is ovally rounded and the shell bears a yellow, somewhat rugose, periostracum. The posterior 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. Sphenia fragilis is apparently the most ubiquitous member of the genus on the Pacific Coast, having been reported from Oregon to Mazatlan, Mexico. The shell is elongate and opaque, but not solid. The periostracum is dull yellow and closely attached, but the surface of the

shell is somewhat nacreous and almost smooth with indistinct annuli. The posterior is attenuated and truncate. 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, this shell can be separated from S. sincera by the yellow periostracum, the attenuated posterior, and the size and position of the adductor scars.

Sphenia antillensis Dall and Simpson 1901 appears to be the closest living species to S. sincera not only in geographic location, being found on the coast of Porto Rico, but also because it appears to be the only other species that is commonly free-living and not a nestler. The shell, however, is quite distinct from S. sincera having more acute umbones, a distinctly flattened anterior margin not curving regularly as in S. sincera, a broader (in lateral view) posterior, and an unusual lateral concavity to the posterior ventral shell which tends to produce a keeled shape to the shell. S. antillensis has a yellow periostracum but, apparently, this is often missing. In any case, this distinctive shell can be easily separated from Sphenia sincera by the prominent characters indicated.

Separation of the species of <u>Sphenia</u> can be difficult because of their small size and often extreme distortion resulting from the nestling habit. Most, however, have some distinctive morphological features that provide means of species separation. <u>Sphenia</u> <u>sincera</u> presents an idealized morphological ground plan that by its perfection separates the shells from all other members of the genus.

## SUMMARY

1.      *Sphenia binghami* was described by Turton in 1822, and Gray (1847) designated *S. binghami* as the type species for the genus *Sphenia*. A modern lectotype, from what is believed to be Turton's original material, was selected in this study and deposited in the U. S. National Museum.

2.      The genus *Mya* has a circumarctic and circumboreal distribution, but *Sphenia* is far more cosmopolitan and is found north and south of the equator. This broad geographic distribution gives additional support for *Sphenia* as the ancestral genus of the family Myidae.

3.      *Sphenia sincera*, sp. nov. is established from specimens collected on the coast of Maine, and represents the first member of the genus from the Atlantic coast of the United States and Canada.

4.      The ratio of shell length to shell height was not diagnostic in separating the three species *Mya arenaria*, *Mya truncata*, and *Sphenia sincera*, but *S. sincera* could be distinguished by comparison of the ratios of hinge length to width.

5.     The anatomy of S. sincera is similar to other Myidae. The statement that Sphenia is heteromyarian, and thereby different from all other Myidae, is not valid for the genus. Complete shell calcification and long siphons are characteristic of free-living Sphenia, weak partial calcification and short siphons are characteristic of nestling Sphenia.

6.     Sphenia sincera ranges up to 1 cm in length, with an average length of 5.4 mm in mid-coastal Maine. The growth rate of Sphenia appears to be about 2 mm per year and the life span is about 3 years. Mya arenaria and M. truncata grow much faster, with average juvenile rates of 5 to 6 mm per year.

7.     The reproductive cycle involves identical stages observed in other Myidae, but the preparatory stages are very short and the ripe phase is extremely long. As a result, Sphenia sincera can generally be stimulated to spawn throughout the year. Sexual maturity is achieved early in life, commonly in the first year, and at a smaller size than has ever been reported for Mya arenaria. When the two species were grown under identical conditions for one year, M. arenaria showed no gonadal development, while S. sincera was fully mature.

8.     Chromosome numbers were established from aceto-orcein stained smears of eggs from *Mya arenaria* and *Sphenia sincera*. In both the 2n was 34 (n = 17). This observation of similar numbers within a family agrees with recently published information on other molluscan families.

9.     *Sphenia sincera* is free-living; in contrast to most other members of the genus, which are nestlers. It lives in water depths up to 81 meters in soft sediments of silt and clay. Most common faunal associates are the bivalve *Nucula proxima* and the polychaetes *Nephthys incisa* and *Sternaspis scutata*. Major predators are bottom-feeding fish such as cod, haddock, and flounder. Little is known about the food of *Sphenia*, but it probably consists of algae, bacteria, and other micro-organisms. Like other Myidae, it is relatively free of parasites.

10.     Starch-gel electrophoretic patterns of serum proteins showed distinct differences between *Mya arenaria* and *Sphenia sincera*. Although the technique is not definitive, it offers a possible additional tool in separating specimens that intergrade in other characteristics.

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APPENDIX

PLATE I:  Lectotype specimen of <u>Sphenia</u> <u>binghami</u>

Turton USNM No. 171240 by subsequent

designation Hanks (This Dissertation).

A.& B.  - Outer surface of left and

right valves.

C.& D.  - Inner surface of left and

right valves.

E.      - Chondrophore of left valve.

PLATE II:   Paralectotype of <u>Sphenia</u> <u>binghami</u> from

Turton's original material.

A.& B.  - Outer surface of left and

right valves.

C.& D.  - Inner surface of left and

right valves.

E.      - Chondrophore of left valve.

F.      - Small juvenile nestling in old

oyster shell.
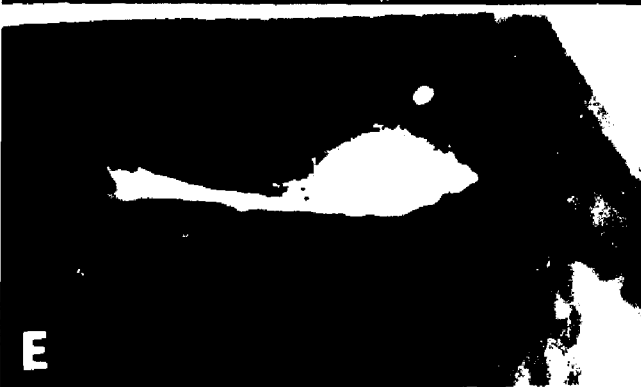
PLATE III:  Type specimen of <u>Sphenia</u> <u>sincera</u> Hanks,

sp. nov. USNM No. 679164.

A.& B.  - Outer surface of left and

right valves.

C.& D.  - Inner surface of left and
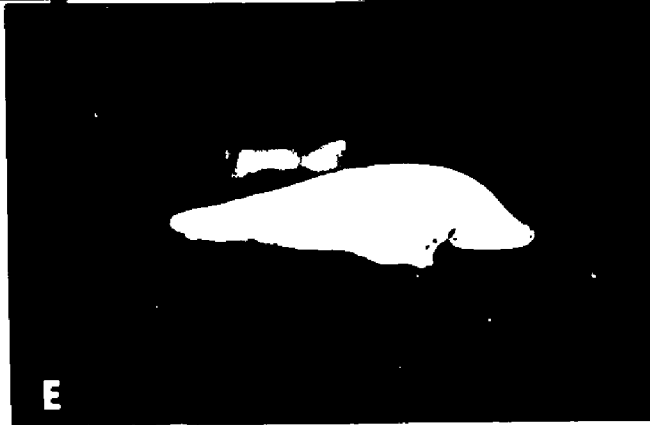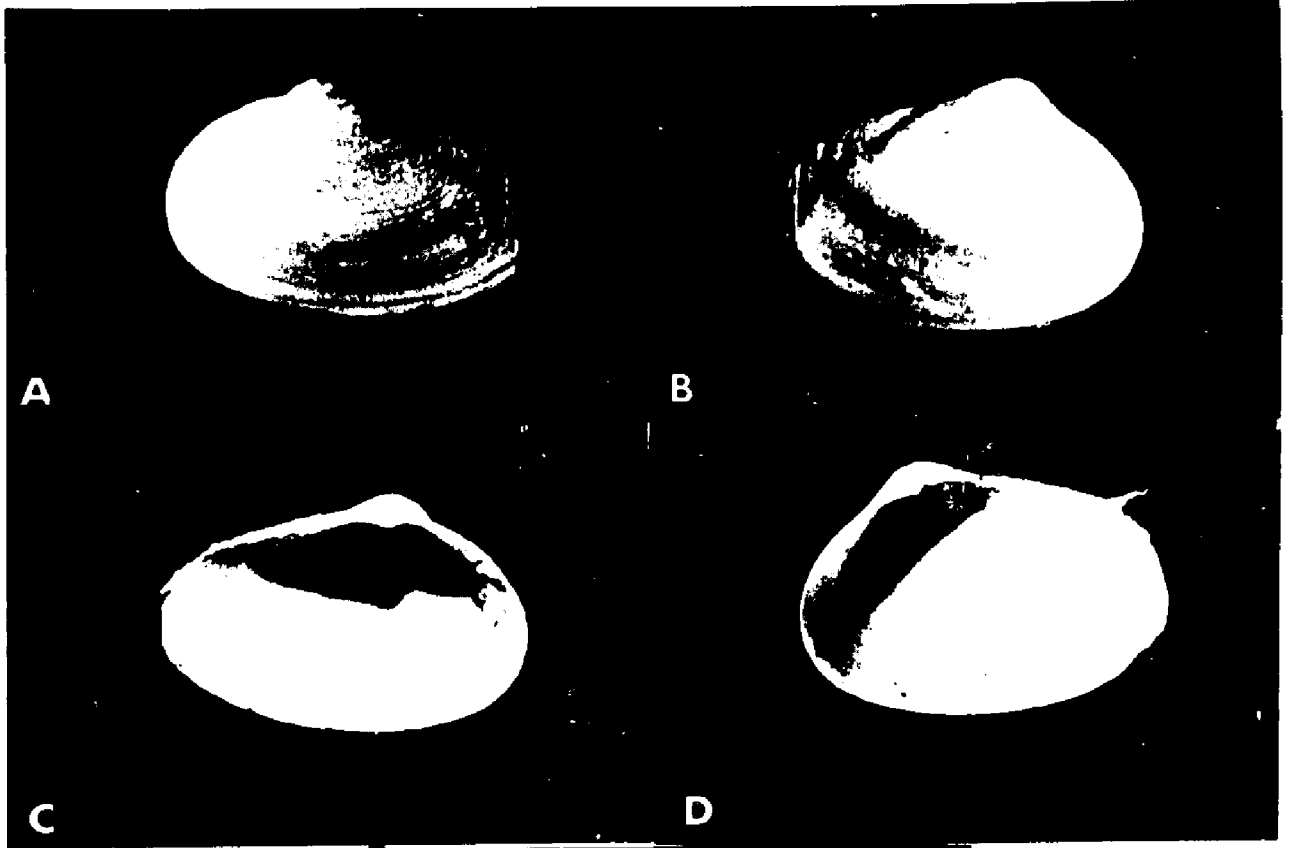
right valves.

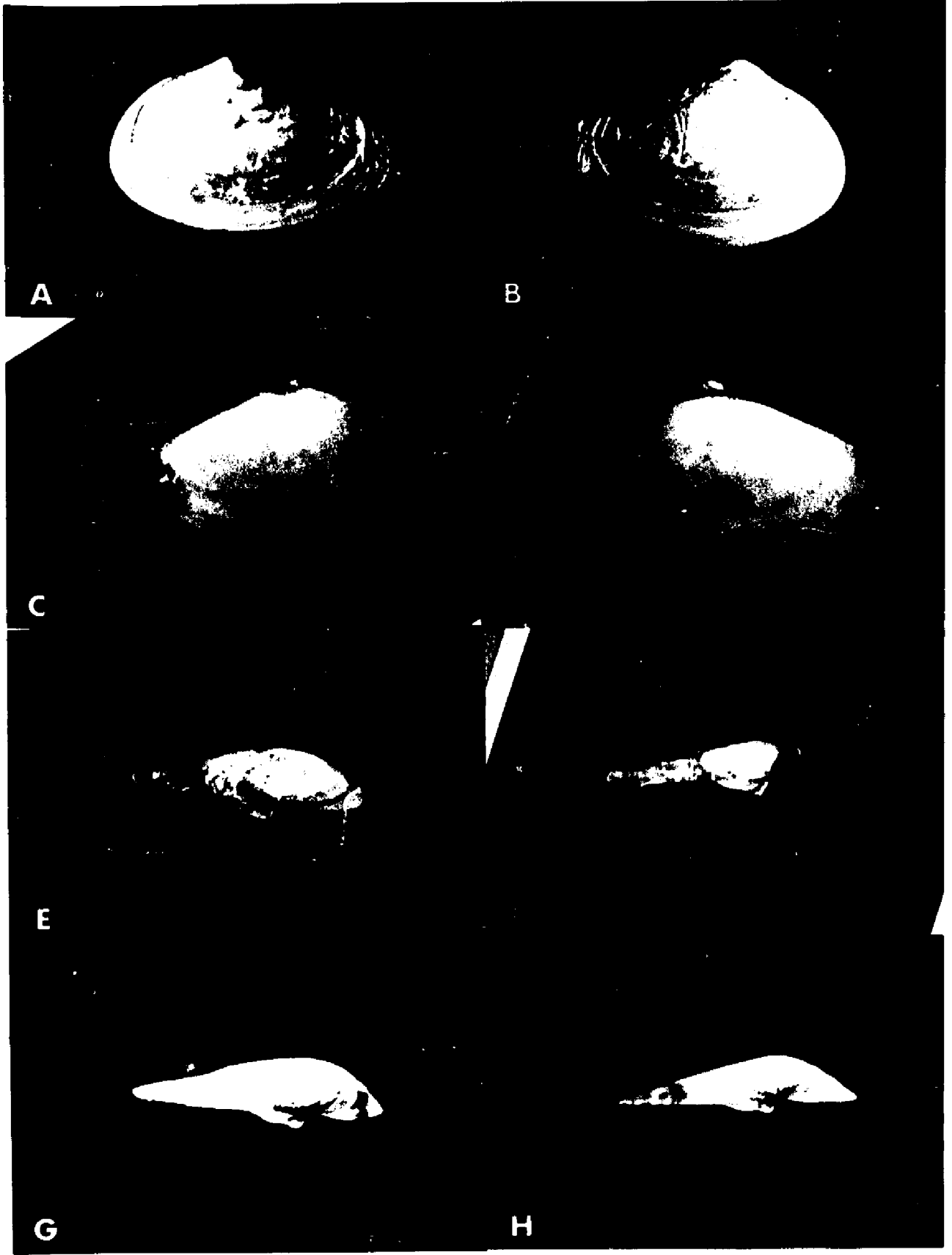E.      - Chondrophore of left valve.

PLATE IV:  Paratype of <u>Sphenia</u> <u>sincera</u> Hanks,

sp. nov. USNM No. 679165.

A.& B. - Outer surface of left and

right valves.

C.& D. - Inner surface of left and

right valves.

E., F., G., & H. - Chondrophores of

left valves showing variation in hinge

shape and sculpture.

A

B

C

E

G                                        H

PLATE V: Juvenile <u>Mya</u> <u>truncata</u> from the coast of Greenland.

      A.& B. - Outer surface of left and right valves.

      C.& D. - Inner surface of left and right valves.

      E.& F. - Chondrophores of left valves.
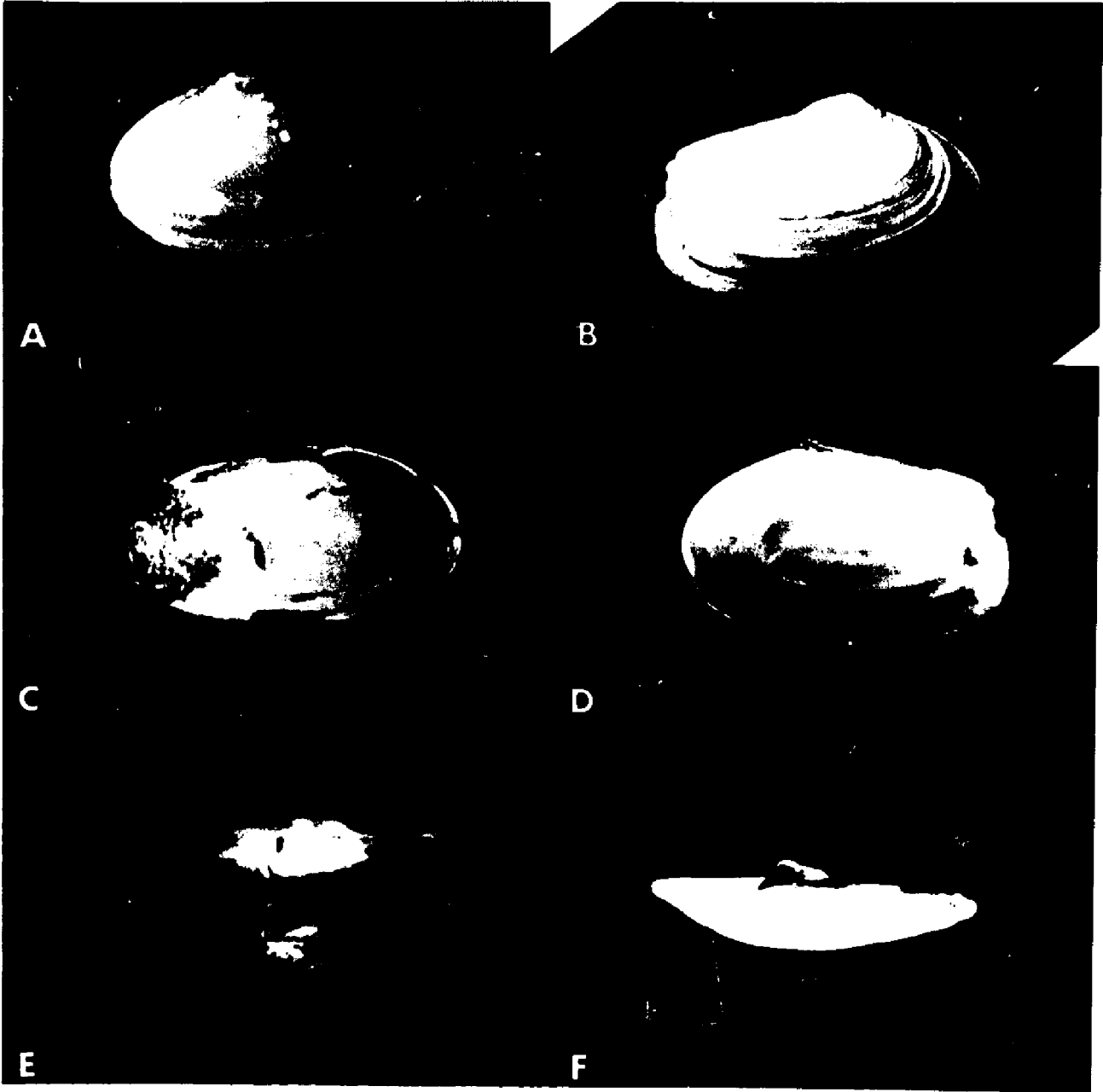
A     B

C     D

E     F

PLATE VI:   Juvenile <u>Mya</u> <u>arenaria</u> from central Maine

Coast, U. S. A.

A.& B. - Outer surface of left and

right valves.

C.& D. - Inner surface of left and

right valves.

E.       - Chondrophores of left valve.