

The eastern Pacific species of *Sphenia* (Bivalvia: Myidae)

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ABSTRACT

There are four eastern Pacific Ocean species of the genus *Sphenia*: (1) *Sphenia fragilis* (H. Adams and A. Adams, 1854), occurs in a variety of nestling situations from the intertidal zone to shallow water, from Santa Barbara County, California, to Guayas Province, Ecuador, and has as synonyms *S. fragilis* Carpenter, 1857; *S. pacificensis* de Folin, 1867; and *S. trunculus* Dall, 1916; as well as the western Atlantic *Corbula iheringiana* Pilsbry, 1897; and *S. antillensis* Dall and Simpson, 1901. (2) *Sphenia gulfensis*, a new species, is restricted to soft bottoms in the Gulf of California. (3) *Sphenia hatcheri* Pilsbry, 1899, occurs, probably in relatively soft substrata, from Rocha Department, Uruguay, through the Estrecho de Magallanes, as far north as Isla Chiló, Chile; *S. subequalis* Dall, 1908, is a synonym. (4) *Sphenia luticola* (Valenciennes, 1846), occurs offshore in rock cavities from Jefferson County, Washington, to San Diego County, California, and has as synonyms *S. pholadidea* Dall, 1916; *Cuspidaria nana* Oldroyd, 1918; and *S. globula* Dall, 1919. *Sphenia bilirata* Gabb, 1861, may have been based on Recent specimens of *Hiatella arctica* (Linnaeus, 1758). *Sphenia ovoidea* Carpenter, 1864, is based on a juvenile *Mya*, most probably *M. arenaria* Linnaeus, 1758.

INTRODUCTION

Bernard (1983: 58) provided the most recent list with synonymies of the eastern Pacific species of the myoid genus *Sphenia*. He recognized three: *S. hatcheri* Pilsbry, 1899, in southern Chile; *S. luticola* (Valenciennes, 1846), with a number of synonyms, from northern California to northern Peru; and *S. ovoidea* Carpenter, 1864, from southeastern Alaska to Puget Sound, Washington. At the same time he erected a new subfamily, the Spheniinae, based on two morphological features (Bernard, 1983: 58, 70).

My attention was drawn to some material that proved to belong to *Sphenia* from the Golfo de California and that had been misidentified as a new species of *Basterotia*, a genus of the Sportellidae, which I was then studying. When that review was completed (Coan, 1997; 1999), I returned to this material, which proved instead

to be a new species of *Sphenia*. Examination of the available eastern Pacific material of *Sphenia*, including the type material of the described species, has resulted in conclusions that differ significantly from those of Bernard (1983).

Previous taxonomic lists and studies of *Sphenia* include those of A. Adams (1851), Tryon (1869: 67), E. A. Smith (1893), Lamy (1927: 176–184), Lewis (1968), and Hanks and Packer (1985). Bałuk and Radwański (1979) discussed the morphological variability of the Miocene *Sphenia anatina* (Basterot, 1825: 92) caused by its nestling site.

Forbes and Hanley (1848: 189–193) were the first to describe the anatomy of a species of *Sphenia*, *S. binghami* Turton, 1822, from notes provided by William Clark. Yonge (1951) reviewed the functional morphology of *S. binghami*, and Narchi and Domaneschi (1993) that of *S. antillensis* Dall and Simpson, 1901.

Some species, such as *S. binghami*, nestle in rock crevices and similar situations, whereas others, such as *S. antillensis*, are somewhat more widespread nestlers, occurring among colonial ascidians, polychaete tubes, and the byssal threads of mytilid clams. *Sphenia sincera* Hanks and Packer, 1985, occurs in soft bottoms, but there is not yet an account of how its functional morphology differs from the two taxa studied thus far.

FORMAT

In the following treatment, each valid taxon is characterized by its synonymy, description, information on type specimens and type localities, notes on distribution and habitat, and an additional discussion.

The synonymies include all major taxonomic accounts about the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes given in parentheses.

The distributional information is based on Recent specimens I have examined, except as noted. Fossil occurrences are taken from the literature.

The following abbreviations are used in the text: AMNH, American Museum of Natural History, New

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York, New York, USA; BM(NH), The Natural History Museum, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; LACM, Natural History Museum of Los Angeles County, California, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UMML, Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, USA; Skoglund Collection, collection of Carol C. Skoglund, Phoenix, Arizona, USA.

MORPHOLOGICAL CHARACTERS

Due to the nestling habitat of most species, overall shell shape is not an easily used character in identification of species. Variability in shape is illustrated in the material figured herein. Some species of *Sphenia*, such as *S. luticola* and *S. anatina*, are highly variable in shape, inhabiting pre-established cavities in relatively hard substrata. *Sphenia fragilis*, nestling amongst such materials as bryozoan colonies, is only slightly less variable. Those species occurring in softer substrata, such as *S. sincera*, and presumably *S. gulfensis* and *S. hatcheri*, retain a more defined shape.

While the shape of the ends, especially the posterior end, is also variable, the degree of elongation and inflation of the anterior end is a useful character that helps, for example, to distinguish *S. fragilis* from *S. gulfensis*.

The periostracum differs among species. The extent to which the periostracum and, in one case, the outer shell layer, extend the posterior end is particularly important in species distinction.

The chondrophore in the left valve, while exhibiting variability in size and shape, provides at least three useful characters. In small specimens of all species, it is approximately horizontal. As some species reach their maximum size, it may become more vertical, such as in *S. luticola*. Also useful is the degree of elongation of the posterior attachment (the "posterior buttress") and the length of the posterior ridge (figures 1, 18–22).

The placement of the anterior muscle scar—located either close to the ventral margin or more toward the middle of the anterior margin—proves to be a useful specific character. The extent to which the posterior adductor muscle scar and the pallial sinus are recessed from the posterior end is also a useful character. These features are illustrated with line drawings (figures 18–22).

Finally, the size of the discontinuous scars defining the pallial sinus differs among the four eastern Pacific species.

The most important specific characters are given in Table 1.

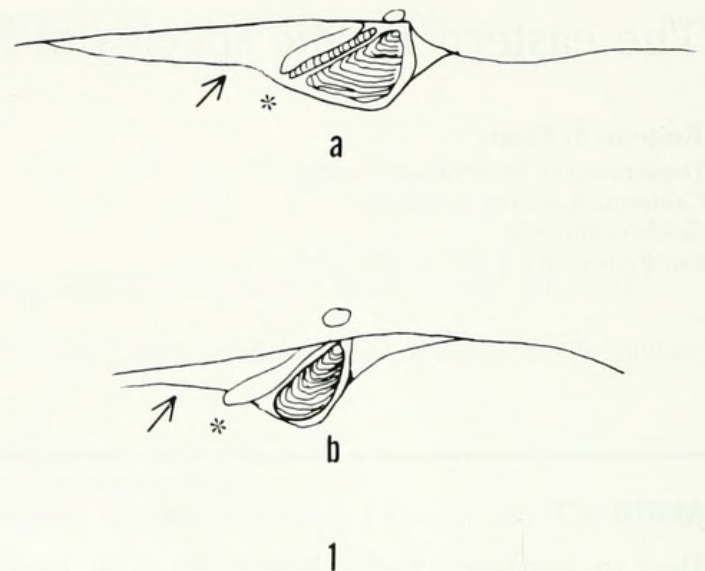


Figure 1. Contrasting features of the chondrophores of two species of *Sphenia*. (a) *S. gulfensis* and (b) *S. luticola*. The first has a long posterior buttress (arrow) in contrast to the latter. The second has a long, projecting posterior ridge (asterisk) in contrast to the first.

SYSTEMATICS

Family Myidae Lamarck, 1809: 319, as "Myaires"
Subfamily Cryptomyinae Habe, 1977: 279

This subfamily is thus far distinguished from the Myinae only on the basis its short siphons and shallow pallial sinus.

Bernard (1983: 58, 70) proposed the Spheniinae based on two characters: (1) the "resilifer" in the left valve was said to be "only superficially similar" to the "chondrophore" of *Mya*, and (2) "the lateral tubercles of the right valve have no counterpart in *Mya*."

I believe that this rationale is indefensible. In the first instance, a chondrophore is merely a hollowed-out, projecting resilifer, and the left valves of both *Sphenia* and *Mya* have similar structures. *Mya* attains a much larger size than *Sphenia*, and its chondrophore ultimately becomes more prominent. However, at an equivalent size, the chondrophores and their features in the two genera are virtually identical. Indeed, in describing a new species of *Sphenia*, Hanks and Packer (1985) use terminology for chondrophore features first proposed for those of *Mya* by MacNeil (1965) and earlier authors. Bernard's reference to "lateral tubercles" in *Sphenia* is equally perplexing. The eastern Pacific species of *Sphenia* have a small, slightly projecting anterior cardinal tooth in the right valve, varying in prominence among species; there is no posterior tooth. There is no projecting anterior cardinal tooth in *Mya* of equivalent size, but the posterior end of its anterodorsal margin may be expanded and turned ventrally just anterior to the resilifer. The presence or absence of a small tooth may differentiate members of the two genera, but it does not seem to be a fundamental difference.

Bernard's differentiation of the Spheniinae from *Mya*

Table 1. Key differentiating characters, size, and frequency of eastern Pacific *Sphenia*. Total 204 lots.

	Shell thickness/ shape	Anterior end	Chondrophore orientation/ posterior ridge	Anterior adductor muscle scar	Posterior adductor muscle scar and pallial sinus	Max. size, mm	Number of eastern Pa- cific lots studied
<i>Sphenia fragilis</i>	Thin/variable— ovate, ovate- elongate, sub quadrate	Proportionately inflated	Horizontal, but a little ventrally/ ridge not pro- jecting	Near ventral margin	Close to pos- terior end	12.7	138
<i>Sphenia gulfensis</i>	Thin/elongate	More inflated, but tapering gradually	Horizontal/ridge not projecting	Central	Recessed from poste- rior end	13.1	31
<i>Sphenia hatcheri</i>	Moderate/elon- gate	More inflated, but tapering gradually	Equal horizontal- ly and ventral- ly/ridge slightly projecting	Near ventral margin	Recessed from poste- rior end	30.1	1
<i>Sphenia luticola</i>	Thick/variable— ovate, elongate	More inflated, but tapering gradually	More ventral/ ridge project- ing	Near ventral margin	Close to pos- terior end	20.6	34

is still more puzzling, because *Sphenia* had until then been placed in the Cryptomyinae Habe, 1977, which he also recognized. It was originally erected for myids with short siphons, and into it Habe placed *Cryptomya* Conrad, 1849: 121; *Distugonia* Iredale, 1936: 283; *Paramya* Conrad, 1860: 232 [*nomen novum pro Myalina* Conrad, 1845: 65, *non* Konnick, 1842: 125]²; *Sphenia*; and *Venatomya* Iredale, 1930: 403.

Overall relationships among the genera of Myidae could be inferred from cladistic analysis of an array of anatomical and shell morphological characters. The subfamily Cryptomyinae currently stands on minimal grounds.

Genus *Sphenia* Turton, 1822

Sphenia Turton, 1822: xvii, xxiii, 36–38, 261 (*ex* Leach ms, according to Gray, 1847). Type species: *Sphenia binghami* Turton, 1822: xxiii, 36–37, 257, 277, pl. 3, figs. 4, 5; by the subsequent designation of Gray (1847: 190). A lectotype for this species was designated and figured by Hanks and Packer (1985: figs. 1, 2).

Shaenia, *Spaena*, *Sphaena*, *Sphaenia*, *Sphaeria*, *Sphena*, *Spenia*, *Sphenica*, *Sphoenia*, *Syphonia*, misspellings of authors.

Tyleria H. Adams and A. Adams, 1854: 418. Type species: *Tyleria fragilis* H. Adams and A. Adams, 1854: 418; by monotypy.

² Placement of the genus *Paramya* remains a mystery. The resiliifers in the two valves are equally recessed and U-shaped, very different from those of other myids. There is no pallial sinus, and the external shell surface is pustulose, the latter suggesting to Campbell (1993:33) that it the species might be a member of the Sportellidae. Moreover, like the sportellid genus *Anisodonta* Deshayes, 1858:542, *Paramya* has a thick internal radial rib just posterior to the anterior adductor. However, sportellids have not been reported to have large internal ligaments. Only an examination of the anatomy of this genus will resolve its taxonomic position.

Tileria, misspelling of authors.

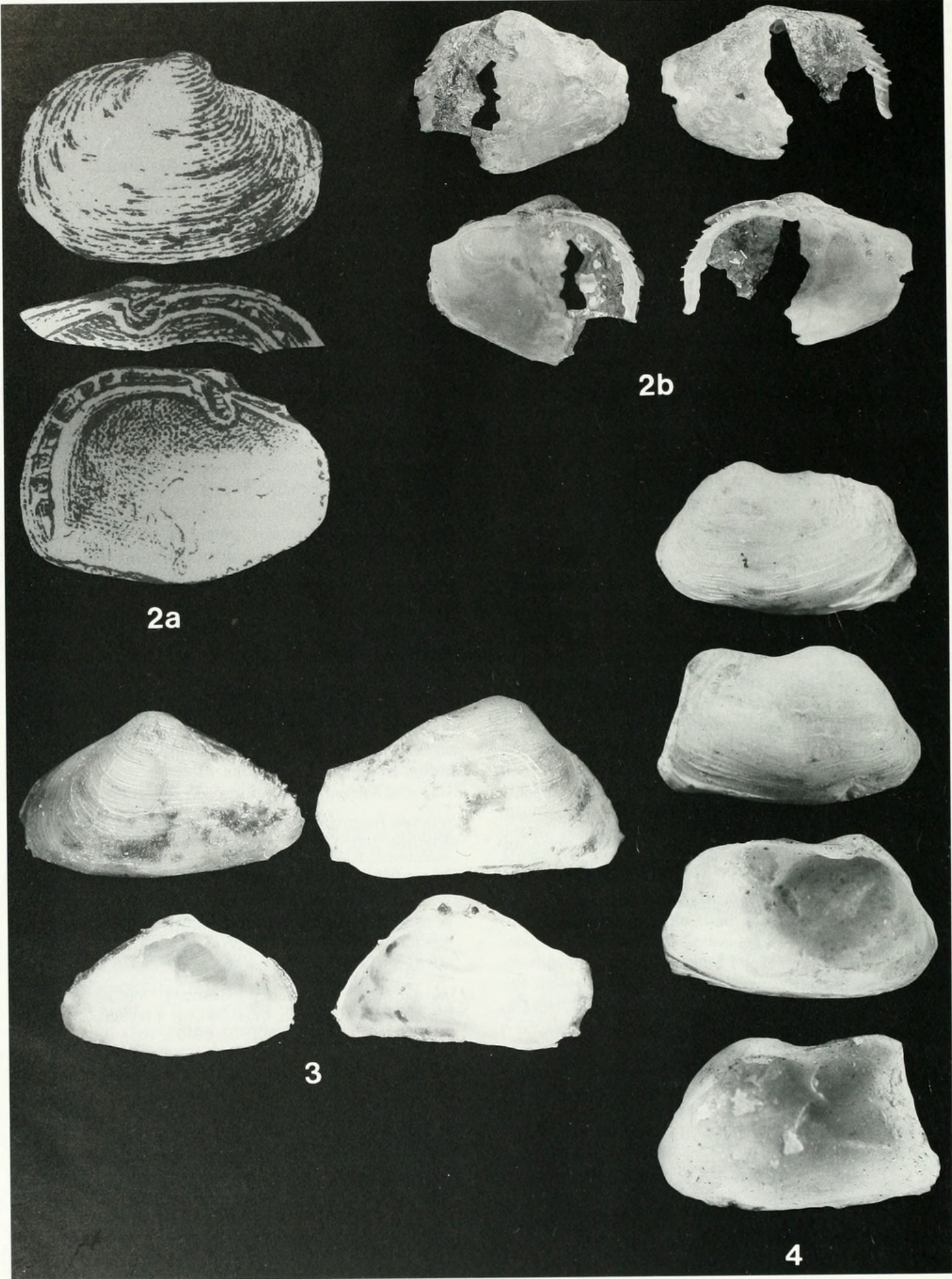
Description: Shell medium-sized to small, irregular in shape in nestling species. Posterior end truncate. Chondrophore narrow to somewhat projecting. Small anterior cardinal present in right valve. Pallial sinus shallow. Pallial line a series of discontinuous scars. Siphons short and united, with tips surrounded by single, common row of short tentacles. Incurrent siphon circled by additional row of tentacles, excurrent siphon with tubular valvular membrane. Ctenidia large and unplicated, inner demi-branch larger, with supra-axial extension. Palps small and differing in size between species. Foot small, narrow, serving in *S. binghami* and *S. antillensis* to attach the byssus to hard substrata.

Sphenia fragilis (H. Adams and A. Adams, 1854)
(Figures 2–6, 18, 24)

Tyleria fragilis H. Adams and A. Adams, 1854: 418; 1856: 368, pl. 97, figs. 3, 3a; Carpenter, 1857a: 245, 300; 1857b: 25 (as a possible synonym of *Sphenia fragilis* Carpenter), 547–548 (as something unique); Keen, 1968: 400–401 (as a senior synonym of *S. fragilis* Carpenter); Bernard, 1983: 58 (as a synonym of *S. luticola*)

Sphenia fragilis Carpenter, 1857a: 244, 300, *nomen nudum*; 1857b: 24–25, 530; 1864: 543 (as a possible synonym of *P. luticola*), 553, 619 (1872: 29, 39, 105); de Folin, 1867: 53 [= 15], pl. 2, figs. 7–9; Tryon, 1869: 67; E. A. Smith, 1893: 279; Oldroyd, 1924: 62–63; 1925: 200; Lamy, 1927: 179–180 (as a synonym of *P. luticola*, but under the heading of *S. fragilis*); Palmer, 1951: 13, 1958: 116; Keen, 1958: 207, fig. 521; Franc, 1960: 2120–2121, fig. E; Olsson, 1961: 424–425, 550, pl. 77, fig. 9, 9a, b; Brann, 1966: pl. 6, fig. 35 (tablet 80); Keen, 1968: 394, 400–401, fig. 22a–c; 1971: 262, 263–264, fig. 673; Bernard, 1983: 58 (as a synonym of *S. luticola*)

Sphenia pacificensis de Folin, 1867: 53–54 [= 15–16]; de Folin and Périer, 1867: 8 (as *pacificensis*); Crosse, 1868: 218 (as *pacifica*, unjustified emendation); von Martens, 1868:



586 (as *pacifica*); E. A. Smith, 1893: 280, pl. 15A, fig. 7 (as *S. pacifica*); Keen, 1958: 207 (as a variety of *S. fragilis*); Kisch, 1960: 149, 162; Lamy, 1927: 181; Keen, 1971: 263 (as a synonym of *S. fragilis*); Bernard, 1983: 58 (as a synonym of *S. luticola*)

Corbula iheringiana Pilsbry, 1897a: 8, *nomen nudum*; 1897b: 295, pl. 7, figs. 24–26; Figueiras and Sicardi, 1970a: 411, pl. 5, fig. 78

Sphenia antillensis Dall and Simpson, 1901: 474, pl. 55, fig. 14; Lamy, 1927: 181; Warmke and Abbott, 1961: 205–206, pl. 43, fig. e; Abbott, 1974: 537; Vokes and Vokes, 1983: 44, 65, 164, pl. 48, fig. 17; Narchi and Domaneschi, 1993: 195–210; Rios, 1994: 291, pl. 99, fig. 1419

Sphenia trunculus Dall, 1916a: 41, *nomen nudum*; 1916b: 415; Oldroyd, 1925: 201; Lamy, 1927: 181; Bernard, 1983: 58 (as a synonym of *S. luticola*)

Sphenia luticola Valenciennes, *autt.*, non Valenciennes, 1846. Gemmell et al., 1987: 58, fig. 71

Description: Shell thin, ovate to ovate-elongate to subquadrate; shape variable, depending on habitat; right valve slightly more inflated, often overlapping left valve at postero-ventral margin in less distorted specimens; anterior end generally short, broadly rounded, particularly inflated; posterior end from short to produced, truncate posteriorly, sometimes twisted to left or right, often extended by periostracum, slightly gaping. External surface with fine commarginal ribs; periostracum thin, dark to light tan, adherent. Left valve with medium-sized to large, triangular chondrophore, projecting towards right valve, but also somewhat ventrally; posterior buttress short; posterior ridge not much extended beyond ventral edge of chondrophore. Right valve with resilifer under beaks, more deeply recessed than that of *S. luticola*, and with small anterior cardinal tooth. Anterior adductor muscle scar positioned ventrally. Posterior adductor scar and pallial sinus close to posterior end. Pallial sinus a series of 2–4 narrow scars; pallial line a discontinuous series of small, rounded scars (Figure 18). Length to 12.7 mm (USNM 733245; Fort Amador, Canal Zone, Panamá); in the western Atlantic, to 14.6 mm (Narchi and Domaneschi, 1993: 196, misprinted as “146 mm”).

Type material and localities:

T. fragilis—BM(NH) 1878.1.28.64, holotype (figure 2a, b); length, 6.3 mm; height, 5.0 mm; thickness cannot be measured because of breakage. Mazatlán, Sinaloa, México (23.2°N); nestling in a sand-filled cavity in a *Spondylus* valve; R. W. Tyler. The holotype is now badly broken. Copies of the original figures as well as photographs of the present state of the specimen are provided here.

S. fragilis—BM(NH) Carpenter Mazatlán Collection 1857.6.4.82/1 [species 35, tablet 82], lectotype herein designated, the largest set of paired valves, length, approxi-

mately 8 mm; height, approximately 4.9 mm; thickness cannot be measured because specimen glued on slide (Figure 3); this specimen was figured by Keen (1968: figs. 22a, b). Paralectotypes: BM(NH) 1857.6.4.82/2, one left valve glued on same slide; 1857.6.4.81/1–6, 5 smaller pairs, some of which are broken, on slide, one loose valve; 1857.6.4.80/1–14, 10 still smaller pairs and four valves on slide; USNM 715649, 40 pairs, valves, and fragments. Mazatlán, Sinaloa, México (23.2°N); inhabiting the burrows of worms and mollusks in shells of chamids and *Spondylus*; also in dead barnacles on *Strombus*; F. Reigen.

S. pacificensis—BM(NH) 196460/1, lectotype herein designated, the only intact pair; length, 5.8 mm; height, 3.6 mm; thickness, 3.4 mm (Figure 4). BM(NH) 196460/2–3, paralectotypes, 1 pair with right valve broken anteriorly, length, 5.2 mm; 1 pair with both valves broken, length, approximately 6.2 mm. Archipiélago de las Perlas, Panamá (approximately 8.4°N).

C. iheringiana—ANSP 70541, lectotype herein designated, closed pair; length, 9.0 mm; height, 5.6 mm; thickness, 3.8 mm (Figure 24); ANSP 401333, paralectotypes, 1 right valve, length 7.4 mm; 1 open pair, length, 6.5 mm; 1 closed pair, length, 3.9 mm. Bahía Maldonado, Maldonado Department, Uruguay (34.9°S); 3–6 fms. [6–11 m].

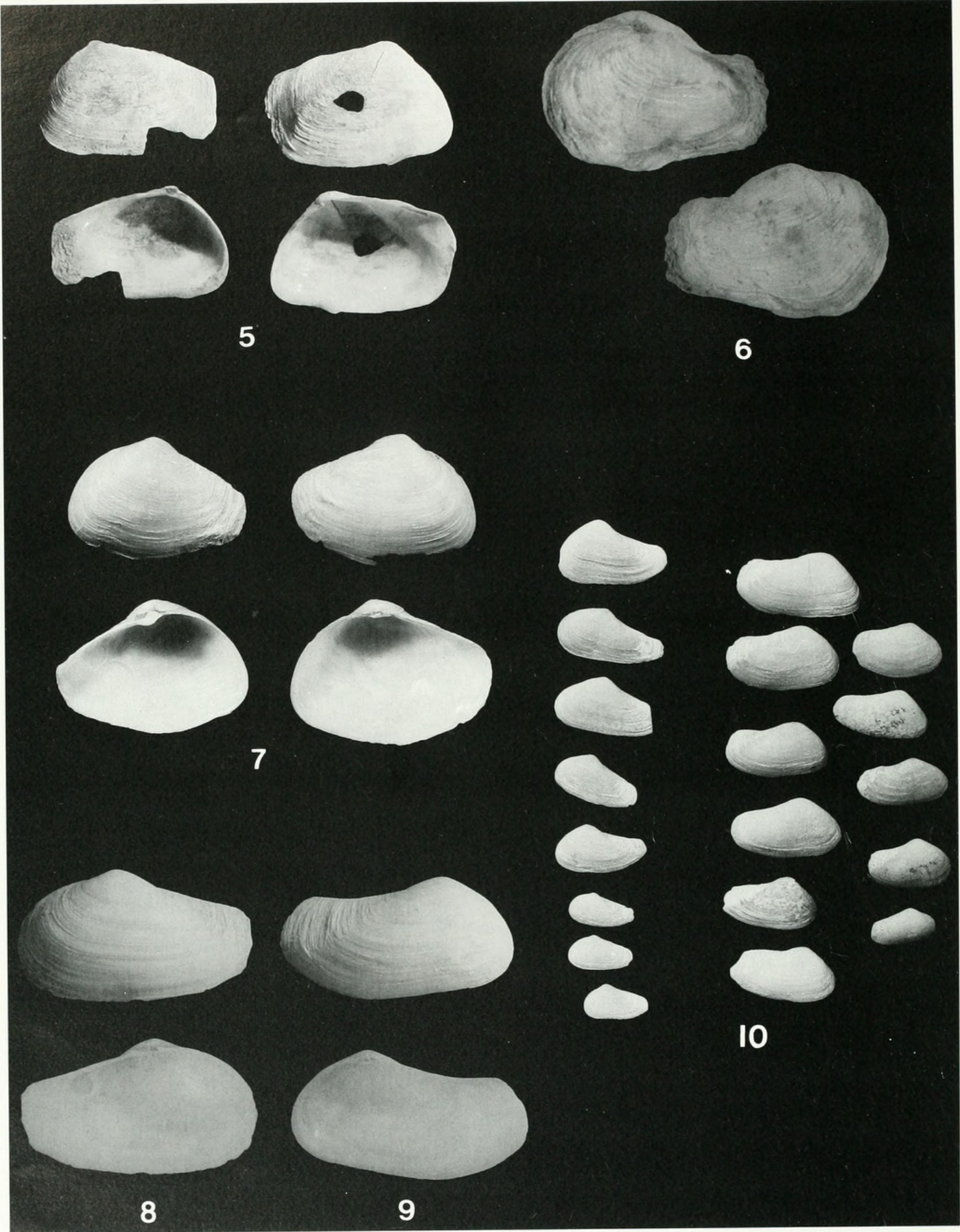
S. antillensis—USNM 160495, holotype, pair; length, 4.0 mm; height, 2.5 mm; thickness, 4.5 mm (Figure 5). Playa del Ponce, Puerto Rico (18.0°N, 66.6°W). The right valve of this pair is now split but not broken.

S. trunculus—USNM 160116, lectotype herein designated, closed pair; length, 6.9 mm; height, 5.0 mm; thickness, 3.8 mm (Figure 6); USNM 880250, paralectotype, smaller closed pair; length, 6.6 mm. San Diego, California (32.7°N); among barnacles on wharf piles.

Distribution and habitat: Carpinteria, Santa Barbara County, California (34.6°N) (LACM 77-30.22, SBMNH 31575), throughout the Golfo de California, to its head at Puerto Peñasco, Sonora, México (31.3°N), south to Salinas, Guayas Province, Ecuador (2.2°S) (CAS 110971); intertidal zone to 55 m⁽³⁾ (mean, 4 m; n = 50), nestling in pre-existing holes in rock, wood, and other mollusks, and among bryozoan colonies and in similar situations. A record from Zorritos, Tumbes Province, Perú (3.7°S) (Olsson, 1961: 425), could not be verified and was perhaps based on a specimen of *Aligena* (UMML 30.10456); in the western Atlantic from Hunting Island State Park, South Carolina (32.3°N) (L. D. Campbell, in correspondence, 19 July 1997), Saint Lucie

³ The specimen forming the basis of Durham's (1942:121) record of “*Sphenia* sp.” from 393 m west of Isla Tiburon, Sonora, México, cannot now be located in the UCMP, and thus a deep record of either this or the next species cannot be confirmed. The specimen might have proven to belong to some other genus and has now been filed elsewhere.

Figures 2–4. *Sphenia fragilis* (H. Adams and A. Adams). **2.** Holotype of *Tyleria fragilis* H. Adams and A. Adams, BM(NH) 1878.1.28.64, length = 6.3 mm. (a) Figures of H. Adams and A. Adams (1856); (b) photographs of current state of specimen. **3.** Lectotype of *Sphenia fragilis*, BM(NH) Carpenter Mazatlán Collection 1857.6.4.82/1, length = 8 mm (external view through glass slide). **4.** Lectotype of *Sphenia pacificensis*, BM(NH) 196460/1, length = 5.8 mm.



(USNM 861964) and Sanibel Island (SBMNH 144631), Florida, and South Padre Island, Texas (Abbott, 1974), to Santa Catarina State, Brazil (approx. 28°S) (Rios, 1994), and south to Bahía Mandonado, Maldonado Department, Uruguay (34.9°S) (type locality of *Corbula iheringiana*; SBMNH 145228). I have seen 138 eastern Pacific lots and about 30 western Atlantic lots.

Discussion: *Tyleria fragilis* was proposed as a new genus and species by H. Adams and A. Adams in 1854 for a “curious little shell” found nestling in a sand-filled cavity in a *Spondylus* valve. Figured by these authors two years later, it was characterized as having a chondrophore and a short pallial sinus like a *Sphenia*, but it was also said to have a partly external ligament and the anterior end was said to have a ridge below the dorsal margin supported by a series of calcareous septa dorsal to it (figure 2a).

When Carpenter (1857b: 24) first discussed *Tyleria fragilis* (in a portion of the Mazatlán Catalogue typeset in 1855), and having seen only a drawing of it, he said, “I have occasionally noticed valves of *Sphenia* with a tendency towards the same crenation at the posterior end, apparently through the irritation of sand.” (He evidently confused or misstated which end had the “crenation.”) Later, in a portion of his book typeset in 1857 (p. 547), he said that he had seen the actual specimen and concluded that it was unique, not a *Sphenia*; in the same work he described *Sphenia fragilis* as a new species, thus selecting the same species name.

When Myra Keen examined the holotype of *Tyleria fragilis* in The Natural History Museum in London she concluded that it really was a pathological specimen of *Sphenia* in which the shell material was “either not deposited or was resorbed” along the dorsal margin, leaving “a few islands of solid calcium carbonate embedded in what is mostly periostracum” (Keen, 1968). (Periostracum bridging the two valves probably accounts for the Adams’ observation of an external ligament.)

The holotype of *Tyleria fragilis* remains a puzzle. I have been able to examine only photographs of the specimen, which is now too fragile to travel. The specimen was badly eroded from the start and has since been much broken; the outer periostracal layer is now mostly gone. The “calcareous septa” seen by the Adams’ and the “islands of solid calcium carbonate” observed by Keen now appear with loss of the periostracum to resemble short radial ribs (figure 2b). No other specimens of *Sphenia* have been seen like this, and it may have been caused by the animal’s nestling site. On the other

hand, the shallow pallial sinus defined by a series of discontinuous scars comports with *Sphenia*. The chondrophore and resilifer also fit this genus; while both seem distorted, such distortion is not unusual. A greater comfort level with the identity of the specimen could be achieved by close examination of the chondrophore, because that of myids has unique features. While I have not seen other specimens of *Sphenia* with its singular morphology, no other known nestling clam better explains the specimen, and it is best to leave the synonymy of the two species named *fragilis* as it is.

The type specimen of *Sphenia antillensis* is small, flat, and now chipped (figure 5). All other western Atlantic material I have examined, including the 23 lots available in the USNM, specimens in museums on the west coast, and a set of the material studied by Narchi and Domaneschi (1993) [SBMNH 145246], is indistinguishable from eastern Pacific specimens of *Sphenia fragilis* in all features here found to be useful here in distinguishing species *Sphenia*—shell shape and thickness, maximum size, chondrophore orientation and morphology, pallial sinus details, and positions of the adductor muscle scars, as well as in reported habitat.

The nomenclatural situation is further complicated by the fact that *Sphenia antillensis* is not even the earliest name available in the western Atlantic. The first name proposed for a Recent western Atlantic *Sphenia* is *Corbula iheringiana* based on material from Uruguay, with a lectotype figured here with a photograph for the first time (figure 24).

Because of the fact that western Atlantic material cannot be distinguished from eastern Pacific material by any criteria found useful at the species level in this genus, it is inescapable to use the first name proposed until such time as significant differences are discovered.

Given its shallow habitat and presence in fouling communities, it is not impossible that *Sphenia fragilis* has been transported by ship traffic during the last 300 years either to the east or the west. As evidence that such transport can occur in this genus is the recent discovery of a few specimens of *Sphenia* in Pearl Harbor, Oahu, Hawaii (SBMNH 144633). This material has been tentatively identified as the western Pacific *Sphenia coreanica* Habe, 1951:76, based on its heavier commarginal sculpture and pallial sinus positioned further from the posterior end. (Habe’s original material was small and oval, and had not grown the elongate posterior end typical of larger specimens.) However, the relationships of this material and of western Pacific *Sphenia coreanica*

Figures 5–7. *Sphenia fragilis* (H. Adams and A. Adams). **5.** Holotype of *Sphenia antillensis*; USNM 160495; length, 4.0 mm. **6.** Lectotype of *Sphenia trunculus*, USNM 160116, length = 6.9 mm. **7.** SBMNH 144630, Puerto Peñasco, Sonora, Mexico, length = 9.1 mm.

Figures 8–10. *Sphenia gulfensis* new species. **8.** Holotype, left valve, SBMNH 144627, length = 11.7 mm. **9.** Paratype, right valve, SBMNH 144628, length, = 0.6 mm. **10.** Lot showing variability in shape, SBMNH 144345, Puertecitos, Baja California (Norte), 18 m.

to the eastern Pacific *S. fragilis* merits additional study, ideally augmented with information from biochemical genetics.

Sphenia gulfensis new species
(Figures 1a, 8–10, 19, 20)

Description: Shell thin, elongate; anterior end produced, broadly rounded, tapering in thickness gradually from anterior to posterior end; right valve more inflated, generally extending well beyond posteroventral margin of left valve; posterior end often very elongate, tapered vertically, broadly truncate, sometimes flared, narrower in left valve, not extended by periostracum, slightly gaping. External surface with fine commarginal ribs. Periostracum thin, very light tan, adherent. Left valve with narrow chondrophore, projecting horizontally toward right valve, even in large specimens; posterior buttress elongate in large specimens; posterior ridge not extending beyond ventral margin of chondrophore. Right valve with resilifer more deeply recessed than that of *S. fragilis*, and with more conspicuous anterior cardinal tooth. Anterior adductor scar at middle of anterior end. Posterior adductor scar and pallial sinus well recessed from posterior margin. Pallial sinus a series of 3–4 narrow scars; pallial line a discontinuous series of small, rounded scars (figures 19, 20). An additional lot is illustrated to show the variability in shape of this species (Figure 10). Length to 13.1 mm (SBMNH 144345; Puertecitos, Baja California [Norte], Golfo de California).

Type material: SBMNH 144627, holotype, left valve; length, 11.7 mm; height, 6.6 mm; thickness, 2.2 mm (Figure 7, 19); SBMNH 144628, figured paratype, right valve; length, 10.6 mm; height 5.9 mm; thickness, 1.9 mm (figures 8, 20); SBMNH 144629, four additional paratypes, of lengths 12.8 mm (right valve), 12.0 mm (left valve), 11.1 mm (right valve), 11.0 mm (left valve), all from type locality, Peter and Sally Bennett, March 1976.

Type locality: San Felipe, Baja California (Norte), Gulf of California, Mexico (31.0°N, 114.8°W), 15–22 m, mud bottom.

Distribution: Puerto Escondido, Baja California Sur (25.8°N) (CAS 112929), northward to the head of the Gulf of California at Bahía Cholla, Puerto Peñasco, Sonora (31.4°N) (SBMNH 115752, UCMP E8398, Skoglund Coll.), south to Mazatlán, Sinaloa (23.2°N) (UCMP E9704), Mexico, from the intertidal zone to 61 m (mean = 15 m; n = 13), on soft bottoms. I have examined 31 lots.

Discussion: This species has sometimes been separated in collections as differing from *S. fragilis*. Stillman

Berry recognized it in material he had collected at Puerto Peñasco, Sonora, in 1949 and 1952 (SBMNH 115752), and I isolated it aside in material I had collected at San Felipe, Baja California (Norte), in 1963 (UCMP E9705).

This new species differs from *S. fragilis* as follows: (1) the anterior end of *S. gulfensis* is longer and proportionately less inflated; (2) overall, it is more elongate; (3) while varying somewhat in shape, not as much as *S. fragilis* and never as irregular, suggesting a non-nestling habitat, (4) the right valve overlaps the left valve more extensively postero-ventrally; (5) the chondrophore in the left valve, while varying somewhat in shape, is normally smaller and projects more horizontally, and has a longer posterior buttress; the resilifer in the right valve is consequently more deeply recessed; (6) the cardinal tooth in the right valve is more conspicuous; (7) the posterior end is sometimes flared and is not extended by periostracum; and (8) the posterior adductor and the pallial sinus are positioned further from the posterior end.

In the Golfo de California, where their distributions overlap, specimens of *S. fragilis* and *S. gulfensis* smaller than 2 mm are difficult to differentiate. In such material, *S. fragilis* is most easily distinguished by its more rounded outline, more inflated posterior end, its more posteriorly positioned pallial sinus, and its proportionately larger chondrophore.

This new species differs from *S. sincera* Hanks and Packer, 1985, which inhabits soft bottoms in 30 to 63 m in northern New England, in being longer and more tapered posteriorly, having a narrower, less projecting chondrophore, having a thinner, almost transparent periostracum, and in attaining a larger size.

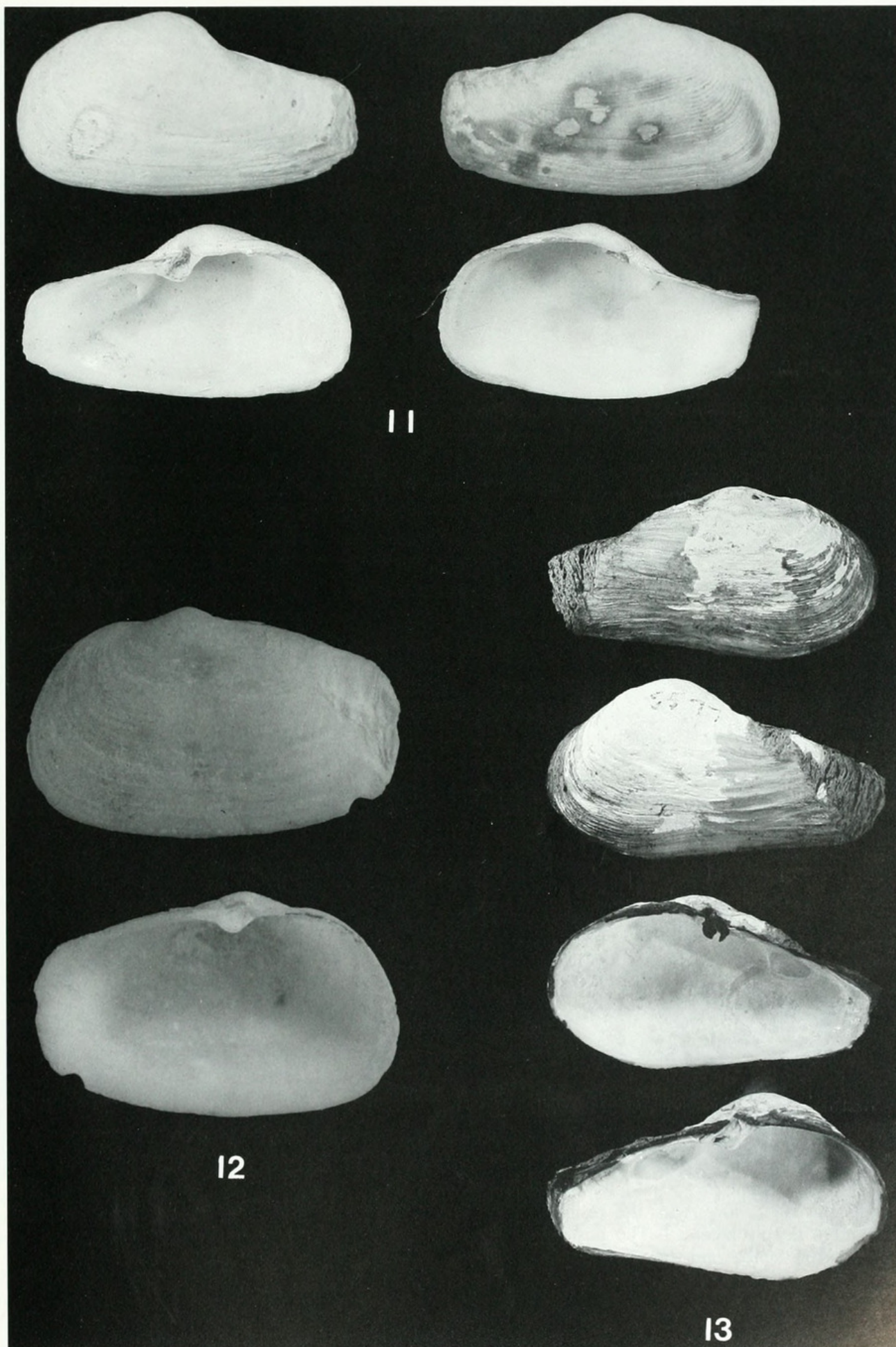
Etymology: The name *gulfensis* refers to the fact that the known distribution of this new species is chiefly restricted to the Gulf of California.

Sphenia hatcheri Pilsbry, 1899
(Figures 11–13, 21)

Sphenia hatcheri Pilsbry, 1899: 128, pl. 1, fig. 5, 6; Lamy, 1927: 181; Carcelles, 1950: 82, pl. 5, fig. 94; Carcelles and Williamson, 1951: 347; Castellanos, 1965: 173–175, pl. 1, figs. 1–8; Figueiras and Sicardi, 1970b: 22, pl. 7, fig. 103; Castellanos, 1970: 278–279, 348, pl. 25, figs. 9–11 [349]; Bernard, 1983: 58.

Sphenia subequalis Dall, 1908: 422–423; Lamy, 1927: 181–182; Carcelles, 1950: 82; Castellanos, 1965: 174 [as a synonym of *S. hatcheri*]; Bernard, 1983: 58 [as a synonym of *S. hatcheri*].

Description: Shell of moderate thickness, elongate; subequivalve; anterior end produced, rounded, width tapering gradually towards posterior end; posterior end



elongate, tapering, truncate posteriorly, extended by periostracum, scarcely gaping. External surface with fine to moderate commarginal ribs. Periostracum of moderate thickness, thicker on posterior slope, light tan, eroded in large specimens. Left valve with a large chondrophore, projecting as much ventrally as horizontally; anterior buttress wide; posterior buttress short; posterior ridge extending a little beyond ventral margin of chondrophore. Right valve with resilifer not very deeply recessed, with a conspicuous anterior cardinal tooth. Anterior adductor placed antero-ventrally. Posterior adductor and pallial sinus recessed from posterior margin. Pallial sinus of one broad and several smaller scars; pallial line a discontinuous series of small scars (Figure 21). Length to 30.1 mm (SBMNH 144635; Isla Chiloé, Chile).

Type material and localities:

- S. hatcheri*—ANSP 18083, holotype, pair; length, 17.2 mm; height, 9.2 mm; thickness, 7.3 mm (Figure 11). "Cape Fairweather" (Cabo Buen Tiempo), Santa Cruz Province, Argentina (51.5°S).
- S. subequalis*—USNM 110719, holotype, left valve; length, 6.9 mm; height, 4.3 mm; thickness, 1.3 mm (Figure 12). Segunda Angostura, eastern end of Estrecho de Magallanes, Magallanes Province, Chile (52.6°S, 70.2°W); *Albatross* stn. 2779; 20 fms. [37 m], on gravel.

Distribution: La Paloma, Rocha Department, Uruguay (34.6°S) (Figueiras and Sicardi, 1970b); Mar del Plata, Buenos Aires Province (38.0°S) (Castellanos, 1970: 279; MACN 10757, not seen); Puerto Madryn, Golfo Nuevo, Chubut Province (42.8°S) (ANSP 170466), and Cabo Domingo, Tierra del Fuego Province (53.7°S) (ANSP 236074), Argentina, in the Estrecho de Magallanes, at 52.6°S (USNM 110719), and north in the eastern Pacific to Isla Chiloé, Chiloé Province, Chile (approx. 43°S) (Figure 13) (SBMNH 144635). The only depth record available is that with the type specimen of *S. subequalis*, 37 m. The material that has been illustrated and that I have studied is of similar shape, suggesting that the species occurs in relatively soft substrata. Records from north of the Golfo Nuevo—the Uruguayan and Mar del Plata specimens cited above—probably represent sporadic larval settlement. Only a single eastern Pacific lot has thus far come to my attention, and I have been unable to discover what material Bernard (1983) relied upon for his eastern Pacific record of this species.

Discussion: The largest species of the genus, *S. hatcheri* is most similar to *S. luticola*. The former differs in having a thinner, more regular shell with a broader posterior end. The chondrophore in the left valve projects more toward the right valve, with the resilifer in the right valve more deeply recessed. The posterior ridge does not extend as far beyond the ventral edge of the chondrophore.

Sphenia luticola (Valenciennes, 1846)
(Figures 1b, 14–17, 22)

Corbula luticola Valenciennes, 1846: pl. 24, fig. 6, 6a; Carpenter, 1864: 543 (as *Sphenia*, and as a possible senior synonym of *S. fragilis*); E. A. Smith, 1893: 279; Lamy, 1927: 179–180 (as *Sphenia* and as senior synonym of *S. fragilis*, but under the latter heading); Hertlein and Grant, 1972: 321–322, pl. 56, figs. 21, 22 (as "cf. *luticola*"); Bernard, 1983: 58.

Sphenia pholadidea Dall, 1916a: 41, *nomen nudum*; 1916b: 415; Oldroyd, 1925: 201; Lamy, 1927: 181; Bernard, 1983: 58 (as a synonym of *S. luticola*)

Cuspidaria (Tropidomya) nana Oldroyd, 1918: 28; Oldroyd, 1924: 99, pl. 13, figs. 8, 9; J. T. Smith, 1978: 350; Bernard, 1983: 58 (as a synonym of *S. luticola*); Coan and Kellogg, 1990: 178.

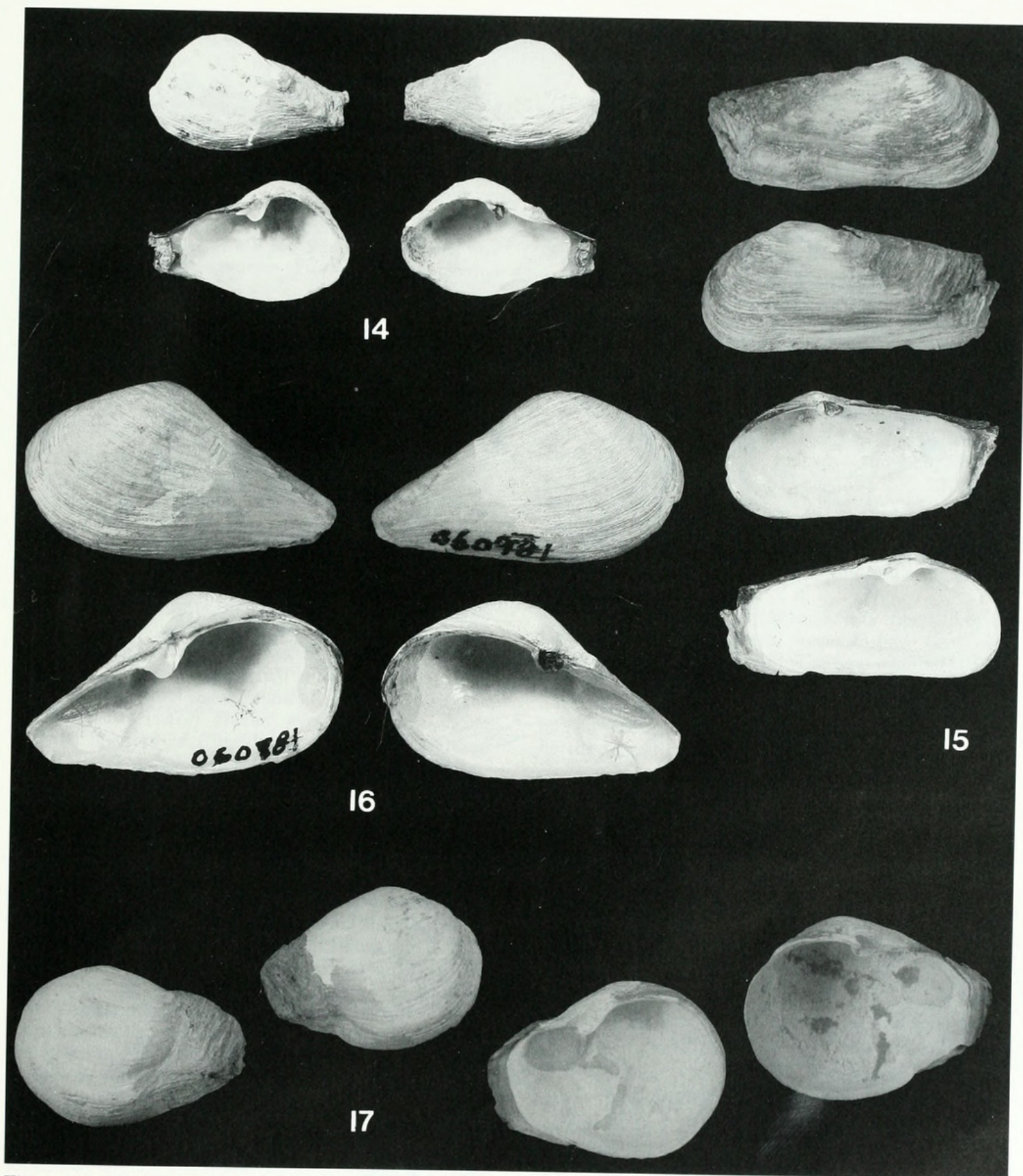
Sphenia globula Dall, 1919: 370–371; Oldroyd, 1925: 201; Lamy, 1927: 181; Schenck and Keen, 1940: 391, pl. 2, figs. 4–7; Schenck, 1945: 517, 519, pl. 67, figs. 5–8; Woodring and Bramlette, 1951: 66, 91; J. T. Smith, 1978: 340; Bernard, 1983: 58 (as a synonym of *S. luticola*).

Description: Shell relatively thick, highly variable in shape, from oval to elongate; right valve slightly more inflated than left; anterior end short, broadly rounded; tapering in thickness evenly from anterior to posterior ends; posterior end from short to somewhat produced, and from truncate to somewhat pointed, sometimes twisted in various directions depending on crevice or hole inhabited, generally extended by outer shell layer and periostracum, scarcely gaping. External surface with fine commarginal ribs; periostracum light to dark tan, frequently eroded in large specimens. Left valve with large, heavy chondrophore, projecting more ventrally than toward right valve; posterior and anterior buttresses of chondrophore short, thick; posterior ridge often projecting well beyond ventral margin of chondrophore. Right valve with large, heavy, rounded resilifer under beaks, not deeply recessed, and sometimes with slightly projecting anterior cardinal tooth. Anterior adductor scar large, positioned ventrally. Posterior adductor scar and pallial sinus near posterior end. Pallial sinus of two relatively broad, elongate scars, and generally also with one or two smaller scars; pallial line a series of small, discontinuous scars (figure 22). Length to 20.6 mm (paratype of *C. nana*).

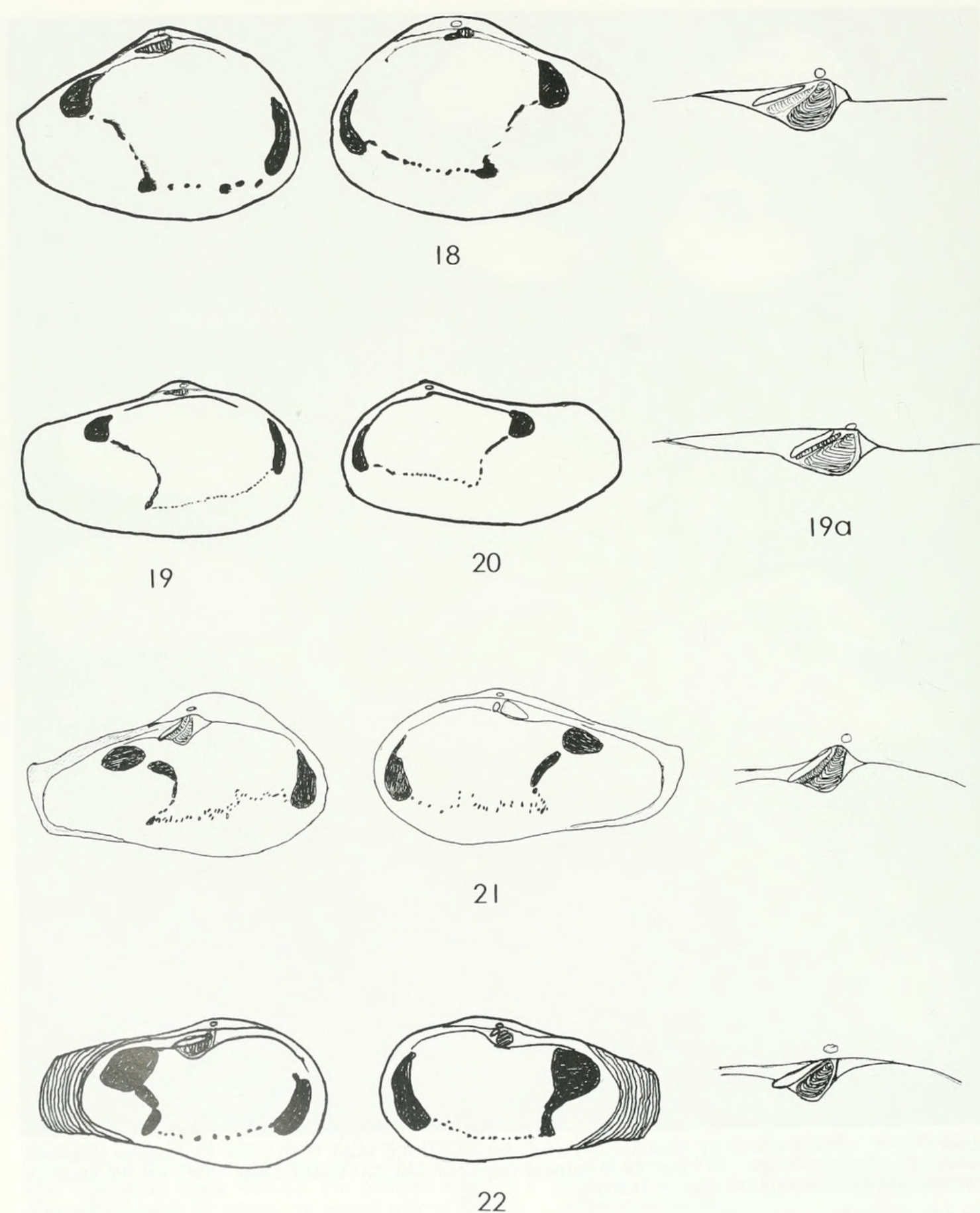
Type material and localities:

C. luticola—MNHN, lectotype herein designated, the larger of two pairs, likely that figured by Valenciennes (1846: pl. 24, fig. 6a) as an opened specimen; length, 10.7 mm; height, 6.3 mm; thickness, 6.0 mm (figure 14). Paralectotype, pair, perhaps that figured by Valenciennes (1846: pl. 24, fig. 6) as a closed pair in situ in a rock crevice; length, 9.3 mm. Locality not given in original account. The label says "Californie," to which someone has added "Mazatlán." The latter is undoubtedly incorrect, and the locality is here restricted to Monterey Bay, Monterey County, California (36.7°N), from where other of Valenciennes' material of bivalves boring or nestling in dredged rocks seems to have come.

S. pholadidea—USNM 2581, holotype, pair; length, 13.1 mm; height, 6.0 mm; thickness, 5.1 mm (Figure 15). Santa Barbara, Santa Barbara County, California (34.4°N); William Rich.



Figures 14–17. *Sphenia luticola*. **14.** Lectotype of *Corbula luticola*, MNHN, length = 10.7 mm. **15.** Holotype of *Sphenia pholadidea*, USNM 2581, length = 13.1 mm. **16.** Holotype of *Cuspidaria nana*, CAS 060981, length = 19.4 mm. **17.** Lectotype of *Sphenia globula*, USNM 218977, length = 12.8 mm.



Figures 18–22. Comparative pallial lines, muscle scars and hinges. **18.** *Sphenia fragilis*, SBMNH 144630, Puerto Peñasco, Sonora, Mexico, length = 9.1 mm. **19, 20.** *Sphenia gulfensis* new species. **19.** Holotype, SBMNH 144627, left valve, length, 11.8 mm. **20.** Paratype, SBMNH 144628, right valve, length = 10.6 mm. **21.** *Sphenia hatcheri*, SBMNH 144635, Isla Chiloé, Chile, length = 30.1 mm. **22.** *Sphenia luticola*, LACM 60–22, Monterey, California, 18 m, length = 14.1 mm.

C. nana—CAS 060981, holotype, pair; length, 19.4 mm; height, 11.1 mm; thickness, 10.1 mm (Figure 16). AMNH 58306, paratype, 20.6 mm. Monterey Bay, Monterey County, California (36.7°N).

S. globula—USNM 218977, lectotype herein designated, open pair; length, 12.8 mm; height, 8.7 mm; thickness, 8.4 mm, the only specimen cited in the original account (Figure 17). CAS 064102, open pair, paralectotype; length, 14.5 mm. CAS 085834, closed pair, paralectotype; length, 9.7 mm. Bolinas Bay, Marin County, California (37.9°N); Henry Hemphill. The last specimen was figured by Schenck and Keen (1940) and Schenck (1945) and may also be the Bolinas specimen of *Cuspidaria nana* referred to by Oldroyd (1918).

Distribution: West of Destruction Island, Jefferson County, Washington (47.7°N) (SBMNH 140087), south to San Diego, San Diego County, California (32.8°N) (USNM 322064, 322065), from 15 to 155 m (mean, 50 m; $n = 15$), nestling in holes in rock and shell. I have seen 34 Recent lots. This species has also been recorded in the Pliocene Foxen Mudstone of Santa Barbara County (Woodring and Bramlette, 1951: 66, 91, as *S. globula*) and San Diego Formation of San Diego County (Hertlein and Grant, 1972: 321–322, pl. 56, figs. 21, 22, as “cf. *luticola*”), California.

Discussion: The type specimens of this species and its synonyms demonstrate the potential of species of *Sphenia* to assume a variety of shapes. Nestling in pre-established cavities in subtidal rocks, the shell conforms to the shape of the available space in the same manner as the European Miocene *S. anatina* discussed by Baluk and Radwański (1979). The lectotype of *Corbula luticola* and the holotype of *Cuspidaria nana* are inflated and acuminate. The holotype of *Sphenia pholadidea* is flattened and truncate posteriorly, and the lectotype of *S. globula* is oval and inflated.

A small specimen (CAS 111000; Monterey, California; length, 5.8 mm) is regular in outline and only somewhat longer posteriorly. It is similar to juvenile *Mya*, but is easily distinguished by its shallow pallial sinus composed of broad pallial scars, as well as by features of its chondrophore, such as those outlined by Hanks and Packer (1985: 324) for their new species of *Sphenia*. In this small Monterey specimen, the chondrophore projects more horizontally and the resilifer in the left valve is more deeply recessed than those of large specimens, demonstrating the morphological change with growth.

Sphenia luticola and *S. fragilis* overlap in southern California. The former can be distinguished by its thicker shell, more ventrally directed chondrophore, with a larger, often projecting posterior ridge, and a pallial line formed by larger scars. It also occurs offshore and attains a larger size.

Of the eastern Pacific taxa, *S. luticola* is the most similar to the type species of the genus, *S. binghami*, which has a more regularly quadrate shape, with a broadly truncate posterior end, and its chondrophore is thinner, more horizontal, and does not have a projecting posterior ridge (USNM 171240 [lectotype], 171245, 337253).

Its pallial sinus is composed of narrower scars, and attains only about 10 mm.

OTHER TAXA

Several fossil taxa of *Sphenia* have been named in North and Central America. While it is beyond the scope of the present paper to analyze their relationships, I list them here to facilitate access to this literature.

Sphenia senterfeiti Gardner (1936: 45, pl. 8, figs. 2–4), described from the Miocene Oak Grove Formation of the Alum Bluff Group of Florida, has an oblique outline, a broadly flared posterior end, and a relatively small, horizontal chondrophore [USNM 372905]. *Sphenia dubia* (Lea, 1843: 2) [originally as *Mya dubia*] from the Pliocene Yorktown Formation of Virginia is relatively thick shelled, variable in shape, but generally short and oval, and it has an especially large chondrophore in the left valve and resilifer in the right; *Mya reflexa* Lea (1843: 2) is regarded as a synonym (Campbell, 1993: 47, 213, fig. 187, 187a) [see also Lea, 1845: 236–237, pl. 34, figs. 9, 10] [ANSP 1588, USNM 403361, SBMNH 144632]. *Sphenia attenuata* Dall (1898: 860, pl. 35, fig. 9) [USNM 107806], from the Plio-Pleistocene Caloosahatchee Formation of Florida, is very similar to *S. dubia* and is perhaps a synonym of it.

Sphenia wallacei Dall (1912: 3), described from the late Pleistocene of Panama, seems to have been overlooked since it was proposed. The type material [USNM 214354] consists of a large right valve (length, 10.3 mm), a medium-sized left valve (length, 9.1 mm), and a small left valve (length, 3.7 mm). The right valve, which would be the logical candidate for an eventual lectotype designation, is oval and inflated and seems to be same thing as the later-named *S. tumida* Lewis (1968: 26–30, pl. 1, figs. 1–4) [USNM 645663–645667] from the Pleistocene of Florida. The larger left valve in the type lot of *S. wallacei* is elongate and may be *S. fragilis*; the other left valve is too small to identify. *Sphenia tumida* was reported from a Texas beach, although it was thought to have possibly been a fossil (Odé and Speers, 1971: 71; Odé, 1971: 74–75). However, *Sphenia tumida* has been reported and figured as living on the coast of Yucatan, Mexico (Vokes and Vokes, 1983: 44, pl. 48, fig. 16). Thus, there may be a second living species of *Sphenia* in the western Atlantic, which should be called *S. wallacei*.

EXCLUDED TAXA

Sphenia bilirata Gabb (1861: 369) was described from Santa Barbara, California, presumably from the Tertiary, as is implied by the paper's title (“Descriptions of new species of American Tertiary Fossils and a new Carboniferous Cephalopod from Texas”). *Sphenia bilirata* was not figured, and the type material has never been located. There must have been more than one original specimen, because the diameter was said to be “variable.” As has been noted by previous workers (Carpenter, 1864: 632 [1872: 118]; Lamy, 1927: 177), the description close-

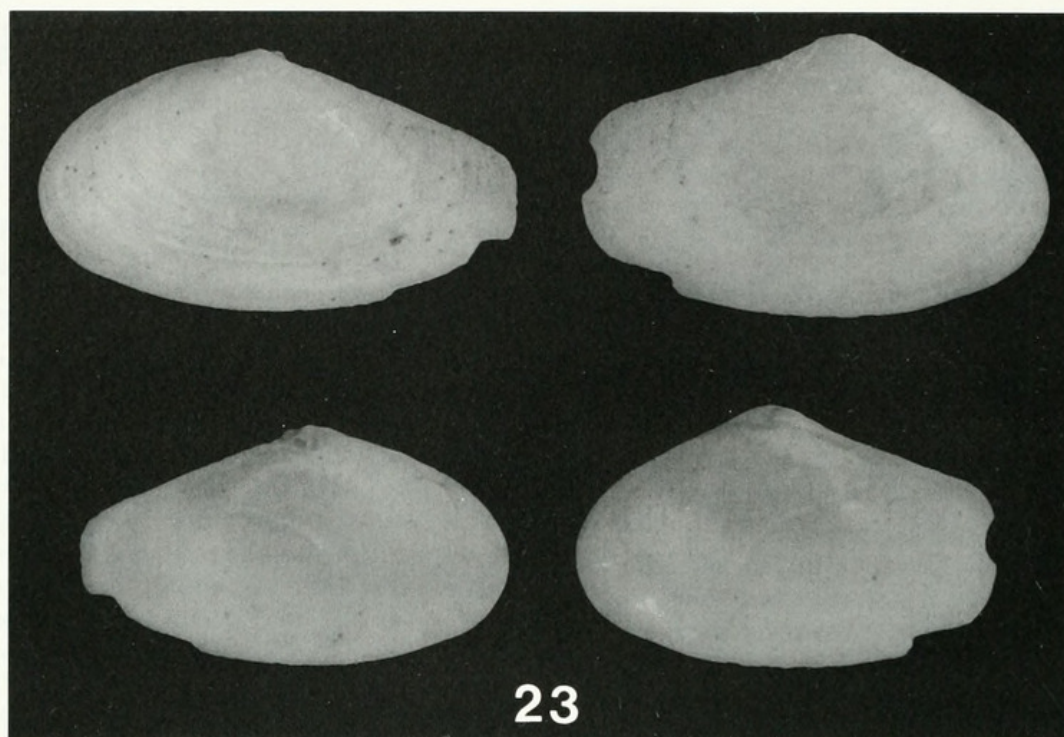


Figure 23. *Mya ?arenaria* Linnaeus, 1758. Holotype of *Sphenia ovoidea*, USNM 4552, length, 7.5 mm.

ly matches small *Hiatella arctica* (Linnaeus, 1758). However, *Hiatella* has not been recorded from the Santa Barbara Formation (Arnold, 1907: 32; Dibblee, 1966: 58), the outcrop of which at Bathhouse Beach is the most likely locality for the rest of the Santa Barbara taxa described in Gabb's paper⁴. Additional study of the Santa Barbara Formation is needed, because its fauna remains poorly documented. It is more likely that *S. bilirata* came from the Recent fauna, because, while it is recorded by Gabb simply as "Santa Barbara Cal.," each of the other Santa Barbara fossil taxa also adds "Miocene" or "Miocene?" (The Santa Barbara Formation is now regarded as being of early Pleistocene age.)

Sphenia californica Conrad (1837: 234, pl. 17, fig. 11) is the original combination for *Cryptomya californica* (Conrad, 1837) (Keen, 1966: 171).

Sphenia? meganosensis Clark and Woodford (1927: 106, 134, pl. 18, figs. 15, 16), from the lower middle Eocene Meganos Formation of central California, is based on two closed specimens [UCMP 31326, 31327]

said to resemble material of *Sphenia* from the Eocene of the Paris Basin. No additional specimens of this species have been recorded, nor has the genus been reported in any other strata earlier than the Pliocene in western North America. Until more material becomes available and a hinge exposed, one cannot be certain that this material represents *Sphenia*.

Sphenia ovoidea Carpenter (1864: 602, 637 [1872: 88, 123], 1865: 54) was described from a single specimen, paired valves obtained in Puget Sound from a fish stomach in the 1860s. (*Sphenia ovalis* Carpenter, 1864: 682 [1872: 168], is a typographical error for *ovoidea* in the same work.) Although previous workers have listed it as a *Sphenia*, examination of the holotype [USNM 4552; length, 7.5 mm; height, 4.5 mm; thickness, 2.8 mm] (Figure 23)⁵, which was well figured by Palmer (1958: 116, 340, pl. 15, figs. 7–10), confirms Carpenter's "mantle bend large" (i.e., a large pallial sinus), demonstrating that it is a juvenile *Mya*, not a *Sphenia*. Juvenile *Mya* are most easily distinguished from *Sphenia* by their larger, continuous pallial sinuses. This specimen appears to be *Mya arenaria* Linnaeus (1758: 670); it presents a quandary because this species, having become extinct in the Pacific Northwest by the Pleistocene (Carlton, 1979: 518–543, 1992: 495), was first recorded in the 1880s, when it became reestablished through introduction from Atlantic populations with imports of *Crassostrea virginica* (Gmelin, 1791). The only *Mya* thought to have been present in the 1860s is *Mya truncata* Linnaeus (1758:

⁴ Another Santa Barbara bivalve described in Gabb's paper, *Cardita monilicosta* (p. 371), has been subsequently recorded from this formation. A third Santa Barbara bivalve, *Venus rhyssomia* (pp. 369–370), which has been regarded as a synonym of *Nutricula tantilla* (Gould, 1853:406) (Carpenter, 1864:632; S. Gray, 1982:108–109, as *Transennella*; generic allocation: Coan and Scott, 1997:14, 25), has not been recorded from the Santa Barbara Formation, but *N. barbarensis* (Arnold, 1907: 440–441, pl. 58, fig. 3, as *Psephidia*) is so recorded, and I thus suspect that *V. rhyssomia* is a senior synonym of Arnold's taxon instead. The two gastropods described from the same station have subsequently been recorded there, both now regarded as junior synonyms of other taxa.

⁵ A broken valve in a separate capsule with the holotype is an unrelated species, most likely a lyonsiid, mixed into the lot between the time of Carpenter and that of Palmer.

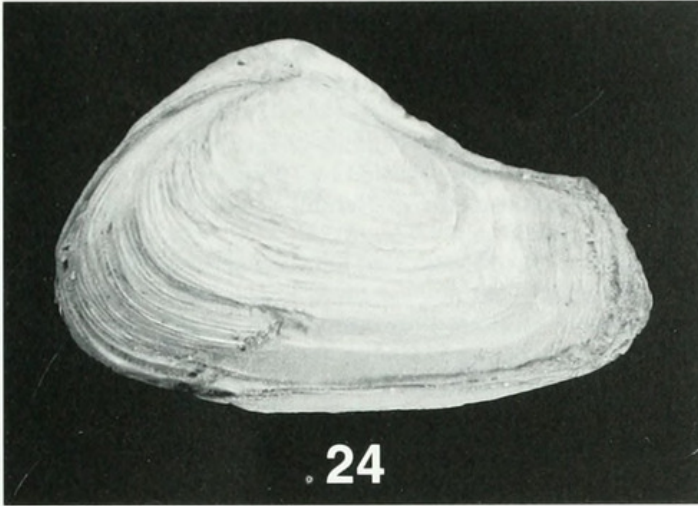


Figure 24. *Sphenia fragilis*. Lectotype of *Corbula iheringiana* Pilsbry, 1897; ANSP 70541, length, 9.0 mm.

670)⁶, but small specimens of that species are very different from those of *arenaria*. It is possible that: (1) the specimen might not actually have come from Puget Sound, although all the other material collected there by C. B. R. Kennerley of the Northwest Boundary Survey has proven to be authentic; or that (2) *Mya arenaria* was actually present in Puget Sound 20 years earlier than previously thought as a result of introduction with oysters or ship fouling (J. T. Carlton, e-mail, 19 November 1997).

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University of California, Berkeley. Carol C. Skoglund generously made available material from her collection, as did the late Elsie Marshall. David B. Packer of the National Marine Fisheries Service, Highlands, New Jersey, provided specimens of *Sphenia sincera*, and Lyle Campbell, of Spartanburg, South Carolina, provided specimens of the Pliocene *Sphenia dubia* and the Recent *S. antillensis*. Osmar Domaneschi of the Universidade de São Paulo provided Brazilian specimens of *S. antillensis*. I obtained advice from Roland Anderson, Seattle Aquarium; James T. Carlton, Williams College, Mystic, Connecticut; Nora Foster, University of Alaska; Akihiko Matsukuma, Kyushu University, Fukuoka, Japan; Fabrizio Scarabino, Museo Nacional de Historia Natural, Montevideo, Uruguay; and Richard L. Squires, California State University, Northridge. Lyle Campbell, Osmar Domaneschi, Lindsey T. Groves, Paula M. Mikkelsen, Walter Narchi, David B. Packer, Paul Valentich Scott, and Carol C. Skoglund provided useful comments on the manuscript. Sharon Williams helped to prepare the plates.

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⁶ The second species of *Sphenia* described by Turton (1822) along with the genus and *S. binghami*, its type species, was *S. swainsoni* (pp. 37–38, pl. 2, fig. 3, pl. 19, fig. 2). It was regarded as having been based on a juvenile *Mya truncata* by MacNeil (1965:38).

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