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REVISION OF *SYNCYCLONEMA* (UPPER CRETACEOUS)  
AND COMPARISON WITH OTHER SMALL  
PECTINID BIVALVES AND *ENTOLIUM*

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## ABSTRACT

New descriptions and figures are given for *Pecten rigida* Hall & Meek (= *Pecten halli* Gabb), the type species of *Syncyclonema* Meek, and for the type species of genera to which *Syncyclonema* is often compared: *Entolium* Meek, *Eburneopecten* Conrad, *Pectinella* Verrill, *Hyalopecten* Verrill, *Camptonectes* Agassiz, *Micronectes* Ichikawa & Maeda, *Pseudamussium* Mörch, and "*Pseudamussium*" H. & A. Adams. *Syncyclonema* is shown to be a valid genus. A lectotype is designated for *Syncyclonema halli*, and on the basis of its chlamyiid shape, deep byssal notch, and hinge morphology *Syncyclonema* is placed in the family Pectinidae. These characters invalidate synonymy of *Syncyclonema* with *Entolium* and its assignment to the family Entoliidae Korobkov.

## INTRODUCTION

Hall & Meek's (1856, p. 381, pl. 1, figs. 4a-c) original description of *Pecten rigida*, the type species of *Syncyclonema* Meek (1864a), was brief and the accompanying figures rather indefinite. Consequently, the systematic position of *Syncyclonema* and its relationships to other genera have been confused and controversial. Staesche (1925, p. 90) considered *Syncyclonema* a distinct genus and a smooth chlamyiid with a very weak byssal notch. Verrill (1897, p. 62) hesitantly accepted *Syncyclonema* as a valid genus and compared it to his recent genus *Hyalopecten*. *Syncyclonema* was classed as a subgenus of *Pecten* by Woods (1902, p. 145), who also thought it was probably synonymous with *Entolium* (Meek, 1865, p. 478; type species by original designation, *Pecten demissus* Phillips, Middle Jurassic). Stephenson (1941, p. 133) considered it of uncertain generic status, but included it as a subgenus of *Pecten*. Arkell (1930, p. 91) made *Syncyclonema* synonymous with *Entolium* to which he gave priority. Stewart (1930, p. 120) and Feldtmann (1951, p. 10), who followed the same procedure, more correctly gave *Syncyclonema* priority. In contrast Hayami (1965) concluded that *Syncyclonema* is distinct from *Entolium*. Both Dall (1898, p. 752) and Cox (1952, p. 35) thought the genus too poorly known to be certain of its status. Because of the inadequacy of Hall & Meek's (1856) original description of *Pecten rigida* for detailed systematic comparisons the conclusions of Dall and Cox are the most correct.

So much difference of opinion indicates the need for a redescription and discussion of the morphological features of *P. rigida*. The new data provides a base for considering the relationships between *Syncyclonema* and other similar small pectinid genera with which it has often been compared.

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Specimens mentioned and figured in this paper are held at the following institutions:

Academy of Natural Sciences, Philadelphia (ANSP)  
American Museum of Natural History (AMNH)  
British Museum of Natural History (BMNH)  
Museum of Comparative Zoology, Harvard University (MCZ)  
Osaka City University (OCU)  
Peabody Museum of Natural History, Yale University (YPM)  
Texas Bureau of Economic Geology (BEG)  
U. S. National Museum (USNM)  
World Mollusca Collection, New Zealand Geological Survey (NZGS-WM)  
Yorkshire Museum



DISCUSSION OF THE STATUS OF *SYNCYCLONEMA*  
AND ITS TYPE SPECIES *PECTEN HALLI*

HISTORY OF THE TYPE SPECIES OF *SYNCYCLONEMA*

Meek (1864a, p. 31) proposed the genus *Syncyclonema*, with *Pecten rigida* Hall & Meek (1856, p. 381, pl. 1, figs. 4a-c; non *Pecten rigida* Sowerby, 1818, p. 5, pl. 205, fig. 8; = *Pecten halli* Gabb, 1861, p. 214), Upper Cretaceous, as the type species by original designation. Meek, on p. 31, used the spelling *Syncyclonema* in the heading to a short description and discussion of the genus as follows: "195 = *SYNCYCLONEMA*, Meek. Type *Pecten rigida*, Hall & Meek", but on an earlier page in a check list he (p. 7) used a second spelling, "195. *Syncyclonema rigida*, (Hall & Meek) Meek. Dak.". It is important to note that Meek used the spelling *Syncyclonema* in his generic description and designation. This spelling was used consistently by Meek in later publications and on labels accompanying collections he examined. Most other workers since Meek have preferred the spelling *Syncyclonema*. It is therefore concluded that the spelling *Sincyclonema* was probably a typological or editorial error, and under the terms of the first reviser, Article 24 of the "International Code of Zoological Nomenclature" (Stoll, *et al.*, 1961), *Syncyclonema* is designated as the valid spelling.

*Pecten rigida* was erected by Hall & Meek (1856, p. 381) for a small pectinid collected by F. V. Hayden from the upper Pierre Shale at Sage Creek, South Dakota. Gabb (1861) noted the preoccupation of the name *rigida* by *Pecten rigida* Sowerby (1818), a quite different species, and renamed Hall & Meek's species as *Pecten hallii* Gabb. Following the recommendation of the International Commission of Zoological Nomenclature (Stoll, *et al.*, 1961, p. 107) the ending *-i* rather than *-ii* is used here. Gabb's new name was ignored by Meek (1864a, p. 31) when he proposed the genus *Syncyclonema*, although he clearly knew that the name *rigida* was preoccupied and his species distinct from Sowerby's. Meek (1876) later redescribed *rigida* and gave a more complete diagnosis of the genus *Syncyclonema*, but placed Gabb's name *halli* in synonymy under his *rigida*. Since 1876 the only other work of importance discussing this species is that of Whitfield

(1880) who described and illustrated specimens of *S. halli* (USNM 12272) from the Cheyenne River, Black Hills.

Whitfield (1901, p. 424) reported that the American Museum of Natural History held "the Gen. and Sp. Type. *Syncyclonema* Meek rigidum . . . H. & M.", from Sage Creek, Wyoming (AMNH 5351/1). The full label accompanying this collection, now numbered as AMNH 9347, lists "*Syncyclonema rigida*, H & M sp. TYPE. Mem. A. Ac. Sci. & Arts, vol. 5, p. 381, pl. 1, fig. 4, Cretaceous No. 4, Fort Pierre Gp. Sage Creek, Nebraska (Wyoming)." Professor N. D. Newell kindly examined the collection and reported (written communication Oct. 17, 1966) that the specimens of *S. halli* "do not agree in detail with the original figures" of Hall & Meek. Comparison of photographs (pl. 1, figs. 1-3) of right and left valves most closely resembling Hall & Meek's drawings, here reproduced as figs. 6 and 7, pl. 1, support Professor Newell's conclusion. Hall & Meek's drawings were probably idealized by the artist, especially as the specimens are small. Gross similarities are evident, but differences in size, shape and ornament make it impossible to be sure that the specimens in AMNH 9347 are the originals from which the drawings were made.

Because Hall & Meek's original collections were dispersed I examined collections at the United States National Museum, Washington, and the Academy of Natural Sciences, Philadelphia, but found no specimens matching the original drawings. Collection USNM 347 is listed (Schuchert, 1905, p. 636) as containing "Cotypes" of *S. halli*. As this collection is from "The Cheyenne and Moreau Rivers, South Dakota", and not from Sage Creek, it cannot be the original collection of Hall & Meek. Consequently, the specimens of *S. halli* in this collection are not cotypes but probably include all or some of the specimens on which Meek (1876) based his redescription of the species and possibly his figures (1876, pl. 16, figs. 5a, b; but see below). Correspondence with Dr. Kilfoyle, New York State Museum, Albany, and Professor Popenoe, University of California, Los Angeles, established that these institutions do not hold collections likely to contain Hall & Meek's original specimens of *S. halli*.

Collection USNM 347 includes three specimens of *S. halli*; a left valve (347a), a partly buried valve with concentric sculpture (347b), and a partly buried interior showing fine radial striae (347c).

Specimen 347a is labeled as being the original of fig. 5b of the pl. 16 of Meek (1876) (pl. 3, fig. 4). But this specimen, and also the drawing, is a left valve and not a right valve as stated in Meek's caption. Judging from his descriptions Meek (1876, p. 27) probably mixed the captions of his figures 5a and 5b. In addition, correspondence of the specimen with fig. 5b is unlikely because the specimen retains most of the shell on the ventral half of the valve, and it lacks the fine radial striae and widely spaced concentric ornament shown on Meek's illustration of the steinkern (pl. 1, fig. 4). The differences are too great to be accounted for by artistic license, for even though Meek idealized many of his illustrations to varying degrees, he usually recorded gross morphological characteristics and imperfections. In many cases I have been able to identify positively Meek's specimens because of imperfections recorded on the drawings. Although USNM 347a is unlikely to be the original of fig. 5b, the original specimen should be located to prove positively this contention.

There is no trace of the original of Meek's (1876, pl. 16) fig. 5a in USNM 347, and this specimen also appears to have been lost.

Although it is not possible to be absolutely certain that the specimens represented by the original illustrations of Hall & Meek are conspecific with the specimens of *S. halli* in AMNH 9347 their gross similarity strongly suggests that they are conspecific (see pl. 1, figs. 1-3, 6, 7). Examination of Meek's (USNM 347) and Whitfield's (1880, USNM 12272, pl. 1, fig. 8) specimens shows they are conspecific with each other and also with the specimens in AMNH 9347 and collections made by Professor K. M. Waage and myself from the type area of the Fox Hills Formation. Meek's identification and labeling as *Pecten rigida* of specimens in USNM 347, which were collected from the "Cheyenne and Moreau Rivers", a locality lying within the type area of the Fox Hills Formation, gives additional support to my conclusion that Hall & Meek's species concept includes the specimens in the collections discussed above.

No holotype or lectotype has been designated for *S. halli*. In order to fix the concept of the species, and genus, it is necessary to select a lectotype. Although it can never be certain that AMNH 9347 is the original collection studied by Hall & Meek,

or that it contains the originals of their illustrations, all the evidence indicates that it most probably is the original collection. Consequently, the almost complete right valve (AMNH 9347/1.1; pl. 1, fig. 3) from this collection, 4 mm long and 5 mm high, showing nine shallow concentric plicae on the ventral half of the shell, and a distinct byssal notch, but with the anterior auricle incomplete, is here selected as the lectotype.

#### SYSTEMATICS OF *SYNCYCLONEMA* AND ITS TYPE SPECIES

##### GENUS *SYNCYCLONEMA*

AUTHOR. Meek, 1864a, p. 31, 7.

TYPE SPECIES. By original designation, *Pecten rigida* Hall & Meek (1856, p. 31, pl. 1, figs. 4a-c; non *Pecten rigida* Sowerby, 1818, p. 5, pl. 205, fig. 8; = *Pecten halli* Gabb, 1861, p. 214), Sage Creek, South Dakota, Pierre Shale, Upper Campanian-Maastrichtian.

EMENDED DIAGNOSIS OF *SYNCYCLONEMA*. The following diagnosis is based on study of the type species *halli* (see below):

Small, subequivalve, subequilateral. Shell of vitreous appearance, thin, of three layers: thin outer homogeneous or prismatic layer, middle layer of zigzag lamellar structure, and thin inner complex cross-lamellar layer. Ornament sub-macroscopic, except on ears, of fine non-punctate diverging radial striae, fine growth striae, and coarser irregular growth lamellae tending to give reticulate pattern. Radial striae strongest at ventral margin and on dorsal flanks of disc of shell, sometimes absent on center of disc. Concentric lamellae strong on ears. Interior of shell sometimes with low faint rounded concentric ridges and fine radial striae. Concentric undulations sometimes evident on external surface, particularly on the right valve.

Anterior auricle equal to or significantly larger than the posterior. Anterior auricle of the right valve distinctly separated from disc of shell, fasciole very narrow, and byssal sinus deep, open V-shaped. No ctenolium. Dorsal margin of right valve overlaps that of the left valve. Each auricle with one thin cardinal crus below the ligament band, that on the posterior auricle of each

valve extending usually only about two-thirds of the distance towards the posterior margin (pl. 3, figs. 1, 5). One relatively long strong tooth-like process on either side of the resilifer pit of the right valve (pl. 2, fig. 5; pl. 3, figs. 2, 5). No auricular crura. Adductor muscle impression small, subcircular, sited above two-thirds the height of shell adjacent to basal part of posterior auricle. Pallial line continuous.

DISCUSSION. Several morphological features of the type species, *S. halli*, require discussion before the status of *Syncyclonema* is fully clarified.

1. Byssal sinus. *Syncyclonema halli* has a deep byssal sinus on the right valve (pl. 2, figs. 1, 5). Careful examination of the internal and external surfaces of right valves provided no evidence of a ctenolium at any stage of growth. *S. halli* was probably a free swimming pectinid. Stewart (1930, p. 120) thought the small specimens of *S. halli* described by Hall & Meek (1856) and Meek (1876) might be juveniles of a species of *Entolium*, but growth lines show the presence of a relatively large byssal auricle at all stages of growth, and for this reason *S. halli* cannot be classed in *Entolium* (see below). The normal occurrence of specimens 10 to 13 mm long, but none larger than this, suggests that the largest specimens are adults of a small species.

2. Musculation. The adductor muscle impression is weakly impressed and was observed on only a few specimens. It is small, subcircular, sited postero-dorsally, with its base at or above two-thirds of the height of the shell adjacent to the basal part of the posterior ear (pl. 2, fig. 3; pl. 3, fig. 6). Whitfield (1880, pl. 7, fig. 1) illustrated the adductor scar which, as he noted, occurs in an unusual position. Examination of his specimen (USNM 12272; pl. 1, fig. 8) shows that the impression is partially masked by a pattern of vermiculated markings. The pallial line sometimes coincides with the contact of the inner and outer shell layers and has a small oval inflated impression near its postero-ventral extremity (pl. 3, fig. 6).

3. Auricular crura. No auricular crura are developed, although a few right and left valves have the internal surface of the anterior ear slightly thickened along the junction with the main disc of the shell.

4. Ornament. Meek (1864a, p. 31), in his original diagnosis of the genus, described the ornament of the right and left valves as "surface with fine obscure concentric striae and sometimes on the right valve, small rounded concentric ridges." In his (Meek, 1876, p. 26) later, more detailed diagnosis he stated "surface showing only concentric striae, and sometimes stronger, regularly defined concentric ridges on the right valve." Although he uses the word "sometimes" in this description, on p. 27 he stressed the discrepancy of ornament between the valves.

In their original description of *S. halli* Hall & Meek (1856) described but did not emphasize the discrepancy in ornament.

Clearly the emphasis should have been on the similarity of the ornament on each valve, and on the uncommon occurrence of weak concentric plicae. Misinterpretation of Meek's diagnosis and discussion has undoubtedly contributed to the uncertain status of the genus. Most of the specimens from the Fox Hills Formation, admittedly younger stratigraphically than those of Hall & Meek (1856) from Sage Creek, have similar ornament on each valve. Weak concentric ridges are sometimes present on the inner surface of the shell of either valve (pl. 3, fig. 4), and tend to show up more strongly on steinkerns. Strong concentric lamellae are rarely developed. The lamellate ornament, like the internal concentric ridges, tends to be accentuated by the removal of the thin outer prismatic layer of the shell.

The concentric ridges are more regular on the steinkern illustrated by Whitfield (1880, pl. 7, fig. 1; see pl. 1, fig. 8), and on the right valves in AMNH 9347 (pl. 1, figs. 1, 3), than on any specimen collected from the type area of the Fox Hills Formation. Compared with the overall similarity of the other morphological features, the difference in this one character is not considered of species rank, particularly as the concentric ridges are stronger on small than large specimens (compare pl. 1, figs. 1, 3, 8, with pl. 3, fig. 4).

COMPARISONS. Other virtually smooth small pectinids assigned to *Pecten*, *Camptonectes*, and *Syncyclonema*, may also be congeneric with *S. halli*. Possible Upper Cretaceous species include *Pecten (Camptonectes) kaufmanensis* Stephenson (1941, pl. 21, figs. 7-9), *P. (C.) cavanus* Stephenson (1952, pl. 19, fig. 7), *P.*

(*Syncyclonema*) *trivisanus* Stephenson (1941, pl. 22, fig. 1), and specimens placed under *Pecten simplicius* Conrad (e.g. Wade, 1926, pl. 20, fig. 7). Inclusion of these species would necessitate modifying the diagnosis to cover species with ornament varying from smooth to with strong concentric striae, with the byssal notch deep to moderate, and the fasciole narrow to moderately wide.

*Syncyclonema halli* (Gabb)

(Pl. 1, figs. 1-9; pl. 2, figs. 1-5; pl. 3, figs. 1, 2, 4-6)

*Pecten rigida* Hall & Meek, 1856, p. 381, pl. 1, figs. 4a-c (non Sowerby, 1818, p. 5, pl. 205, fig. 8).

*Pecten hallii* Gabb, 1891, p. 214. (*Nom. nov.* for *P. rigida* Hall & Meek).

*Syncyclonema rigida* (Hall & Meek). Meek, 1864a, p. 7.

*Syncyclonema rigida* (Hall & Meek). Meek, 1864a, p. 31. Meek, 1876, p. 27, pl. 16, figs. 5a, b. Whitfield, 1880, p. 383, pl. 7, fig. 1.

LECTOTYPE. Here selected (p. 7), AMNH 9347/1.1, a right valve, 4 mm long and 5 mm high (pl. 1, fig. 3), Sage Creek, South Dakota, Pierre Shale, Upper Campanian-Maastrichtian.

MATERIAL. One hundred and seventeen specimens, including eight articulated or displaced bivalved.

OCCURRENCE. In the type area of the Fox Hills Formation *S. halli* is virtually restricted to the Timber Lake Member (Waage, in press).

The species, recorded by Fisher, *et al.* (1960), as *Syncyclonema hallii*, from the lower part of the Pierre Shale and in the Sego Sandstone in western Colorado and eastern Utah, and by Griffiths (1949) as *S. rigida*, from the "Rocky Ridge sandstone member of the Hygiene zone" of the Pierre Formation in Colorado, is apparently rare in the Upper Cretaceous sequences of the Western interior. It is found mainly in sandstone units.

DESCRIPTION. Small, length of specimens 3.5 to 13.2 mm, subequivalve, equilateral to slightly inequilateral, compressed, valves equally inflated. Orbicular, with height, width of one valve, length

of dorsal margin (between extremities of ears), and anterior length respectively, 101.4 to 129.2 ( $n=28$ ,  $\bar{x}=111.7\%$ ), 4.6 to 13.3 ( $n=25$ ,  $\bar{x}=9.1\%$ ), 48.2 to 64.6 ( $n=19$ ,  $\bar{x}=54.9\%$ ), and 45 to 55.9 ( $n=28$ ,  $\bar{x}=49.2\%$ ) per cent of length, and length of anterior ear 50 to 63.2 ( $n=19$ ,  $\bar{x}=55.7\%$ ) per cent of length of dorsal margin. Umbones weakly prosogyrous, project slightly above dorsal margin. Antero- and postero-dorsal margins of the disc of shell straight or slightly concave, form an angle of 87.5 to 100 degrees, and meet the rounded ventral margin at distinct angulations. Dorsal margins of ears straight, intersect at a small angle, the anterior is more steeply inclined. Margin of right valve, especially that of the anterior ear, projects above and overlaps the margin of left valve. Anterior ear equal to or larger than posterior. Ears of left valve, and posterior ear of right valve, weakly delimited from disc of shell, although the margin of disc becomes overhanging ventrally, with straight or rounded anterior or posterior margins which form a rounded or angled junction with the dorsal margin of the ear. Anterior ear of right valve sharply delimited from the overhanging margin of the disc, with a narrow fasciole at base, at the ventral end of which is a narrow moderately deep V-shaped byssal sinus. Ctenolium apparently lacking.

Ornament similar on both valves, of submicroscopic vermiculating *Camptonectes*-striae, 40 to 50 per millimeter at ventral margin, fine growth striae and coarser irregular growth lamellae tending to give a reticulate pattern. Striae are sometimes very weak on the center of disc and, with the growth striae, are often very strong on the antero- and postero-dorsal flanks of disc and sometimes on ears. Either the striae or growth lamellae may dominate on the ears. Internal surface of shell sometimes with irregular or regular shallow rounded concentric costae and fine radial striae.

Resilifers triangular, internal, do not extend to ventral margin of hinge-plate. Resilifer of right valve bordered on either side by a short strong tooth-like process which extends the length of the resilifer and fits into sockets on each side of the resilifer of the left valve. Ligament groove narrow, submarginal, extends most of length of ears, bordered below by a weak cardinal crura. No auricular crura. Pallial line continuous, extending in a loop across shell at about one-quarter of the height above base, becomes indefinite antero-dorsally at base of the fasciole. The pallial line has a small



subquadrangular scar situated at about one-third the height of the shell; and a large subcircular adductor scar is situated near the base of the posterior ear in the dorsal quarter of the shell. Muscle scars on the left valve unknown.

Ostracum less than 0.2 mm thick, of three layers. A very thin outer layer, probably prismatic, bearing the *Camptonectes* striae, a translucent middle layer, apparently of zigzag lamellar structure (Bøggild, 1930, p. 267), that thickens towards the ventral margin, and an inner white layer of complex cross-lamellar structure that is thickest in the umbonal region and ceases within one to two millimeters of ventral margin (pl. 2, fig. 1). Outer surface vitreous, but with irregularly distributed, radially elongated patches of matt appearance (pl. 2, fig. 4).

DISCUSSION. Left and right valves of *S. halli* are equally inflated and their other measurements have approximately the same range of values and means. In spite of the extremely fragile shell few specimens from concretions in the type area were broken during deposition. Complete specimens are very difficult to extract and the ears are especially prone to damage. At Yale loc. 288, Solen, North Dakota, where the sediment is a limonite-cemented medium-grained sandstone with little argillaceous matrix, many specimens were broken during transportation. The tripartite layering of the shell described above requires confirmation by thin section studies. As interpreted it is similar to the shell of "*P. textorius* (Liassic)" of Bøggild (1930, p. 267). The very thin outer prismatic layer bears the *Camptonectes*-like striae and, although always present on well preserved specimens, it is easily removed by abrasion, weathering or extraction. The shell then appears smooth or with concentric lamellae only. Species of *Camptonectes* recorded in the literature as being smooth and striate should be re-examined to ascertain that the outer layer, if this is characteristic of the genus, has not been lost, especially in the case of small species.

Whitfield (1880, pl. 7, fig. 1) illustrated a different pattern of muscle scars on a steinkern from "the forks of the Cheyenne River, Black Hills." He commented on the unusual position of the muscle scar. Examination of recent pectinid species held in the collections of the Peabody Museum, Yale University, showed

that some, for example *Cyclopecten (Delectopecten) vitreus* (Chemnitz), *Pseudamussium striatum* (Müller), and *P. septemradiatum* (Müller), have an elongated or oval scar in a comparable position close to the base of the posterior ear of the right valve. The ventral small subquadrangular scar in the pallial line is present on several specimens and seems to be a valid scar. It may represent a gill suspensory attachment (Newell, 1937, p. 21).

COMPARISONS. Specimens of *Pecten (Camptonectes) kaufmanensis* Stephenson (1941, pl. 21, figs. 7-9) and *P. (C.) cavanus* Stephenson (1952, pl. 19, fig. 7) closely resemble *S. halli*. Other specimens from Gulf and Atlantic Coastal Plains sequences classed under *Pecten* or *Syncyclonema* resemble *S. halli* in shape and size but apparently lack the fine *Camptonectes*-striae. Some, for example *P. (Syncyclonema) trivisanus* Stephenson (1941, pl. 22, fig. 1), show traces of radial ornament, while others, like *P. simplicius* Conrad (Wade, 1926, pl. 20, fig. 7) and the right valve of *P. trivisanus* (Stephenson, 1941, pl. 22, fig. 2), have relatively strong lamellae like *S. halli* when its outer prismatic layer is lost.

#### THE FAMILY PLACEMENT OF *SYNCYCLONEMA*

Pectinid-like genera have been classified into either the Pectinidae Rafinesque (1815) or the Amusiidae Ridewood (1903). The placing of genera in the Amusiidae is primarily based on anatomy (Cox, 1952, p. 33), and in the absence of anatomical information the classification of some fossil and Recent genera is difficult, especially small, thin-shelled, weakly ornamented forms which possess a small byssal notch and lack internal ribs and muscle impressions. Most paleontologists have accepted only one family, the Pectinidae (Marwick, 1928; Grau, 1959). Newell (1965, p. 18) follows this procedure in his proposed classification of the Bivalvia for the "American Treatise of Invertebrate Paleontology."

Korobkov (1960) subdivides the Pectinidae into five subfamilies, including the Amusiinae and Pectininae. Detailed revision of the morphology and anatomy of pectinid genera is required

to confirm the validity of some of these subfamilies. A new subfamily proposed by Korobkov, the Entoliinae, was raised to family rank by Newell (1965). Characteristics of the family include an equivalve or subequivalve inflated shell, weak ornamentation, a small or no byssal sinus, and usually strong auricular and cardinal crura. The following is a translation of the diagnosis of the subfamily Entoliinae given by Korobkov (p. 83) as prepared by the Translation Service of the New Zealand Department of Internal Affairs:

“The shell is prosocline or acline, often gaping; the ears of the left valve are raised, those of the right valve are almost identical and not raised, the resilifer cavity is almost symmetrical and comparatively small; dentate ridges are strongly developed on the ears, at their base they appear more weakly; the byssus notch is entirely absent or can be seen only in the early stages of development; the outer surface is smooth or has regular concentric riblets, more rarely having radial striae. Carboniferous to Cretaceous.”

Genera included by Korobkov in the Entoliinae are *Pernopecten* Winchell (1865), *Entolium* Meek (1865), and doubtfully *Syncyclonema* Meek (1864a). Other possible members are *Pseudentolium* Cox (1948; not synonymous with *Eburneopecten* as suggested by North, 1951) and *Cteniopleurium* Feldtmann (1951). *Somapecten* Kimura (1951), Jurassic, should perhaps be included, although it has a distinctive interlocking hinge apparatus and may be an aberrant offshoot of a pectinid or entoliid stock.

Recognition of the Pectinidae and Entoliidae separates two morphologically different groups of genera, chlamyid-like and entoliid-like respectively, and is supported by the writer. Detailed paleontological studies are required to prove whether the Entoliidae is monophyletic or polyphyletic. The occurrence throughout the late Mesozoic and Tertiary of pectinid genera, e.g. *Lentipecten* Marwick (1928), and amusiid-like genera, closely resembling entoliids suggests that the Entoliidae may be polyphyletic and include convergent end members of branches from a pectinid stem.

The morphology of *Syncyclonema* indicates placement in the Pectinidae and clearly excludes it from the Entoliidae, as is shown in the next section.

*ENTOLIUM*, AND A COMPARISON WITH  
*SYNCYCLONEMA*

GENUS *ENTOLIUM*

AUTHOR. Meek, 1865, p. 478.

TYPE SPECIES. By original designation, *Pecten demissus* Phillips (1829, p. 124, 140, pl. 6, fig. 5), Middle Jurassic, England and Europe.

DISCUSSION. Diagnoses of the genus *Entolium* (Arkell, 1930, p. 91; Cox, 1952, p. 34) stress external morphological features, especially the relatively smooth thin shell, dorsally projecting auricles (particularly on the left valve), and the lack of a byssal notch (at least on adult specimens). The external characteristics as shown by the holotype of *E. demissum* (pl. 3, fig. 3) are rather constant, although the shape of a species may be extremely variable (Staesche, 1925, p. 100).

Less is known of the internal features of species of *Entolium*. One of the three groups of Staesche (1925), that of *E. cingulatum* Goldfuss, has fine internal ridges on the main disc of the shell close to each auricular margin. The generic significance of these ridges is uncertain. Most species possess strong auricular crura and one cardinal crus on each auricle close to the dorsal margin (Korobkov, 1960, p. 83; *E. sanchuense*, Hayami, 1965, p. 315; *E. fossatum*, Marwick, 1953). The auricular crura in part reflect the strong grooves which separate the auricles from the disc of the shell on many species. Some species appear to lack cardinal crura, although others have two strong cardinal crura on the right valve (*E. irense* McLearn, 1933, pl. 1, fig. 10; NZGS-WM 5403) or possibly two crura and tooth-like processes on each side of the resilifer, [*E. orbicularis* (Sowerby) Woods, 1902, pl. 27, fig. 14].

I attempted to obtain suitable specimens to clarify the hinge morphology of the type species *E. demissum*. Unfortunately, these were not available from the collections of the British Museum, Oxford University, or Cambridge University. Considerable work is required before the taxonomy of entoliids is clear.

COMPARISON OF *ENTOLIUM* WITH *SYNCYCLONEMA*. Many authors, as summarized in the Introduction (p. 2), have suggested synonymizing *Syncyclonema* under *Entolium*. The inadequacy of the original descriptions and illustrations of *S. halli* undoubtedly has led workers to assume that it had approximately equal auricles and lacked a distinct byssal sinus.

Nevertheless, *Syncyclonema* is easily distinguished from *Entolium* by its chlamyid rather than orbicular shape, the possession of a deep byssal sinus, which is lacking on *Entolium*, and the occurrence of radial ornament on the auricles, which is also not present on *Entolium*. Internally, *Entolium* lacks the distinct tooth-like processes present on either side of the resilifer on the right valve of *Syncyclonema*. Other differences in internal morphology, for example musculation, may prove to be significant.

The differences prove that *Syncyclonema* should not be synonymized under *Entolium*.

#### COMPARISON OF *SYNCYCLONEMA* WITH OTHER SMALL PECTINID GENERA

*Syncyclonema* superficially resembles a number of pectinid genera and this similarity has been a source of confusion. In particular, *Syncyclonema* has been compared with *Camptonectes* Agassiz, *Eburneopecten* Conrad, *Pectinella* Verrill, *Micronectes* Ichikawa & Maeda, *Hyalopecten* Verrill, and *Pseudamussium* (see below).

Study of these genera has been hampered by a lack of knowledge of morphological features and variation within the genera, particularly as most of the genera are known largely from the type species.

Shape and ornament are the characters used to separate most pectinid genera. Poorly known and little used morphological features of potential systematic importance include shell structure, details of muscle impression patterns, hinge morphology—especially the number and length of the cardinal crura and whether or not the dorsal one bears the ligament—and the consistency and length of the tooth-like process on either side of the resilifer of the right valve.

To facilitate comparison of several of the above genera with *Syncyclonema* the opportunity is taken in the following sections to redescribe the type species of the poorly known genera *Pectinella*, *Hyalopecten*, *Pseudamussium* Mörch, and "Pseudamussium" H. & A. Adams. The formal systematic data for the genera and their type species are presented and discussed where appropriate. Presentation of full synonymies of the type species is not practicable for this paper.

### 1. GENUS *CAMPTONECTES*

AUTHOR. Agassiz, in Meek, 1864b, p. 28, 39.

TYPE SPECIES. By original designation, *Pecten auritus* Schlotheim (1813; = *P. lens* Sowerby, 1818), Middle and Upper Jurassic, England and Europe.

DISCUSSION. The authorship of *Camptonectes* is controversial. Meek (1864b, p. 39) clearly indicates that the concept of the genus, and the virtual selection of a type species, was due to Agassiz (MS) and under the Rules of Zoological Nomenclature (Stoll, *et al.*, 1961, p. 49, Art. 50) the name should be accredited to Agassiz. Stoliczka (1871, p. 425) was the first to use the word type with reference to *P. lens*.

COMPARISON WITH *SYNCYCLONEMA*. Typical small and large species of *Camptonectes* are clearly distinguished from *Syncyclonema* by their macroscopic and frequently punctate (but see Cox, 1952, p. 22) "Camptonectes" ornament, large byssal ear with a wide fasciole, very deep byssal sinus, strong ctenolium, and thick shell (see pl. 4, fig. 3).

The internal features of species of *Camptonectes* are poorly known. Cox (1952, p. 22) states that cardinal crura are lacking on the type species *C. auritus*, but they are present on *Pecten (Camptonectes) moodyi* Stephenson (1952, p. 79). A small specimen of *C. auritus*, prepared for the writer by Dr. L. R. Cox and his assistant, Mr. C. P. Palmer, shows a weak cardinal crus on each auricle of the right valve (pl. 4, figs. 1, 3). On the internal surface of the byssal auricle this specimen also has a

strong ridge extending in an arc from the umbone to the antero-ventral margin of the auricle. This ridge is strongest antero-ventrally and coincides on the external surface with the dorsal margin of the wide fasciole. Dr. Cox (written communication, June 29, 1965) describes the hinge features as follows: "There is a very weak cardinal crus on each side close to the hinge margin and best developed some distance from the beak. In addition, there is a strong ridge running from the beak to the lower margin of the part of the anterior auricle above the byssal notch. This ridge is also well seen in a second specimen. A comparable but weaker ridge is present in some Recent specimens of *Chlamys*. Auricular crura, running from the beak along the lower margin of complete auricles, are absent." The anomaly of no crura on some specimens and weak crura on small specimens may be accounted for by the degeneration and loss of crura with increasing size and age.

The general position of many small, weakly ornamented, species placed in *Camptonectes* is uncertain. Some may belong to *Micronectes* and others to *Syncyclonema*.

## 2. GENUS *EBURNEOPECTEN*

AUTHOR. Conrad, 1865, p. 140.

TYPE SPECIES. By monotypy, *Pecten scintillatus* Conrad (1865, p. 140, pl. 10, fig. 4), Moodys Branch Marl, Jackson Group, Upper Eocene, Garlands Creek, Clarke County, Mississippi.

COMPARISON WITH *SYNCYCLONEMA*. Externally *Syncyclonema* very closely resembles species of *Eburneopecten*, which differ significantly only by the presence of a strong ctenolium, prominent radial costae, a more distinct fasciole on the anterior ear of the right valve, and less prominent lamellae on the auricles. The discovery by Stenzel, *et al.* (1957, p. 85), of specimens of *Eburneopecten* lacking radial ornament on the anterior auricle suggests that this feature may be of specific rank only.

*Eburneopecten* differs from *Syncyclonema* mainly in internal morphology. *Eburneopecten* has two cardinal crura on each auricle of the right valve and on the anterior auricle of the left valve,

**PLATE SECTION**



PLATE 1

*Syncyclonema halli* (Gabb)

FIG. 1. Syntype, AMNH 9347/1.2. Exfoliated right valve, anterior auricle incomplete. Pierre Shale, Sage Creek, Upper Cretaceous.  $\times 10$ .

FIG. 2. Syntype, AMNH 9347/1.3. Incomplete steinkern of a left valve. Pierre Shale, Sage Creek, Upper Cretaceous.  $\times 10$ .

FIG. 3. Lectotype, AMNH 9347/1.1, here selected. Right valve with an incomplete anterior auricle. Most of shell removed, remainder lacking outer shell layer. Pierre Shale, Sage Creek, Upper Cretaceous.  $\times 10$ . (Photographs for figs. 1-3 kindly supplied by Prof. N. D. Newell).

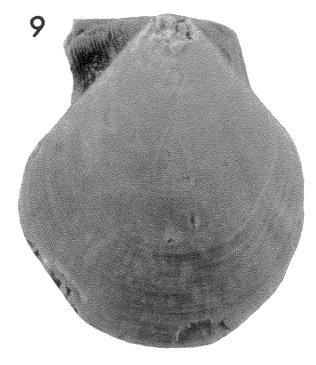
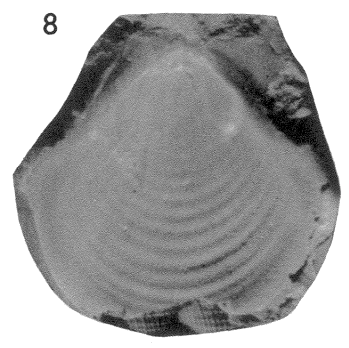
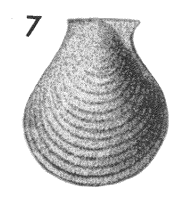
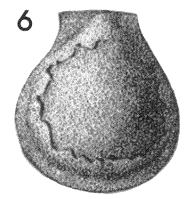
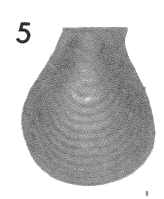
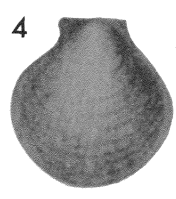
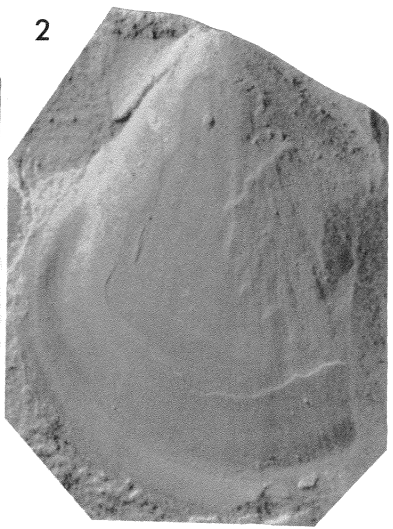
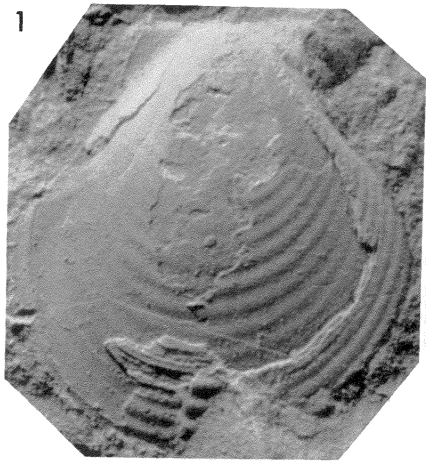
FIG. 4. Fig. 5b of Meek (1876, pl. 16), a left valve and not a right valve as stated in the caption. Supposedly in USNM 347, Pierre Shale, Cheyenne and Moreau Rivers, South Dakota, Maastrichtian. Not found, assumed lost.  $\times ca. 2$ .

FIG. 5. Fig. 5a of Meek (1876, pl. 16), a right valve and not a left valve as stated in the caption. Anterior auricle probably incomplete. Supposedly in USNM 347, not found, assumed lost.  $\times ca. 2$ .

FIGS. 6, 7. Figs. 4c and b respectively of Hall & Meek (1856, pl. 1), left and right valves respectively. Pierre Shale, Sage Creek, Upper Cretaceous.  $\times ca. 2$ . (Photographs kindly supplied by John Howard, Peabody Museum, Yale University).

FIG. 8. USNM 12272; steinkern of a right valve, anterior auricle incomplete, showing concentric ridges and fine radial striae. The original of Whitfield, 1880, pl. 7, fig. 1. Forks of the Cheyenne River, Black Hills, South Dakota, Upper Cretaceous.  $\times 6$ .

FIG. 9. YPM 24129; a left valve from Solen, North Dakota, YPM colln. A-1409, loc. 288, Timber Lake Member, Fox Hills Formation, Maastrichtian.  $\times 6$ .



## PLATE 2

### *Syncyclonema halli* (Gabb)

FIG. 1. YPM 24122; an internal view of the shell of a right valve, showing the inner thin white complex cross-lamellar layer and the translucent middle layer. Note the deep byssal notch and incomplete cardinal crus on the anterior auricle. YPM A-650, loc. 73, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation, Maastrichtian.  $\times 6$ .

FIG. 2. YPM 24126; a left valve showing ornament on the auricles and fine diverging radial striae on the margins of the disc. YPM A-1409, loc. 288, Solen, North Dakota, Timber Lake Member, Fox Hills Formation.  $\times 9$ .

FIG. 3. ANSP 31245; internal view of the postero-dorsal part of the shell of a right valve showing the faintly impressed adductor muscle impression close to the base of the posterior auricle. Pierre Shale, Mingsville, Montana, collector Homer Squyer, Upper Cretaceous.  $\times 12$ .

FIG. 4. YPM 24127; a left valve showing ornament, particularly the diverging radial striae on the margins of the disc. YPM A-1409, loc. 288, Solen, North Dakota, Timber Lake Member, Fox Hills Formation.  $\times 9$ .

FIG. 5. YPM 24123; interior of dorsal part of a right valve, the anterior auricle incomplete and centre of hinge damaged, showing cardinal crura. YPM A-973, loc. 100, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation.  $\times 12$ .

2



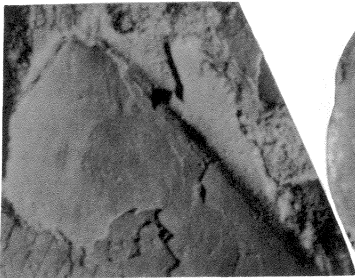
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PLATE 3

*Syncyclonema halli* (Gabb)

FIG. 1. YPM 24124; rubber latex cast of a left valve hinge showing cardinal crura, resilifer, and lack of auricular crura. YPM A-659, loc. 73, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation.  $\times 12$ .

FIG. 2. YPM 24125; right valve hinge, anterior ear and dorsal part masked by matrix, showing tooth-like projections on each side of a narrow resilifer and the lack of ctenolium. YPM A-747, loc. 226, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation.  $\times 12$ .

FIG. 4. YPM 25635; right valve steinkern with some exfoliated shell ventrally, showing radial striae and weak concentric ridges. YPM A-447, loc. 210, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation.  $\times 3$ .

FIG. 5. USNM 347; rubber latex cast of a left valve, supposedly the original of Meek, 1876, pl. 16, fig. 5b, a right valve, showing cardinal crura and resilifer. Compare with pl. 1, fig. 4. Pierre Shale, Cheyenne and Moreau Rivers, South Dakota.  $\times 4$ .

FIG. 6. ANSP 31241; a right valve steinkern showing postero-dorsal adductor scar, pallial line, and postero-ventral swelling. Mingusville, Montana, collector Homer Squyer, Pierre Shale.  $\times 12$ .

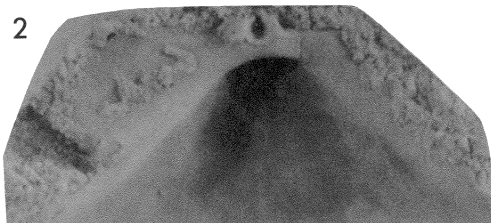
*Entolium demissum* (Phillips)

FIG. 3. Holotype, Yorkshire Museum 202. Kellaways Rock, near Scarborough, Lower Callovian, Middle Jurassic.  $\times 1$ .

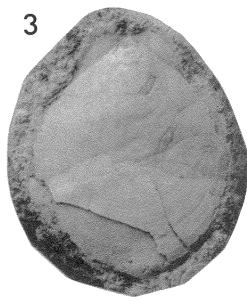
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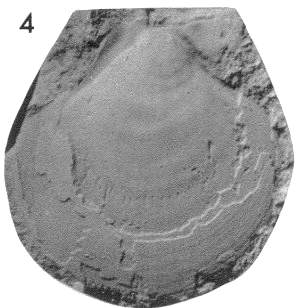
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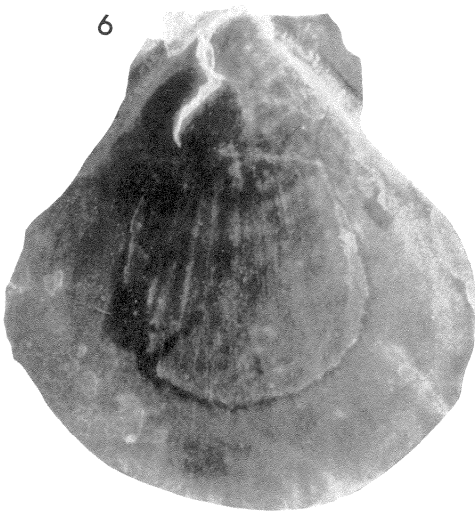
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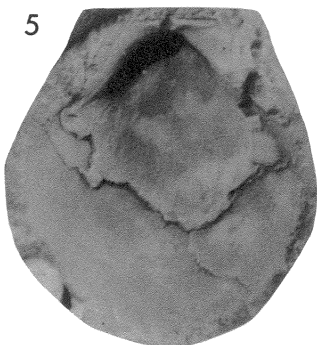
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## PLATE 4

### *Camptonectes auritus* (Schlotheim)

FIGS. 1, 3. BMNH LL 2445; internal views taken under different lighting of the interior of a right valve, showing ctenolium, weak cardinal crura and ridge extending from umbo to antero-ventral extremity of the byssal auricle. Malton, Yorkshire, probably from a "large stone quarry, Coralline Oolite, Upper Oxfordian, Zone of *Perisphinctes plicatilis*" (L. R. Cox, letter, Aug. 2, 1965).  $\times 1.9$ .

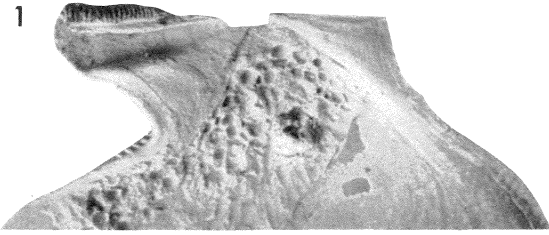
FIG. 6. BMNH LL 2445; exterior of right valve. Note wide byssal notch and fasciole, and punctate "*Camptonectes*" ornament. Locality data as above.  $\times 1.8$ . (Photographs for figs. 1, 3, 6, kindly supplied by Dr. L. R. Cox).

### *Eburneopecten scintillatus* (Conrad)

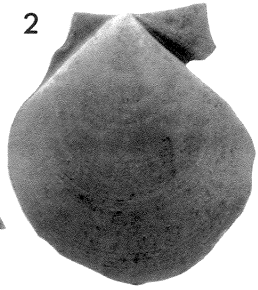
FIGS. 2, 4. Topotype, BEG 20726; photographs of the exterior, fig. 2, and interior, fig. 4, of a right valve showing byssal notch, narrow fasciole, ctenolium, radial costae on the byssal auricle, weak auricular crura, cardinal crura, short tooth-like processes on each side of the resilifer, and the dorsally projecting dorsal margin. Garland's Creek, Moodys Branch Marl, Jackson Group, Upper Eocene (see Stenzel, *et al.*, 1957, p. 82). Fig. 2,  $\times 4$ ; fig. 4,  $\times 6$ .

FIGS. 5, 7. Topotype, BEG 20725; photographs of the interior, fig. 5, and exterior, fig. 7, of a left valve showing weak auricular crura, cardinal crura with finely striated areas on each side of the resilifer, and large subcentral adductor scar. Locality data as above. Fig. 5,  $\times 6$ ; fig. 7,  $\times 4$ .

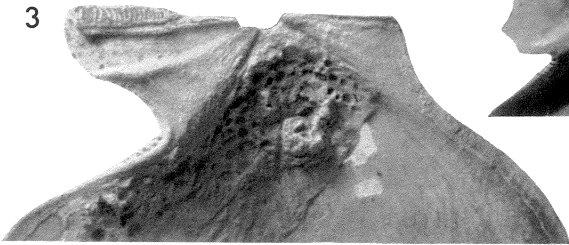
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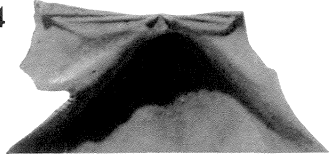
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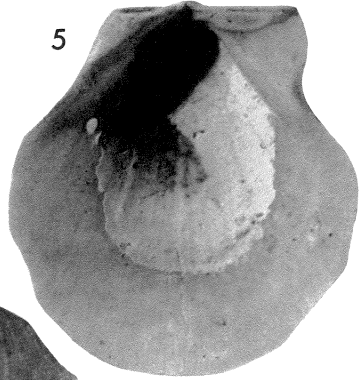
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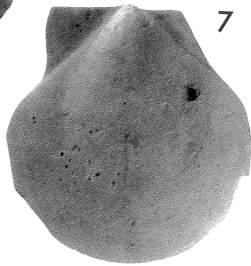




PLATE 5

*Micronecies bellaturus* Ichikawa & Maeda

FIG. 1. OCU MM 239; plastic cast of the dorsal part of a right valve showing strong radial costae on byssal auricle. Loc. 151, Azenotani — 3, Izumi Mountains, Azenotani Shale. Hetonian Series (Campanian).  $\times 4$ .

FIGS. 2, 3. OCU MM 238; plastic casts of the exterior, fig. 2, and interior, fig. 3, of a left valve, showing ornament, cardinal crura, and dorsal triangular flat-surfaced "crura". Locality data as above.  $\times 6$ .

FIG. 4. OCU MM 239; plastic cast of a right valve showing cardinal crus on the anterior auricle. Area around resilifer poorly preserved. Locality data as for fig. 1.  $\times 6$ .

FIGS. 5, 7, 8. OCU MM 772; plastic casts of a right valve showing large anterior auricle, deep byssal notch, wide fasciole, strong costa directly above fasciole, the hidden ctenolium (fig. 7), the prosoclinal shape, resilifer and cardinal crura. Loc. 115, Takinoike, Izumi-Sano City, Osaka Prefecture, K. Ichikawa collector, 1962, Azenotani Shale. Fig. 5,  $\times 4$ ; fig. 7,  $\times 8$ .

FIGS. 6, 9. OCU MM 246; plastic casts of a valve possibly the left, the photographs taken under different lighting, to show ornament. Locality data as for fig. 1.  $\times 4$ .

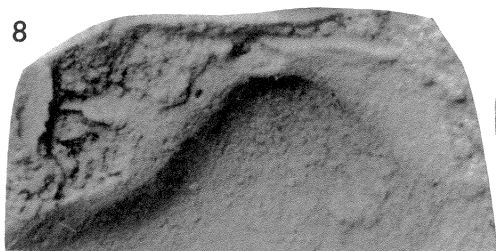
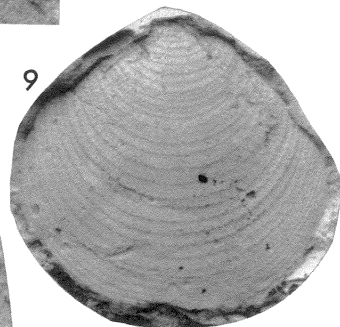
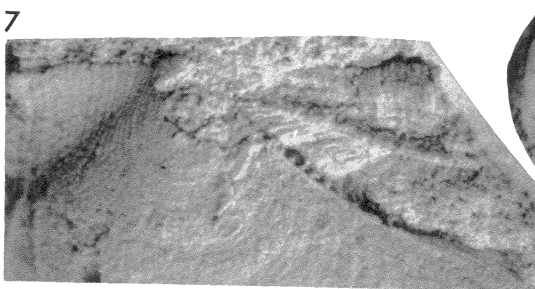
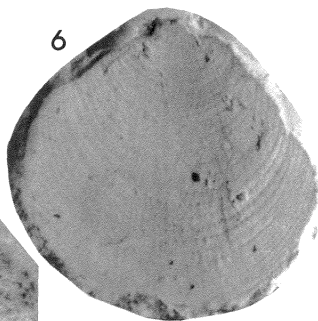
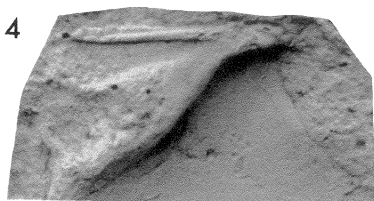
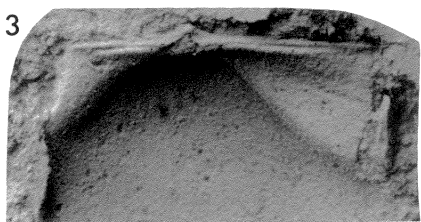
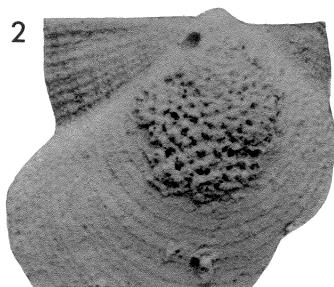
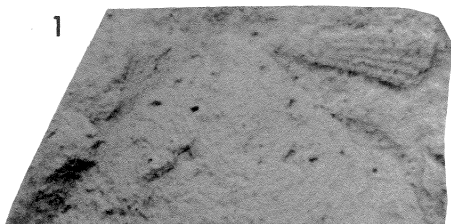


PLATE 6

*Pectinella sigsbeeii* (Dall)

FIGS. 1, 4. Holotype, MCZ 7817; a right valve, the anterior auricle incomplete, not whitened, showing shape, ornament, and hinge morphology. From "off Havana", Recent. Fig. 1,  $\times$  5; fig. 4,  $\times$  10. (Photographs kindly supplied by Dr. W. J. Clench).

FIGS. 2, 3. USNM 62263; a left valve, labeled as "type fig.'d", and probably the matching valve of MCZ 7817, showing shape, ornament, cardinal and auricular crura. Lat 22°10' N, long. 82°20' W, depth 158 fms, Recent.  $\times$  2.8.

FIGS. 5, 6, 7. USNM 503313; a left valve, showing shape, ornament, cardinal and auricular crura. Off English Harbor, Antigua Is., 120 fms, rough coral, Recent. Figs. 5, 7,  $\times$  2.8; fig. 6,  $\times$  4.

*Hyalopecten dilectus* Verrill & Bush

FIGS. 8, 9. Holotype, USNM 44827; matching valves, showing shape, ornament, auricles and byssal notch. Stn 229, 1423 fms, off Maryland, Recent.  $\times$  2.

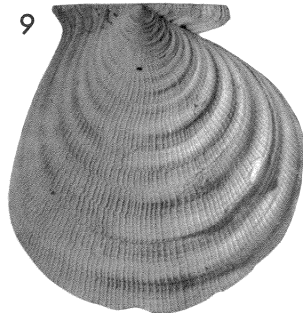
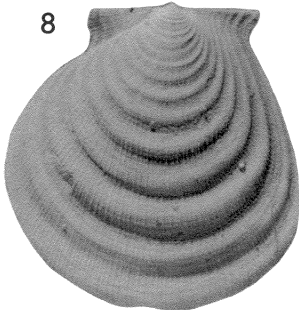
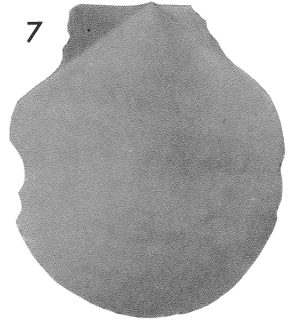
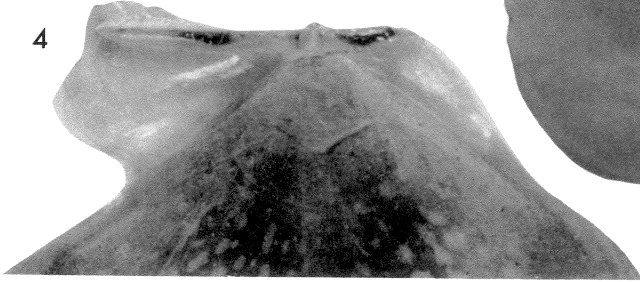
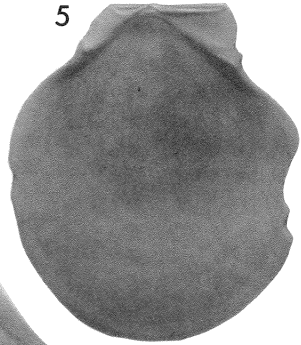
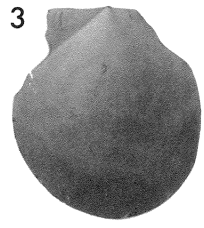
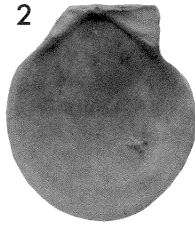
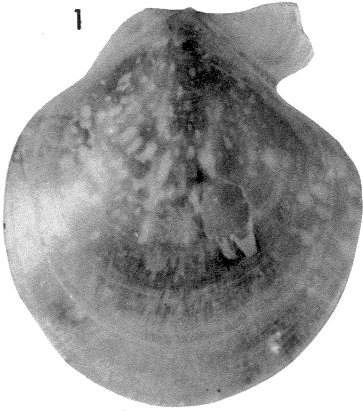


PLATE 7

*Hyalopecten dilectus* Verrill & Bush

FIGS. 1, 2. Holotype, USNM 44827; matching valves, showing hinge morphology, byssal notch and ctenolium. Stn 229, 1423 fms, off Maryland, Recent.  $\times 4$ .

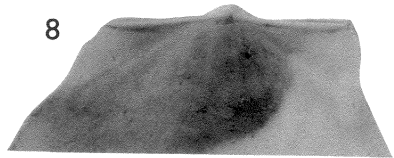
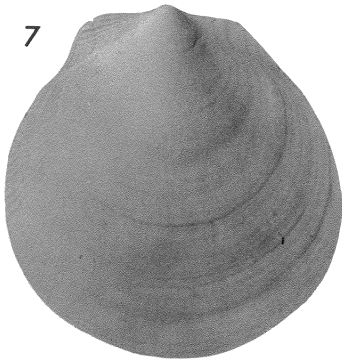
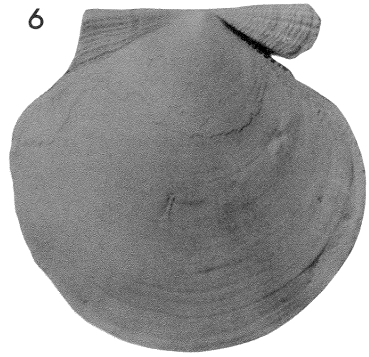
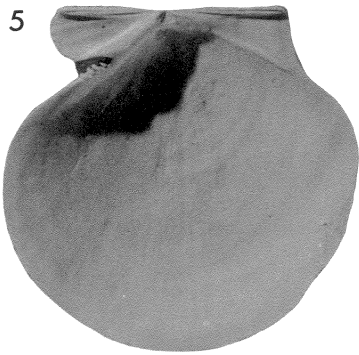
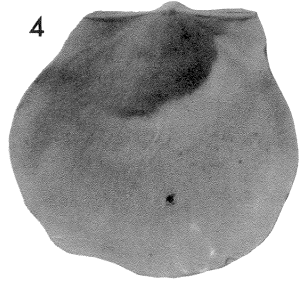
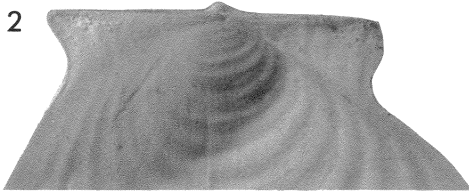
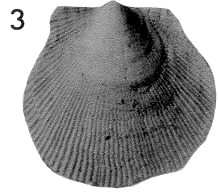
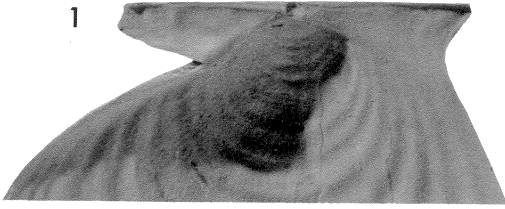
*"Pseudamussium" hybridum* (Gmelin)

(type species of *Pseudamussium* H. & A. Adams)

FIGS. 3, 4, 8. USNM 131671; a small left valve showing ornament, hinge morphology, and adductor muscle scar. From West Africa, Lea collection, labeled as "probably *Pecten dispar* Lam." by Dall?, Recent. Fig. 3,  $\times 2$ , fig. 4,  $\times 3$ .

FIGS. 5, 6. USNM 131671; internal and external photographs of a right valve. Note ornament, hinge morphology and ctenolium. Locality data as above.  $\times 2$ .

FIG. 7. USNM 131671; external view of a large left valve. Compare ornament with that of fig. 3. Locality data as above.  $\times 2$ .



but only one crus on the posterior auricle of the left valve, whereas *Syncyclonema* has one crus on each auricle. The outer ends of the ventral crura on *Eburneopecten* bend upwards to meet the dorsal crura below the dorsal extremities of the auricle thus defining a cuneiform-shaped area (pl. 4, figs. 4, 5). Those on the left valve probably fit inside those of the right valve which are stronger. The dorsal crura and sockets of *Eburneopecten* adjacent to the resilifer are transversely striated (pl. 4, fig. 5). The tooth-like processes on either side of the resilifer on the right valve are short and weak on *Eburneopecten* (pl. 4, fig. 4), but long and strong on *Syncyclonema* (pl. 3, fig. 2). *Eburneopecten* has distinct incipient auricular crura which are stronger on the left valve. The shape and position of the adductor muscle impression are different. The scar of *Eburneopecten* is larger and situated more centrally (pl. 4, fig. 5) than that of *Syncyclonema* which is close to the base of the posterior ear.

These internal morphological differences are sufficient to show there is no close relationship between *Syncyclonema* and *Eburneopecten*.

### 3. GENUS *MICRONECTES*

AUTHOR. Ichikawa & Maeda, 1958, p. 95.

TYPE SPECIES. By original designation, *Micronectes bellaturus* Ichikawa & Maeda (1958, p. 98, pl. 5, figs. 13-17; see pl. 5, figs. 1-9 herein), Late Cretaceous (Campanian-Maastrichtian), Japan.

COMPARISON WITH *SYNCYCLONEMA*. *Micronectes* differs considerably from *Syncyclonema* in external and internal morphology. The strongly inflated valves of *M. bellaturus* have a distinctive ornament of non-punctate, flat- and round-topped radial costae and strong concentric lamellae (pl. 5, figs. 2, 6, 9). The costae become flat-topped on the ventral part of the shell and are three or four times wider than the narrow depressions which, together with the corrugation of the edge of the lamellae and a pseudo-punctate effect produced by the intersection of the lamellae and radial grooves, become the dominant features. This ornament resembles that of species placed by Grau (1959) in *Cyclopecten*

(s.s.) and *C. (Delectopecten)*, but is quite different from the fine submacroscopic radial markings on the compressed valves of *Syncyclonema halli*. The anterior auricle of the right valve of *bellaturus* bears four to six radial costae above a very wide fasciole, the byssal notch is deep and wide, and contrary to Ichikawa & Maeda's statement, there is a strong ctenolium (pl. 5, fig. 7).

By these characters *Micronectes* closely resembles *Camptonectes*, but not *Syncyclonema*. Each auricle has a strong cardinal crus. That on the left valve is separated by a narrow but deep socket from a prominent flat-surfaced crus extending the length of the dorsal margin (pl. 5, fig. 3). The resilifer of the right valve is deeply sunken and appears to lack bordering tooth-like processes. In contrast, *Syncyclonema* lacks the dorsal flat-surfaced crus and has tooth-like processes adjacent to the resilifer.

#### 4. GENUS *PECTINELLA*

AUTHOR. Verrill, 1897, p. 68.

TYPE SPECIES. By original designation, *Pecten sigsbeeii* Dall (1886, p. 223, pl. 4, fig. 2), from "off Havana", Cuba, Recent.

DISCUSSION. Verrill (1897, p. 68) gave the following generic diagnosis.

"Shell small, thin, swollen, nearly smooth, with convex and slightly unequal valves. Auricles very unequal, oblique, the anterior larger, with a deep byssal notch in the right valve, but without pectinidial teeth; posterior auricle small. The surface is smooth except for fine lines of growth. *Camptonectes* sculpture is not present. The texture is not hyaline."

Verrill based his diagnosis of the genus on *P. sigsbeeii*, the only species he included in his new taxon. As the diagnosis is inadequate for present day systematics, and is also erroneous, the opportunity is taken to redescribe the type species. An emended diagnosis is not given as it should await a review of species included in the genus and other closely related taxa.

The redescription of the type species was facilitated by Dr. W. J. Clench, Museum of Comparative Zoology, who kindly



sent me data and photographs of a right valve (MCZ 7817; pl. 6, figs. 1, 4) of *sigsbeeii*, labeled as holotype, from "off Havana", and by Dr. J. Rosewater, U.S. National Museum, who kindly sent me a left valve (USNM 62263; pl. 6, figs. 2, 3) of *P. sigsbeeii* Dall, from "Depth 158 fms., Lat. 22°10'N, long. 82°20'W, U.S. Coast Survey, C. P. Patterson, supt., Gulf Stream and Gulf Mexico Explor., USCG., S. Blake, Alex Agassiz, 1877-78", and labeled "type fig'd." Dr. Rosewater also sent a larger left valve (pl. 6, figs. 5-7) USNM 503313, from "off English Harbor, Antigua, 120 fms, rough coral."

*Pectinella sigsbeeii* (Dall)

(Pl. 6, figs. 1-7)

*Pecten (Pseudamussium) sigsbeeii* Dall, 1886, p. 223, pl. 4, fig. 2.  
*Pectinella sigsbeeii* (Dall). Verrill, 1897, p. 68.

TYPE SPECIMENS. Holotype by original designation MCZ 7817, a right valve from near Havana, Cuba, Lat. 22°10'W, Long. 82°20', 158 fathoms, Recent, and the probably matching left valve USNM 62263 from the same locality.

Several lines of evidence indicate that the left (USNM 62263) and right (MCZ 7817) valves originally came from the one bivalved specimen, and together should be treated as the holotype, especially as these were the only valves available to Dall at the time he described the species.

1. Measurements made on the three valves are as follows:

	MCZ 7817 (right valve)	USNM 62263 (left valve)	USNM 503313 (left valve)
Length	9.5 m	9.4	13.9
Height	10.5	10.5	16.2
Half width	—	1.7	3.2
Length of dorsal margin	4.3	4.2	7.5
Anterior length of dorsal margin	2.9	2.8	c. 4.4 (incomplete)

Even though the measurements of MCZ 7817 are taken from a negative, the coincidence of the measurements of the right valve MCZ 7817 and the left valve USNM 62263 is noteworthy and suggests that the two valves are from one bivalved specimen.

2. The presence of dried body tissue and ligament adhering to the inner surface of the left valve USNM 62263 (this tissue was later removed to improve the specimen for photography) and the apparent presence of similar material on the hinge area of the right valve MCZ 7817.

3. The data on the label accompanying USNM 62263 matches that given by Dall (1886, p. 223) in his original description of the species.

4. Dall recorded "two valves were obtained by Sigsbee", and his description shows he had a left and a right valve. The right valve (MCZ 7817) clearly matches Dall's figure (1886, pl. 4, fig. 2), but to my knowledge, and contrary to the label (see above) the left valve (USNM 62263) has not been figured previously (pl. 6, figs. 1-4).

5. The extremity of the anterior auricle of both the left and right valve is incomplete, suggesting the possibility of breakage when conjoined.

Although Dall (1886, p. 175) notes that the "types of species described will be found in the Museum of Comparative Zoology at Cambridge, and in the U.S. National Museum" it is most unusual that a collection should have been split into two parts. However, in the case of *P. sigsbeei* one valve seems to have been lodged in each institution.

Dall, in his original description, did not select a specific specimen as the holotype. But because the label accompanying the right valve MCZ 7817 is marked as holotype, apparently in Dall's handwriting, and as Dall, in the sentence quoted in the previous paragraph, mentions depositing types in two institutions, the designation of the holotype is taken as being by original designation.

REVISED DESCRIPTION. Small, shell thin, equivalve, inequilateral, strongly inflated. Umbones small, project only slightly above the dorsal margin. Antero-dorsal margin of the right auricle projects dorsally and overlaps the margin of the left valve. Auricles of

the left valve and posterior auricle of right valve not sharply delimited from disc of valve; anterior auricle of right valve with a very narrow fasciole. Anterior auricles much larger than the posterior. Right valve with a deep open V-shaped byssal notch; no ctenolium.

Auricles ornamented with fine raised concentric costae, 11-13 per millimeter, and much finer submacroscopic radial costae which cross only the interspaces between the concentric costae. Disc of shell appears smooth except for occasional growth lines and pauses; but has submacroscopic, very fine, regular, raised concentric striae, about three per 0.1 mm over entire surface of shell. Disc crossed by faint submacroscopic radiating sulci which are impressed only in the interspaces between the raised concentric striae and give the shell a fine pseudo-punctate appearance. Radial sulci diverge and are more distinct on the dorsal flanks of the disc. Radial sulci about one-fourth to one-sixth of the width of the flat-crested interspaces, and about four to six per 0.1 mm.

Left valve with a flat, longitudinally finely striated ligament surface just below the dorsal margin of each valve. Below the flat surface on the anterior auricle is a narrow linear socket followed by a long, strong cardinal crus. Posterior ear similar, with a cuneiform-shaped depression defined ventrally by a cardinal crus which is strongest near the resilifer and at its posterior end, and which extends postero-ventrally and then bends up sharply to meet the end of the flat surface. Right valve with a strong cardinal crus on each auricle. These fit into matching depressions above the crura of the left valve. The presence of flat ligament surfaces on the right valve is uncertain, but probable, judging from the photograph (pl. 6, fig. 4). Base of each auricle has a nodular auricular crura, with the posterior being the stronger. Resilifer small, with on the left valve two shallow depressions on either side. These suggest the presence of short, weak tooth-like processes on either side of the resilifer of the right valve.

Musculature and shell structure unknown.

DISCUSSION. Both left valves are similar except for stronger cardinal crura and more distinct radial ornament on the umbone of USNM 62263.

COMPARISONS. *Pectinella sigsbeeii* is externally similar to *Syncyclonema halli*. The main differences are in the details of ornament, the strong inflation of the valves, and the very small posterior auricle of *P. sigsbeeii*. Both species have similar concentric lamellae on the auricles, but the radial ornament of *S. halli* is much stronger than that of *P. sigsbeeii* and its concentric striae are not so regular or distinctive. Consequently, *S. halli* does not have the pseudopunctate effect of *P. sigsbeeii*. *S. halli* lacks the strong auricular crura of *P. sigsbeeii*, and has strong tooth-like processes on either side of the resilifer against possibly only weak ones on *P. sigsbeeii*. The auricles of the left valve of *P. sigsbeeii* have dorsal flat ligament bearing areas which are lacking on *S. halli*. The cardinal crus on the posterior auricle of the left valve of *P. sigsbeeii* is arcuate and concave upwards (pl. 6, fig. 6), that of *S. halli* is straight (pl. 3, fig. 1). The cardinal crus on the anterior auricle of the left valve of *P. sigsbeeii* is long and strong (pl. 6, fig. 5) whereas that of *S. halli* is weaker, sometimes discontinuous, though relatively strong close to the resilifer and its anterior end where the swollen part is displaced dorsally relative to the rest of the crus (pl. 3, figs. 1, 5).

These morphological differences are sufficient to warrant accepting *Syncyclonema* and *Pectinella* as distinct genera. A knowledge of the musculature might give additional support to my conclusion.

Hayami (1965, p. 318) reclassified a Japanese Lower Cretaceous species, *Pecten miyakoensis* Nagao, under *Pectinella*. Study of casts of *P. miyakoensis* (NZGS-WM 8473) shows that externally the species resembles both *S. halli* and *P. sigsbeeii*. But the strongly projecting dorsal extremities of the auricles of the right valve of *P. miyakoensis* are not matched by either species. *P. miyakoensis* more closely resembles *S. halli* in the strength and form of the radial and concentric ornament and lack of a pseudopunctate effect. As recognized by Hayami the ornament of *P. miyakoensis* tends to be discrepant with stronger concentrics on the right valve and stronger radials on the left valve. Also the ornament of *P. miyakoensis* is markedly finer, and the radial ornament more restricted to the dorsal flanks of the disc.

*P. miyakoensis*, like *S. halli*, lacks auricular crura. Contrary to Hayami's (1965) description, a right valve of *P. miyakoensis*

has cardinal crura. (These are faintly visible on pl. 45, fig. 6, of Hayami, 1965, Gk H6622). On either side of the sunken resilifer, flat longitudinally striaed surfaces pass laterally into narrow crura which extend halfway to the extremities of the auricles. Small rounded protuberances extend ventrally from the triangular surfaces on either side of the resilifer. The form and arrangement of the crura and the strongly projecting auricles of the right valve distinguish *P. miyakoensis* from both *Syncyclonema* and *Pectinella*, and the lack of tooth-like processes on either side of the resilifer distinguishes it from *Syncyclonema*.

Future studies on small, relatively smooth pectinids may warrant placement of *P. miyakoensis* in a separate supra-specific taxon. Until adequate studies are completed, it is best to treat it as a *Pecten* (sensu lato). Except for the large byssal auricle and notch *P. miyakoensis* superficially resembles species of *Entolium* by its possession of strongly projecting dorsal margins and short cardinal crura.

#### 5. GENUS *HYALOPecten*

AUTHOR. Verrill, 1897, p. 71.

TYPE SPECIES. By original designation, *Pecten undatus* Verrill & Smith, in Verrill, 1885, p. 444, pl. 44, fig. 21 (= *Hyalopecten dilectus* Verrill & Bush, in Verrill, 1897, p. 80, pl. 18, fig. 5; see North, 1951), North-west Atlantic Ocean, Recent.

DISCUSSION. To document the differences between *Syncyclonema* and *Hyalopecten* the poorly known type species of the latter is redescribed from its holotype.

Grau (1959) classes *Hyalopecten* as a subgenus of *Cyclopecten* Verrill (1897).

*Hyalopecten dilectus* Verrill & Bush  
(Pl. 6, figs. 8, 9; pl. 7, figs. 1, 2)

*Pecten undatus* Verrill & Smith, in Verrill, 1885, p. 444, pl. 44, fig. 21 (not *Pecten undatus* DeFrance, 1825, p. 257).

*Hyalopecten dilectus* Verrill & Bush, in Verrill, 1897, p. 80, pl. 18, fig. 5.

For a full synonymy refer to North, 1951, p. 234.

TYPE SPECIMEN. Holotype of *H. dilectus* Verrill & Bush, by original designation, USNM 44827, Station 229, Albatross Expedition, 1423 fathoms, off Maryland, Recent.

Holotypes have been proposed for both *Pecten undatus* and *Hyalopecten dilectus*. I agree with both Dall (1898, p. 754) and North (1951) in considering that *P. undatus* Verrill & Smith and *H. dilectus* are conspecific. Consequently, under the Rules of Zoological Nomenclature, Article 72d (Stoll, *et al.*, 1961, p. 75) the holotype selected by Verrill & Smith for their *P. undatus* is valid.

REVISED DESCRIPTION. Shell very thin, equivalve, although umbone of left valve projects above dorsal margin and is more inflated than that of right valve, subequilateral. Measurements: length 18.8 mm, height 20.0 mm, half width 3.0 mm, length of anterior ear from umbone to extremity 5.6 mm, length of dorsal margin 11.0 mm. Dorsal margin of ears does not project above ligament attachment area. Both valves have distinctive ornament of fine radial plicae, subdued on inner shell surface, and concentric growth striae and regular broad plicae. Radial plicae much finer and weaker on the dorsal flanks, consisting of 155 and 140 on the left and right valves respectively. Secondary radial plicae appear by intercalation on upper third of shell, and tertiaries close to ventral margin. Concentric plicae number 17 on left and 14 on right valve. Protoconch of both valves smooth. Auricles small, of approximately equal size, extremity of posterior auricle pointed, and all except byssal auricle of right valve are not demarcated from main disc of shell. Byssal auricle of right valve overhung by margin of main disc of shell, outermost margin of which projects upwards as a thin flange. Strong ctenolium is hidden under overlapping margin. Byssal auricle with wide fasciole covering half of its surface, fasciole ornamented by concentric growth costae, and dorsal half of auricle with five radial costae. Byssal notch deep, narrow, V-shaped. Hinge weak; each auricle with narrow, flat-topped crus (for ligament attachment?) followed below by shallow linear depression and very weak cardinal crus, latter being barely evident on posterior ear. Resilifer very small and shallow, that on right valve bordered on anterior side by very short and weak tooth-like ridge (? abnormal

asymmetry). No auricular crura. Muscle scars not impressed, unknown. Shell of two layers of unknown structure; translucent outer layer and thin white inner layer covering dorsal third of shell.

COMPARISON WITH *SYNCYCLONEMA*. The strongly plicate valves with numerous fine radial costae differ markedly from the virtually smooth non-plicate valves of *S. halli*. *H. dilectus* has small pointed auricles whereas those of *S. halli* are relatively larger and their extremities rounded. A ctenolium is present on *H. dilectus* but lacking on *S. halli*, and the cardinal crura on *H. dilectus* are exceptionally weak compared to those of *S. halli*.

### PSEUDAMUSSIUM

The status of *Pseudamussium* has been controversial. Soot-Ryen (1962, p. 254) correctly points out that the name has been used for two "quite different groups of pectinids"; (1) *Pseudamussium* Mörch (1853) with *Pecten septemradiatus* Müller (1776) as type species, and (2) *Pseudamussium* H. & A. Adams (1858) with *Ostrea hybrida* Gmelin (1791; = *Pecten exoticus* Chemnitz, 1784) as type species (Grau, 1959). The correct application of the name depends on the validity for nomenclatural purposes of Mörch's catalogue. The International Commission of Zoological Nomenclature, Opinion 714 (1964) has validated under the Plenary Powers *Pseudamussium* Mörch, 1853, with *Pecten septemradiatus* Müller (1776) as type species.

#### 6. GENUS *PSEUDAMUSSIUM* Mörch

AUTHOR. Mörch, 1853, pt. 2, p. 59.

TYPE SPECIES. By designation under the Plenary Powers, *Pecten septemradiatus* Müller (1776, p. 248), Eastern Atlantic Ocean, Recent.

#### *Pseudamussium septemradiatum* (Müller)

*Pecten septemradiatus* Müller, 1776, p. 248.

*Pseudamussium septemradiatum* (Müller). Mörch, 1853, p. 59.  
Soot-Ryan, 1962, p. 225.

SYNONYMY. See Grau (1959) and North (1951) for discussions of this species. No restatement of its full synonymy can be attempted here.

TYPE SPECIMENS. Now that the type species has been designated a type specimen should be selected by a worker familiar with the species, preferably from the collections studied by Müller (1776).

DESCRIPTION. "Pectens" of the *septemradiatum* group, sometimes synonymized with *Peplum* Bucquoy, Dautzenberg & Dollfus (1889; Grau, 1959), have strong radial plicae, relatively small ears, with, *fasciculatum* (Hinds, 1845), or without, *septemradiatum*, a ctenolium on adult specimens, a shallow open byssal notch, the auricles are delimited from the disc of the shell, and the byssal auricle of the right valve lacks a definite fasciole and has strong radial costae. The following hinge and musculation details are based on specimens (NZGS-WM 2778) of *Pseudamussium septemradiatum* (Müller).

Right valve has on each side of resilifer a short, transversely striated surface (provinculum) which extends one quarter of distance towards extremity of ear. Commencing above end of these surfaces and continuing to end of ears is a weak cardinal crus possessing a transversely striated upper surface. The short surfaces (provincula) fit into matching concave striated depressions on either side of resilifer of left valve and the cardinal crura into relatively deep depressions situated above weak cardinal crura which extend from ends of the provincula sockets. No tooth-like processes bordering resilifer of right valve and no auricular crura. Adductor impression subcircular, centrally constricted, sited above mid-height close to base of posterior auricle, that of right valve more so, and a series of very small impressions extends up to and across end of umbonal cavity. Adjacent to anterior auricle are two small circular impressions, one at antero-dorsal end of umbonal cavity and one near ventral end of auricle. Pallial line continuous.

COMPARISONS. See below under "*Pseudamussium*" *hybridum*.

*"Pseudamussium" hybridum* (Gmelin)  
(Pl. 7, figs. 3-8)



*Ostrea hybrida* Gmelin, 1791, p. 3318.

*Pecten hybridus* (Gmelin), Dall, 1898, p. 751.

For a detailed synonymy of this species see North (1951) and Grau (1959).

TYPE SPECIMENS. When the supraspecific status of this species has been clarified a type specimen should be selected, preferably from the collections available to Gmelin (1791).

TABLE 1: Measurements of seven valves of *Pecten hybridus* Gmelin held in USNM 131671. All measurements in millimeters.

Valve	Length	Height	Half Width	Anterior Length	Length Dorsal Margin	HAM *
right	21.1	20.4	2.4	6.6	13.7	9.0
"	20.2	19.9	2.8	5.7	11.9	9.2
left	23.3	23.4	4.1	5.2	11.0	10.1
"	23.0	23.7	3.6	4.3	9.1	11.6
"	17.0	16.7	3.7	3.3	7.3	7.6
"	15.2	15.7	2.9	3.8	7.8	—
"	13.0	12.2	2.3	3.7	7.4	—

\* HAM = height of base of adductor muscle impression above the ventral margin.

REVISED DESCRIPTION. A redescription of the characteristic species of the *hybridus* group of Pectinids, *Ostrea hybrida*, based on the collection (USNM 131671) studied by Dall (1898, p. 751), follows:

Small, length of specimens ( $n = 7$ ) 13 to 23.3 mm, dimensions as given in Table 1, equivalve, subequilateral, although umbone of left valve is more inflated and projects slightly above margin of commissure. Left valve with 62 to 87 round-topped radial costae, including rare intercalated secondary costae. Radial costae wider than interspaces. Costae weaker on ventral half of shell, and are worn on available specimens. Valve also ornamented by irregular growth depressions and fine regular growth striae which produce nodes where they cross radial costae and lamellar projections across interspaces. Ornament strongest on juvenile speci-

mens. Right valve has concentric growth depressions, striae, and radial costae only on dorsal flanks of disc and on auricles. Auricles subequal, posterior slightly longer than anterior. Posterior auricles and anterior auricle of right valve not delimited from shell, with four to seven radial costae. Byssal auricle of right valve has a narrow deeply impressed fasciole, and on area above, five to six strong radial costae which become more widely spaced ventrally. Byssal notch narrow, deep U-shaped, bordered ventrally by ctenolium of 19 to 21 nodules.

Each auricle of right valve hinge has one dorsal crus which thickens outwards, is flat-topped with fine transverse striae, followed below on the inner half of auricle by a deep narrow socket and an underlying, raised surface (provinculum) with coarse transverse striae which merges with the dorsal crus at end of socket. Very weak and short tooth-like ridges occur on each side of resilifer. Each auricle of left valve has a relatively strong dorsal crus with a transversely striated upper surface, below which on inner half of ear is a concave striated surface for reception of matching raised surface (provinculum) of right valve.

Adductor muscle impression, situated posterior of center at about mid-height, consists of two overlapping suboval portions (quick and catch muscle impressions), with two discrete small oval impressions antero-dorsally above. Two small oval impressions occur in umbonal cavity adjacent to base of anterior auricle, one at top of umbonal cavity, the other close to byssal notch. Pallial line continuous. Central third of inner shell surface, on outer shell layer, marked by fine radial striae.

COMPARISONS. "*Pseudamussium*" *hybridum* and *P. septemradiatum* differ primarily in external morphology. The former has weak ornament which is discrepant, with the left valve possessing fine radial costae or striae and the right valve being smooth or having weak radial ornament which is best developed on the dorsal flanks of the shell, a narrow fasciole, and a strong ctenolium. *P. septemradiatum* has similar plicate ornament on both valves, and no fasciole or ctenolium. The pattern of muscle impressions and the hinge morphology of both species are similar, except that "*P.*" *hybridum* has weak tooth-like processes at the end of the provincula on either side of the resilifer and its cardinal crura begin

above the outer end of the provincula and not near the resilifer as on *P. septemradiatum*.

These differences, especially of ornament, if consistent over the species included in the groups, possibly warrant separation at the subgeneric level of the "P." *hybridum* group from the *P. septemradiatum* group.

*Syncyclonema* differs in external and internal morphology from both *Pseudamussium septemradiatum* and "P." *hybridum* groups. The radial plicae of *P. septemradiatum* and the radial costae and discrepant ornament of "P." *hybridum* are in no way similar to the virtually smooth shell of *S. halli*. Provincula surfaces and dorsal flat-topped cardinal crura are present on *P. septemradiatum* and "P." *hybridum* but absent on *S. halli*. The cardinal crus on the posterior ear of the left valve of *P. septemradiatum* and "P." *hybridum* are long but are short on *S. halli*. *P. septemradiatum* and "P." *hybridum* have a subcentral muscle impression but that of *S. halli* is close to the base of the posterior ear.

#### GENERAL COMMENTS

Further detailed morphological and nomenclatural studies are required to clarify the generic status and the phylogeny of small pectinids. Data from musculation, hinge morphology, and shell structure, may facilitate classification. Hinge morphology and its terminology warrants close attention. The distinction of cardinal crura which bear ligament attachment areas from those that do not may help classification.

*Syncyclonema* differs from the genera it has been compared to in the past by external or internal morphology, or both. Lack of knowledge of the morphology and biostratigraphy of small Upper Cretaceous and Lower Tertiary pectinids prevents a discussion of the phylogeny of *Syncyclonema*. The occurrence of externally closely similar species in the Cretaceous (*Pecten miyakoensis*), Eocene (*Eburneopecten scintillatus*), and Recent (*Pectinella sigsbeeii*) suggests the widespread occurrence of homeomorphy in the Pectinidae.

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