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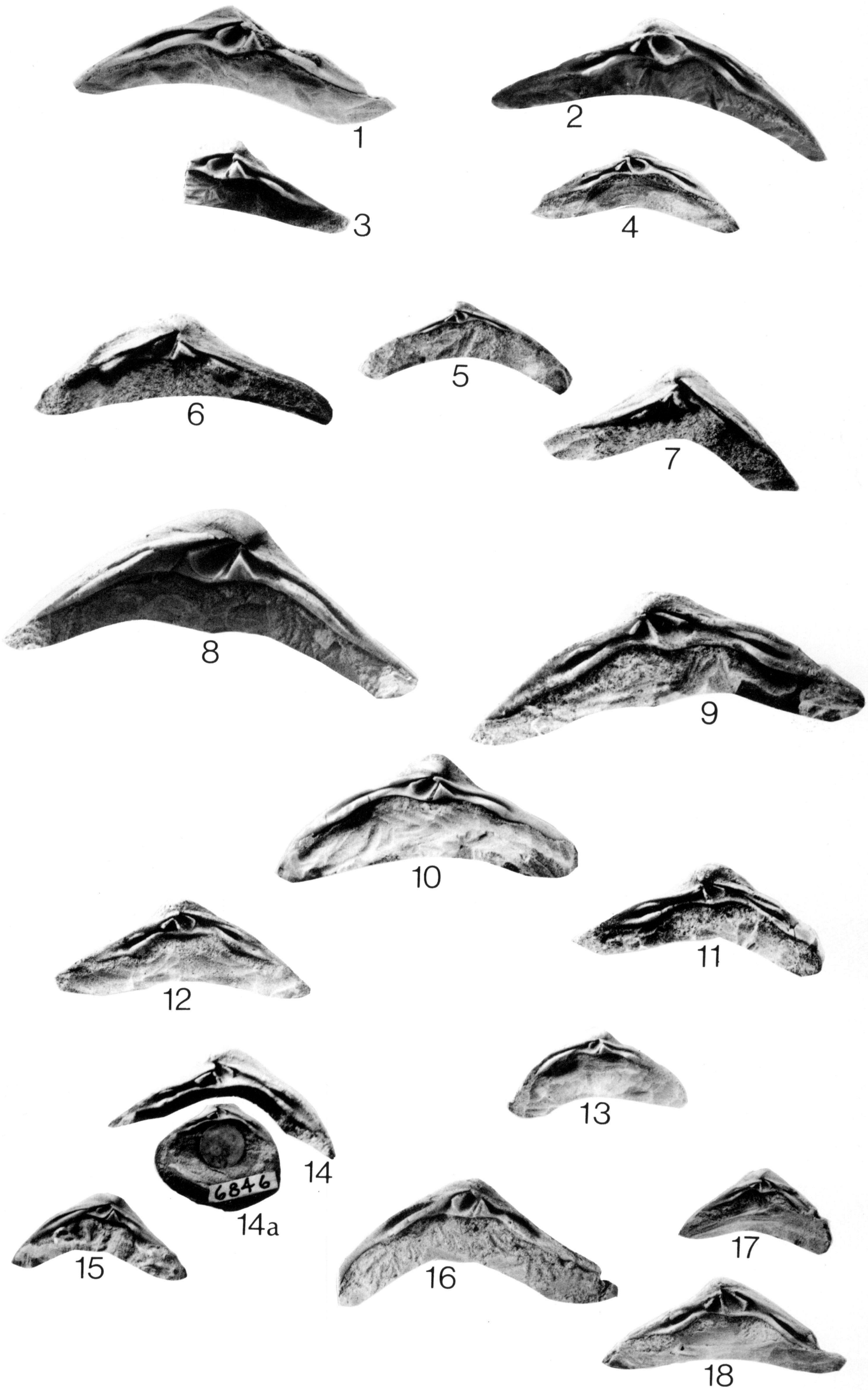
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DESCRIBED OR FIGURED WEST COAST SPECIES OF *CYMBOPHORA*

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ABSTRACT—The type species of *Cymbophora*, Gabb, 1869, *C. ashburnerii* (Gabb) is one of the most commonly reported West Coast Cretaceous bivalves. Specimens so identified are of varying shape and ornamentation and range in age from Albian? to Maestrichtian. In parallel fashion, similar but more strongly ribbed specimens have been assigned to *C. gabbiana* (Anderson). A lectotype is designated for *C. ashburnerii* to provide a standard for recognition of the species and make possible a clearer definition of the genus *Cymbophora*. The mactrids commonly confused with *C. ashburnerii* occur in numerical abundance and specific diversity in arenaceous rocks, but this paper discusses only the eight previously described or figured species. Two, *C. bella* and *C. popenoei*, are here named. These eight species can for the first time be associated with specific stages: *C. gabbiana* (Anderson) middle to late Turonian; *C. stantoni* (Arnold) Campanian; *C. suciensis* (Whiteaves), *C. buttensis* Anderson, and *C. bella* n. sp. early Campanian; *C. popenoei* n. sp. and *C. triangulata* (Waring) late Campanian; and *C. ashburnerii* (Gabb) [? = *Mactra tenuissima* Gabb] Maestrichtian.

Of the eight described or figured *Cymbophora* species, six can be paired on the basis of five relatively stable morphologic features common to both: *C. stantoni-C. ashburnerii*, *C. suciensis-C. triangulata*, *C. gabbiana-C. popenoei*. Paired species exhibit trends involving enlargement and lengthening of the resilifer and lengthening of the pallial sinus which are not synchronous with such trends in other pairs. Both species of each of these three lineage-pairs commonly occur in matrix of similar grain-size. Three lineage-pairs suggests that at least three concurrent species of *Cymbophora* may be found at any given stage in the Late Cretaceous of the West Coast.

INTRODUCTION

In a paper on the origin of the Mactridae (Saul, 1973), I compared the characteristics of *Cymbophora* to other Cretaceous mactrids but failed to take into account the uncertainty that surrounds the type-species of *Cymbophora*, *Mactra ashburnerii* Gabb. Knowledge of the characterictics of its type-species is necessary for a clearer diagnosis of this widely recognized genus ("U. Cret., E. N. Am.-W. N. Am.-Eu," Keen, *in* Moore, 1969, p. N598). Confounding of species as *C. ashburnerii* (Gabb) can only be reduced by an unequivocal selection of a lectotype from Gabb's original material. A lectotype makes possible for the first time the illustration and description of the hinge of *C. ashburnerii*. Seven other described or figured species of

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EXPLANATION OF PLATE 1

FIGS. *1–4*—*Cymbophora ashburnerii* (Gabb). *1,* Left hinge, paralectotype (ANSP 4441a), ×1, photo by T. Susuki. *2,* Right hinge, hypotype (UCLA 48516), ×1. *3,* Left hinge, hypotype (UCLA 48515), ×1. *4,* Right hinge, hypotype (UCBMP 14117), ×1.

5–7—*Cymbophora stantoni* (Arnold). *5,* Right hinge, hypotype (UCLA 48505), ×1. *6,* Left hinge, hypotype (UCLA 48503), ×1. *7,* Right hinge, hypotype (UCLA 48502), ×1.

8–9—*Cymbophora buttensis* Anderson. *8,* Left hinge, hypotype (USMN 187735), ×1. *9,* Right hinge, hypotype (UCLA 48541), ×1.

10–11—*Cymbophora bella* n. sp. *10,* Left hinge, holotype (UCLA 48533), ×1. *11,* Right hinge, paratype (UCLA 48535), ×1.

12—*Cymbophora triangulata* (Waring), right hinge, hypotype (UCLA 48522), ×1.

13—*Cymbophora popenoei* n. sp., left hinge, paratype (UCLA 48492), ×1.

14–15—*Cymbophora suciensis* (Whiteaves). *14-14a,* Right hinge, hypotype (UCLA 6846); *14,* ×2; *14a,* ×1. *15,* Left hinge, hypotype (UCLA 6847), ×1.

16–18—*Cymbophora gabbiana* (Anderson). *16,* Left hinge, holotype (CAS 1), ×1, photo by T. Susuki. *17,* Right hinge, hypotype (UCLA 6853), ×1. *18,* Right hinge, hypotype (UCLA 48490), ×1.

Cymbophora, all of which have been confused with *C. ashburnerii*, are redefined; and each has been found through strata representing a briefer geologic time interval than formerly reported. In addition to *M. ashburnerii* of Maestrichtian age, five previously described species can be placed in *Cymbophora* s.l.: *M. gabbiana* Anderson of middle-to-late Turonian age; *C. buttensis* Anderson and *Laevicardium suciense* Whiteaves of early-to-middle Campanian age; *M. stantoni* Arnold ranging through the Campanian; and *Crassatellites triangulatus* Waring of late Campanian age. Two new species of Campanian age are described: *C. popenoei* associated with *Metaplacenticeras pacificum* (Smith) and based upon specimens figured by W. P. Popenoe (1937, p. 398, pl. 49, fig. 2; Popenoe, 1954, p. 18, fig. 3(4)) and *C. bella* associated with *Submortoniceras chicoense* (Trask).

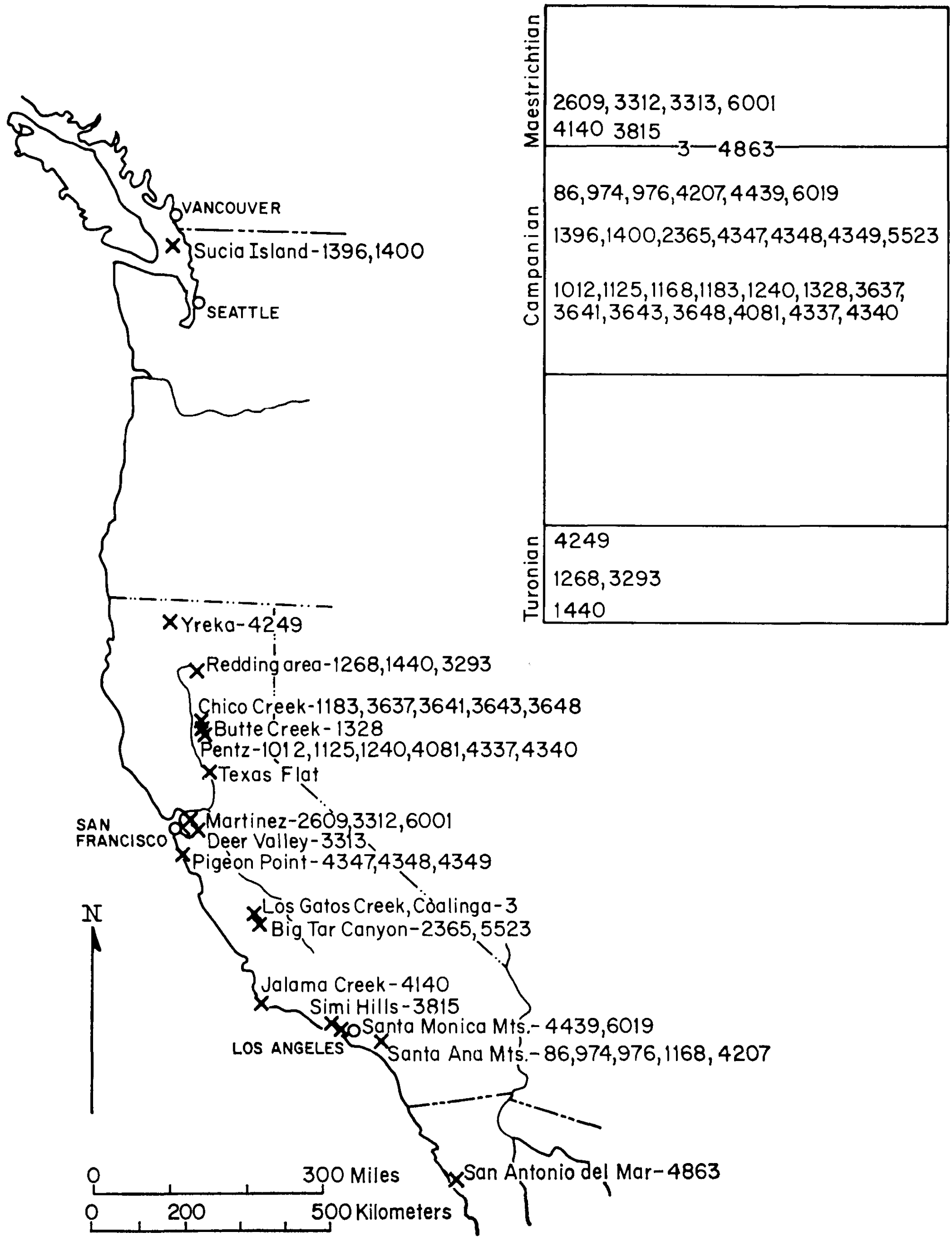
Comparing relatively stable morphologic features of these mactrids results in three pairs of species: *C. stantoni-C. ashburnerii*, *C. suciensis-C. triangulata*, and *C. gabbiana-C. popenoei.* The different geologic time occurrence of each of the members of these pairs suggests that these may represent three lineages. *C. buttensis* and *C. bella* are not, based on the features used, similar enough to each other or to any of the other six species for close relationship to be inferred and may suggest still other lineages. Description of these species has indicated the usefulness of two new morphologic terms: *selenis*, for the area of the anterior slope developed on ectostracum and bounded flankward by a preumbonal groove or a change in sculpture or growth line flexure, and *tensilifer*, for the attachment area of the tensilium.

TYPE SPECIMENS OF *MACTRA ASHBURNERII*

There is no doubt about the name of the type-species of *Cymbophora.* Gabb (1869, p. 180) stated, "I propose this genus for one of the most common fossils of the California Cretaceous, *Mactra Ashburnerii.*" The species is, furthermore, type by monotypy. Confusion has existed in knowing what is *Mactra ashburnerii.* Gabb (1864, p. 153) lists 13 localities at which he recognized this species. Strata at these localities are of various ages ranging from Turonian to late Eocene. Some of Gabb's material for *M. ashburnerii* is still available at the Academy of Natural Sciences of Philadelphia and at the Museum of Paleontology, University of California, Berkeley, but none of the specimens can be recognized as being the basis for Gabb's original figure (1864, pl. 22, fig. 127). Type lots at these two institutions also include specimens collected subsequent to the original description, and there is, in general, no way of separating original (1864) from subsequent material. Both lots include material from more than one horizon and more than one locality, and the locality or localities listed on the labels have only a fortuitous connection to the place of origin of the fossils, but the probable locality and horizon of the specimens can be recognized by comparing them to specimens of known provenance.

Because both the Museum of Paleontology's "original" material and the Philadelphia Academy's "original" material include specimens of Eocene as well as Cretaceous age, it would be possible to choose as lectotype a specimen of Tertiary age. The consensus of paleontologists dealing with this material and with West Coast mactrids of Cretaceous and early Tertiary age has been that *M. ashburnerii* and *Cymbophora* should be based upon Cretaceous specimens and Tertiary specimens are therefore excluded. Gabb's description and figures (1869, p. 180, pl. 29, fig. 69, 69a) of the hinge of *Cymbophora* are no doubt in large measure responsible for restricting *Cymbophora* to the Cretaceous, as no Eocene mactrids have been found having a prominent internal nymph bounding the dorsal side of the resilifer. This internal nymph forms one side of the spoon-shaped process for which the genus is named.

There remain in Gabb's collections at the two institutions specimens that can be recognized as coming from Pentz, Chico Creek, and Martinez, California. All but one of the Berkeley specimens are marked "California Geological Survey coll. 136"; three specimens have been catalogued as paratypes UCBMP cat. nos. 14925–14927. Preservation, matrix, and recognition of the species indicates that these three paratypes are all from Pentz. One of these, 14925, is labelled in Gabb's handwriting "*Mactra Ashburnerii* G., Pence's, Martinez, Marsh's & Alizo Creek," but both it and 14926 which is from the F. L. A. Pioche collection are ribbed forms. Gabb included the ribbed forms in *M. ashburnerii* (1864, p. 153) but his original illustration is of a smooth form like UCBMP cat. no. 14927. Unfortunately, this latter specimen has a handwritten label, "*Cymbophora Ashburnerii* G." and is therefore post 1864. Because Gabb figured a smooth form and the ribbed forms have been excluded from *C. ashburnerii* since the 1902 description of *M. gabbiana* Anderson, only



TEXT-FIG. *1*—Index map. Numbers refer to fossil localities. Fossil localities are listed in numerical order following a geographical place name and their relative ages are given in the column. Fossil localities of approximately equal age are listed in numerical order.

smooth specimens have been considered in choosing a lectotype for *M. ashburnerii.* Perversely, none of the excavated hinges of smooth forms is as similar to Gabb's 1869 figures of the hinge of *C. ashburnerii* as is the hinge of the ribbed form from Pentz, *C. bella* n. sp.

Richards (1968, p. 33) citation of a lectotype for *Cymbophora ashburnerii* Gabb is defective on all counts. The species was described in 1864 as *Mactra ashburnerii*, not 1869 as *Cymbophora ashburnerii*; Stewart (1930, p. 213) did not select a lectotype; he wrote: "It is hoped that a better specimen of the originals than the one figured here may yet be found, but it may be necessary later to designate this specimen the lectotype." The hinge of the species represented by the specimens ANSP cat. no. 4441 is not that figured in the reference Richards cites: Gabb, 1869, pl. 29, fig. 69 (why not also 69a?). Richards gives the locality as Texas Flat without any questioning notation although Stewart explained that whereas the label of ANSP cat. no. 4441 reads "Texas Flat," the preservation and matrix of these specimens is not that of Texas Flat but is that of Martinez. The species represented by ANSP cat. no. 4441 occurs in the vicinity of Martinez but does not occur at Texas Flat.

The specimen figured by Stewart (1930, pl. 5, fig. 6, 6a) has served as a model for *C. ashburnerii* for forty years, and there is no compelling reason for choosing another of the smooth forms. The specimen figured by Packard (1916, pl. 27, fig. 1) is apparently lost, and there is no indication that it was part of the original material. It may have been from Pentz, that being where Packard (1916, p. 299; also Anderson, 1958, p. 144) claimed the type of *C. ashburnerii* was found, but specimens similar to Packard's figure are also found at the top of the section at Chico Creek. The relatively smooth form from Pentz, here referred to *C. stantoni* (Arnold) is a little more similar in shape to Gabb's original figure than is the form illustrated by Stewart, and there are several such specimens in the "original" lots, but none have been figured and so they have had little or no influence on anyone's concept of the species *M. ashburnerii*. The label of ANSP cat. no. 4441 in Gabb's hand suggests that it was part of the original material upon which Gabb based *M. ashburnerii* and the specimen figured by Stewart is here designated the lectotype.

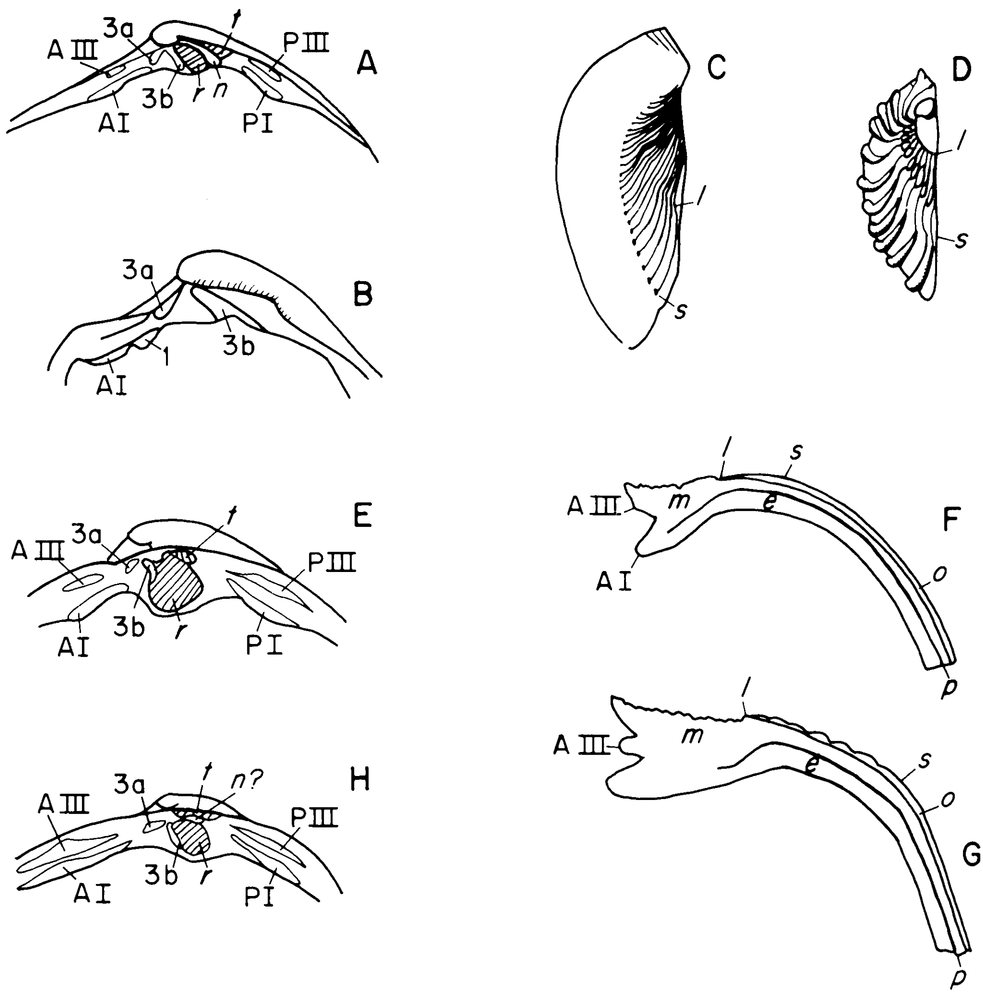
How the specimens ANSP cat. no. 4441 came to be labelled as being from Texas Flat is unknown, but this error is matched by the labels of other "original" lots. That of the California Geological Survey coll. 136 at University of California, Berkeley, reads, "Martinez, Carquinez Strait quad., Cal." but nine of these specimens are probably from Pentz, one probably from Chico Creek and one may be Eocene and from some place nearer Martinez (Text-fig. 1). The lectotype (ANSP cat. no. 4441) and lectoparatype (ANSP cat. no. 4441a) are clearly on the basis of preservation, matrix, and occurrence of the species, from the Maestrichtian beds in the vicinity of Martinez, Contra Costa Co., California; and Martinez must be the type locality of *Mactra ashburnerii* Gabb.

COLAMINAR, SELENIS, AND TENSILIFER

Three morphological terms require mention before discussing the hinge of *Cymbophora* s.s. and characteristics common to these eight West Coast species of *Cymbophora* s. l.

Colaminar.—According to Casey (1952, p. 124) *colaminar* is applied to "A cardinal tooth more or less in alignment and in continuity with a lateral, forming with the lateral a virtually single lamina" (Text-fig. 2B). Rather than introduce a new term, Casey's term colaminar is used more broadly than he defined it and applied to the whole of the anterior lateral either AI (Text-fig. 2A) or AII when the lateral has a bimodally curved profile and a narrowing of the lamina followed by a swelling at its dorsal end. It is this swollen end to which Casey's definition would apply; but to recognize as cardinals, teeth not yet separated from the laterals and not in a cardinal position, seems descriptively confusing. To refer to the whole lateral as colaminar and discuss its degree of division expresses the actual morphologic state without obscuring probable relationships and evolutionary trends. A basically Bernard system of notation is used for the hinge teeth because mactrid hinge teeth are homologous to those of arcticids, corbiculids and venerids (Saul, 1973); and the evolution of the mactrid hinge is similar, except for the resilifer, to the evolution of corbiculoid hinges traced by Casey (1952). Some of the Cretaceous mactrids have a readily recognized arcticoid hinge type with colaminar laterals AI and AII.

Selenis.—Many mactrids have a distinctive area on the anterior slope of the valve (Pl. 3, figs. 2, 5, 7, 12, 15, 17, 19; Text-fig. 2C). This area differs from the flank in sculpture; it may be set off from the flank by a groove that radiates from beneath the beak and reaches the valve margin near, usually just anterior to, the anterior angulation; or this area may be set off from the flank by an aligned emargination of the growth lines. In all specimens so far seen, the boundary of this area lies along the path of the anterior adductor muscle scar. To simplify descriptions, I am referring to this area as the *selenis*.



TEXT-FIG. 2—Diagrams for colaminar, selenis, and tensilifer. *e* = endostracum or inner layer of shell; *l* = boundary of lunule; *m* = mesostracum or middle layer of shell; *n* = nymph; *o* = ectostracum or outer layer of shell; *p* = myostracum or shell layer underlying pallial and adductor muscles; *r* = resilifer; *s* = boundary of selenis; *t* = tensilifer; 3a, 3b, 1 = cardinal teeth; AI, AIII, PI, PIII = lateral teeth. *A, Cymbophora ashburnerii* (Gabb) (UCLA 48516, hypotype), ×1. Lateral tooth AI has a bimodally curved profile and a swelling at its dorsal end and is thus colaminar. The tensilifer lies along the dorsal side of an internal nymph. *B*, an arcticoid hinge after Casey (1952, text-fig. 1B) showing Casey's use of colaminar which applies to that portion of AI labeled cardinal 1 by Casey. *C, Cymbophora suciensis* (Whiteaves) (UCLA 48520, hypotype) ×2, a mactrid in which the selenis is defined by a change in sculpture, a shallow radial groove, and a slight emargination of the growth lines; the lunule is obscurely indicated by a shallow flexure of the growth lines. *D, Placamen isabellina* (Philippi) (UCLA 48915, hypotype, Holocene, Queensland, Australia) ×1, a venerid in which the selenis is defined by a broad shallow radial trough and an emargination of the growth lines. The lunule is clearly marked by a groove, *E, Mulinia edulis* (King) after Lamy (1917, p. 329). The tensilifer is internal and has no shelly separation from the resilifer. *F, Mactromeris polynyma alaskana* (Dall) (UCLA 51268, hypotype, Holocene, Dall Island, Alaska) ×2, a section of shell 14 mm. from the beak, cut perpendicular to the hinge line in which four shell layers, endostracum, myostracum, mesostracum, and ectostracum, can be differentiated. The lunule is underlain by mesostracum—the same shell layer of which the hinge is constructed; the selenis is underlain by ectostracum. *G, Mactra veneriformis* Reeve (UCLA 48914, hypotype, Holocene, Japan) ×4, a section 4 mm. from the beak, analogous to that of *F* with lunule underlain by mesostracum and selenis by ectostracum. *H, Mactra corallina* (Linnaeus) after Lamy (1917, p. 177). The tensilifer is separated from the resilifer by a shelly shelf = a residual nymph?

Lunules of these eight species of *Cymbophora* are expressed only as an obscure depression near the beak bounded by a low, broad welt that is the external track of the anterior end of the hinge (Text-fig. 2C). In general the lunule of mactrids is usually not strongly enough marked to be descriptively useful, but it can be recognized (Carter, 1967, pl. 35B, J). A section of shell cut through the anterior hinge area perpendicular to the valve margin shows that as in the venerids, cardids, and lucinids discussed by Carter (1967, text-fig. 1), the lunule of mactrids is made up of the same shell layer as is the hinge (Text-fig. 2F-G) and is apparently a more fundamental structure than the selenis. If a depressed lunule is a hinderance in rapid burrowing as suggested by Kauffman (*in* Moore, 1969, p. N168), the lack of a well-bounded, depressed lunule in such venerids as *Tivela* and *Meretrix* and in most mactrids might be related to their recurring need to burrow rapidly into the wave and/or current disturbed, sandy substrate most of them inhabit.

I have no suggestion as to the origin or usefulness to the clam of a selenis, but such a structure is a boon to the paleontologist trying to differentiate relatively featureless, similarly shaped mactrid shells. Furthermore characteristics of ornament and boundry definition appear to link some species and so may aid in relating species into phylogenies.

The selenis is especially well marked in such West Coast Cretaceous species as *C. gabbiana* (Anderson), *C. popenoei* Saul, *C. suciensis* (Whiteaves) and in the Indian *C. tripartita* (Forbes) (Stoliczka, 1870, p. 57, pl. 5, fig. 8–11). Among Holocene mactrids equipped with a selenis are *Mactra chinensis* Philippi, "*Spisula*" *sachalinensis* (Schrenck), and *Mactra corallina* Linnaeus. A selenis is also present in the venerids *Bassinia*, *Placamen* (Text-fig. 2D), and *Dosinorbis*.

Tensilifer.—Cox (p. N49), Trueman (p. N58–64), and Kauffman (p. N174–175) (all *in* Moore, 1969) discuss terminology, structure, and morphology of the ligamenture of bivalves, but do not supply a term for the attachment area of the tensilium (Tebble, 1966). This area is here called the *tensilifer*. As an analogue of resilifer, the term tensilifer seems so useful in descriptions of fossil bivalves which have the ligament separated into two parts that it can hardly be a new term, but I have been unable to find it used.

In mactrids the tensilifer may be either wholly external (Text-fig. 2H), partially external (Text-fig. 2A), or wholly internal (Text-fig. 2E). It may lie along the inner edge of the valve margins (Text-fig. 2E), or along the valve margins and in part on a small inner shelf (a residual nymph?) separating the tensilium from the resilium (Text-fig. 2H), or along nymphae which may be either wholly external (Saul, 1973, text-fig. 4m-o), partially external (*ibid*, p-q), or internal (Text-fig. 2A). Use of the term tensilifer for this attachment area in Cretaceous mactrids does away with the objectionable use of "ligamental area" which was formerly used for the attachment area of the "ligament proper or external ligament" rather than the whole of the ligament.

Although by analogy with Holocene mactrids the tensilifer was probably the attachment area for the lamellar layer of the ligament just as the resilifer was probably the attachment area for the fibrous layer (Trueman, *in* Moore, 1969, p. N58), the ligament itself is not preserved in Cretaceous specimens. Holocene Semelidae have both lamellar and fibrous layers in the tensilium and resilium of their ligament (Trueman, 1953) and such terms as resilifer and tensilifer, which are non-committal as to the composition of those parts of the ligament attached thereto may be useful for hinge descriptions of that family as well as for mactrids. Very early mactrids with small resilial notches probably did not have the lamellar and fibrous layers so neatly segregated as do Holocene mactrids. The tensilium of such early Cretaceous mactrids probably contained both layers although it is likely that the resilium did not.

Marks made by the attachment of the resilium can be seen in the resilifer on most of the hinges of *Cymbophora* exposed for this paper. The attachment of the tensilium is much less clearly marked. In specimens of *Cymbophora* which are well enough preserved to show marks of attachment, they occupy the deep, narrow, wedge-shaped trough formed by the dorsal side of the submerged nymph and the shell margin, and like the resilium the posterior end of the tensilium traces an arcuate bulge on the hinge plate.

HINGE OF *CYMBOPHORA* S.S.

Comparisons of the hinge of *Cymbophora* to those of other genera have been based on Gabb's figures which are probably of *C. bella* n. sp., on illustrations of several Gulf Coast species assigned to *Cymbophora* but which have striated rather than granulated laterals;

and on Popenoe's figure (1937, pl. 49, fig. 1) of *C. triangulata* (Waring). Not one of these hinges is typical of *Cymbophora* s.s. The exposed hinges of *C. ashburnerii* (Gabb) show that the genus characteristically has two cardinal teeth in each valve (see Pl. 1, figs. 1–4; Text-fig. 2A). The cardinals of the right valve are lamellar and form an inverted V; cardinal 2b of the left valve is bifid and 4b is very thin. Three of the cardinals, 3b, 2b, and 4b extend to the edge of the hinge plate. The laterals are distant from the beak, elongate, and lamellar; the right valve has two anterior and two posterior laterals, the left valve has one of each. Laterals AI, AII, PI, and PII are ornamental by fine granulations on the upper part of their dorsal surfaces. The tensilifer is as long as the resilifer, extending from a point just behind the beaks in a wedge-shaped trough. The dorsal side of the trough is made by the inner edge of the shell margin, the anterior side of the trough by the strong, submerged nymph. The resilifer which is more shoe-horn than spoon-shaped lies immediately anterior to the submerged nymph which forms the raised dorsal side. In the left valve the resilifer abuts against cardinal 4b; in the right valve it is close enough to cardinal 3b so that it appears to have a raised anterior margin in that valve also, but there is actually a narrow space, a socket for 4b, between the resilifer and 3d. Thus, hinges of equal size from the same species appear to have a broader resilifer in the right than in the left valve.

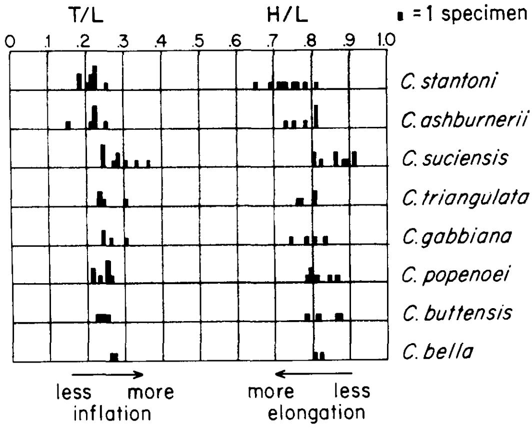
CHARACTERISTICS OF *CYMBOPHORA* S.L.

These aforementioned eight species all have a triangular shape in plan view with the beaks curled forward over a slightly excavated anterodorsal margin. All have some concentric ribs fanning from the beaks. The corcelet of these eight species is made up of two distinct areas; a marginward area lying along the posterior shell margin sculptured by concentric ribs at least near the beak, and an unribbed but usually roughened, acutely triangular area that includes the posterior angulation. In some species (*C. ashburnerii, C. suciensis, C. triangulata, C. gabbiana,* and *C. popenoei*) this second area is a broad welt, in others (*C. bella, C. stantoni,* and *C. buttensis*) it is gently sulcate and in the case of *C. buttensis* is bounded by low but well marked folds.

The arrangement of the granulations on the lateral teeth is such that the granulate dorsal surface is against a smooth ventral surface for all teeth. A similar arrangement of granulations is present in Holocene *"Spisula" sachalinensis* (Schrenck) from Japan. Holocene Atlantic *Spisula* sp. and Cretaceous Western Interior and Gulf Coast *"Cymbophora"* have laterals AII and PII that are vertically striated on both surfaces. Furthermore, these striations face vertical striations of the dorsal surfaces of AI and PI and the ventral surfaces of AII and PIII. These vertical striations can be interpreted as structures which aid in the exact alignment of the closing valves; but the granulations on *Cymbophora* and its allies do not appear capable of improving alignment. Having a roughened surface face a smooth surface is a means of reducing friction (e.g. the base plate of a carpenters plane), but I am uncertain about how much tooth-to-tooth contact there was in *Cymbophora.* Lateral teeth of *"Spisula" sachalinensis* are in closest contact where a granulated surface passes a smooth surface. Obviously, in life this movement takes place in water, and the valve could not be expected to open readily if a vacuum were developed in the socket. Fluid either in mantel tissue or external to it probably replaces the tooth in the socket and moves aside as the valves close. Possibly the granulations provide a space for migration of fluid which could lubricate the movement of the laterals past each other and facilitate opening and closing of the valves. That the presence and position of the granulations is related to reduction of friction, rather than alignment of valves is further suggested by granulations being largest and strongest on long strong laterals which of themselves align the valves neatly and weakest on shorter, slender laterals which are less effective in aligning the valves.

A plot of ratios of thickness/length and height/length for eight species of *Cymbophora* (Text-fig. 3) helps explain why these species have been so easy to confound as *C. ashburnerii.* Deformation of some of the specimens is in part responsible for the spread in a ratio of a single species as, for instance, the H/L ratio of *C. stantoni.* It can be seen that *C. stantoni* and *C. ashburnerii* are usually less inflated and more elongate than the other six species and that *C. suciensis* is the least elongate and the most inflated. Slight differences in average proportion that show up poorly on the graph none-the-less are apparent enough to the eye so that these species can be distinguished on form and ornamentation, and exposing the hinges is not always necessary.

All eight species have a U-shaped pallial sinus which in the following descriptions is



TEXT-FIG. 3—Ratios of T (thickness)/ L (length) and H (height)/ L (length) for eight species of *Cymbophora*. Ratios are from Tables 1–8.

said to be *ascending* if a straight extension of the ventral side of the pallial sinus would intercept or lie dorsal to the anterior aductor scar or *horizontal* if the straight extension would lie ventral to the anterior aductor muscle scar. The relative length of the pallial sinus has been given in two ways: in the tables as a ratio of pallial sinus length to shell length, and in the descriptions length of pallial sinus is compared to the length of the *posterior portion* of the shell. Posterior portion of the shell refers to that area which is posterior to a vertical line dropped from the beak to the ventral margin.

SYSTEMATIC PALEONTOLOGY

The following abbreviations are used in association with locality and catalogue numbers: ANSP = Academy of Natural Sciences of Philadelphia; CAS = California Academy of Sciences; CGS = Canada Geological Survey; CIT = California Institute of Technology; LSJU = Stanford University; UCB = University of California, Berkeley; UCBMP = University of California, Berkeley, Museum of Paleontology; UCLA = University of California, Los Angeles; USGS = U. S. Geological Survey; USNM = U. S. National Museum.

CYMBOPHORA STANTONI (Arnold)

Pl. 1, figs. 5–7; Pl. 2, fig. 4, Pl. 3, figs. 3–6; Table 1

Mactra stantoni Arnold, 1908, p. 357, pl. 31, fig. 3; ARNOLD, *in* BRANNER, NEWSOM, and ARNOLD, 1909, illust., II, fig. 3.
Mactra ashburneri Gabb, ARNOLD, 1909, p. 11, Pl. 1, fig. 4; ARNOLD, *in* ARNOLD and ANDERSON, 1910, p. 60, Pl. 23, fig. 4.
Cymbophora ashburnerii (Gabb) SCHENCK and Keen, 1940, Pl. 17, fig. 3.

Description.—Shell of average size for the genus, thin for its size, of less than average inflation. Beaks moderately prominent; anterior margin nearly straight, sloping to poorly defined anterior angulation, curving in a "duck bill" outline to the slightly curved ventral margin, curvature increased near the posterior angulation, obtusely angled to the convexly curved posterior margin, posterior angulation low but well-marked with two unequal folds and a slight sulcus between. Surface of flank nearly smooth, lightly marked by growth lines between the growth checks which are impressed and emphasized by multiple concentric grooves; anterior slope ornamented by sharp well-spaced concentric ribs fanning from beneath the beak and dying out at the anterior angulation; selenis defined by diminution of ribbing, lightly impressed line, and bend in growth lines and ribbing; posterior slope with similar, more broadly spaced ribs, dying out at the less prominent, more marginward fold on the posterior angulation.

Resilifer extending to the edge of the hinge plate, as high as the widest part of the plate. Hinge of right valve with 3a and 3b equal, 3a parallel to valve margin, petaloid, 3b as long as the width of the hinge plate, slightly shorter than the resilifer; laterals AI and PI ornamented by fine granulations on the upper half of their dorsal surfaces, AI faintly colaminar with a broad beakward slanting groove on its dorsal side. Hinge of left valve with inverted V of 2b half-filled, 4b very thin. Pallial sinus deep, extending nearly across the posterior portion of the shell, nearly horizontal.

Holotype.—USNM cat. no. 31001 (plaster cast UCLA cat. no. 48446).

Hypotypes.—UCBMP cat. no. 14927 (paratype? of *C. ashburnerii* (Gabb)), probably Pentz, Butte Co., Calif.; USNM cat. no. 31074 (hypotype of *C. ashburnerii* (Gabb) plaster cast UCLA cat. no. 48350), Arnold's loc. 3, N. of Los Gatos Creek, Coalinga District, Calif.; UCLA cat. nos. 48502–48503, UCLA loc. 4347, N. of Pigeon Point; UCLA cat. nos. 48505–48506, UCLA loc. 4340, near Pentz; UCLA cat. no. 48507, CIT loc. 1012, near Pentz; UCLA cat. no. 48508, UCLA loc. 4337, near Pentz; UCLA cat. no. 48531, CIT 1328, Butte Creek.

Type locality.—1 mile north of Pigeon Point, Santa Cruz quad., San Mateo Co., California (Arnold, 1908, p. 357).

TABLE *1*—Measurements in mm of *Cymbophora stantoni* (Arnold)

Cat. no.	H	L	T	H/L	T/L	S	S/L	RH	RW	RW/RH	Remarks
48350	21	27	6	.78	.22						distorted
48446	30	46	10	.65	.22						distorted
48502	34	42	9	.81	.21			3.5	1.7	.49	very distorted
48503	34	49	9	.69	.18			4	2.4	.6	slightly distorted
48505	21	29.5	6	.71	.2			1.7	1	.59	
48506	18	25	5.5	.72	.22						
48507	16	22	5	.73	.25	10	.45				
48508	25	33	6	.76	.18	16	.48				
48531	21	28	6	.75	.21	16	.52				

H=height of valve; L=length of valve; T=thickness of valve; S=length of pallial sinus; RH=height of resilifer; RW=width of resilifer.

Age.—Campanian; from *Submortoniceras chicoense* to *Metaplacenticeras pacificum* zones.

Remarks.—UCLA localities 4347, 4348, and 4349 which are near Arnold's type locality, have produced dozens of specimens of this species. All are more or less post depositionally deformed making their outlines dissimilar and difficult to use as a standard for comparison. Both of the illustrated hinges from UCLA loc. 4347 are broken and depressed through the resilifer, the right hinge being much more distorted than the left. Because the holotype and topotypes are distorted, recognition of this species at other localities has depended largely upon the flange-like aspect of the ribbing fanning from beneath the beak, the low inflation of the valves, the slight sulcus between the posterior folds, and the multiple concentric grooving at the growth checks. The description of the pallial sinus is derived from specimens from the Chico Formation of Pentz and Butte Creek, Butte Co., California. The outline of the Butte County specimens is not so distorted as that of those from Pigeon Point, but even the best of these have only small patches of the original shell surface preserved. Etching and peeling of the surface increase the ribbed aspect of the flank of the shell.

Arnold's specimens of *M. ashburneri* (Arnold, 1909, Pl. 1, fig. 4; reprinted by Arnold and Anderson, 1910; Schenck and Keen, 1940) from loc. 3 near Los Gatos Creek, north of Coalinga, Fresno Co., Calif., are poorly preserved. His small figured specimen is high for *C. stantoni* but the inflation of the valve and sculpture near the beak most resemble *C. stantoni*. The occurrence of *Meekia* (*Mygallia*) *daileyi* Saul and Popenoe (Arnold, 1909, Pl. 1, fig. 5 as *M. sella* Gabb) there suggests that Arnold's loc. 3 material is no older than late Campanian. *C. stantoni* (Arnold) is also found in the Pleasants Sandstone of late Campanian age in the Santa Ana Mts., California (Popenoe, 1942, fig. 4, CIT loc. 86 and 974 as *C. ashburnerii*) associated with *Metaplacenticeras pacificum*.

Spisula (*Cymbophora*) *ashburnerii* (Gabb) of Packard (1916, p. 298, Pl. 27, fig. 1) may be this species, but the specimen is lost. The measurements Packard gives fit either a *C. stantoni* of above average inflation or a *C. suciensis* of less than usual inflation and height. Packard's hinge description cannot apply to *C. stantoni*, however, as he describes the laterals as heavy. It could apply to *C. suciensis*, but it may be a rephrasing of Gabb (1869, p. 180). Packard's hinge description contains no new information and repeats all of Gabb's, including the erroneous absence of cardinal tooth 3b. Judging from the figure, Packard's specimen came either from Pentz or Chico Creek, Butte Co., Calif.

Small specimens of *C. stantoni* are common at Pentz, but a few from CIT loc. 1328, Butte Creek, Butte Co., equal the size of those from north of Pigeon Point, San Mateo Co., Calif. Also of similar size is a specimen from UCLA loc. 5523, near Big Tar Canyon, Kings Co., which may be this species, but it is nearly exfoliated. Other mollusks from UCLA loc. 5523, e.g. *Biplica obliqua* (Gabb) suggest a Campanian age. The discrepancy in size of the Pentz specimens, the deformation of the specimens from north of Pigeon Point, the poor preservation of Arnold's two Los Gatos Creek specimens, the usually partially exfoliated shells of the Pentz and Santa Ana Mts. specimens, and the nondescript character of *C. stantoni* make these various identifications and correlations tenuous.

If correctly identified and defined, *C. stantoni* is most similar to *C. ashburnerii*. They both have the elongate, thin laterals with fine granulations, a more delicate hinge than the other species of *Cymbophora* discussed in this paper, and a similar pallial sinus.

TABLE 2—Measurements in mm of *Cymbophora ashburnerii* (Gabb)

Cat. no.	H	L	T	H/L	T/L	S	S/L	RH	RW	RW/RH	Remarks
6849	37	51	11	.73	.22	26	.51				
28775	21	26	4	.81	.15	17	.65				length incomplete
36289	43	53	11	.81	.21						
4441a	39	50	11	.78	.22			4	3	.75	
14117	26	32	8	.81	.25			2.5	2	.8	length incomplete
48515								4	3	.75	
48516	38	51	11	.75	.22			4	3	.75	

H=height of valve; L=length of valve; T=thickness of valve; S=length of pallial sinus; RH=height of resilifer; RW=width of resilifer.

Cymbophora stantoni is found in medium-grained sandstone.

CYMBOPHORA ASHBURNERII (Gabb)

Pl. 1, figs. 1–4; Pl. 2, figs. 1–3; Pl. 3, figs. 1–2; Text-fig. 2A; Table 2

Mactra Ashburnerii Gabb, 1864, p. 153 (in part, pl. 22, fig. 127).
?*Mactra tenuissima* Gabb, 1869, p. 179, pl. 29, fig. 68.
Cymbophora Ashburnerii (Gabb) GABB, 1869, p. 181 (in part); STEWART, 1930, p. 212, pl. 5, fig. 6, 6a.
Cymbophora ashburneri (Gabb) SHIMER & SHROCK, 1944, p. 431, pl. 171, fig. 26 not 27 (fig. 27 = *C. triangulata* (Waring)).

Description.—Shell of average size for the genus, moderately thin, of average inflation, roughly an isosceles triangle in outline with the ventral side longest. Beaks moderately prominent; anterior margin nearly straight, then curving abruptly at the anterior subangulation to the ventral margin; ventral margin smoothly curved, making nearly a right angle at the posterior angulation; posterior margin smoothly convexly curved; posterior angulation well-marked by sharp ridge near the beak becoming more broadly rounded and weltlike near the ventral margin. Surface of flank roughened by growth lines and marked with growth checks; selenis obscurely defined by faint groove and slight bend in growth lines, lightly irregularly concentrically ribbed close to the beak only; marginward areas of corcelet lightly concentrically ribbed only near the beak.

Resilifer broadly shoe-horn shaped, deep, set into the hinge plate, extending to the edge of the hinge plate in which it occupies the widest area. Hinge of right valve with 3a petaloid, close to but not paralleling the valve margin, 3b twice as long as 3a and as long as the width of the hinge plate, shorter than the resilifer; laterals AI and PI ornamented by fine granulations on the upper half of their dorsal surfaces, AI long, broadly slant-grooved on dorsal side, with bimodally curved profile, clearly colaminar, AIII half as long as AI and paralleling the anterior end of AI. Hinge of left valve with inverted V of 2b half-filled, 4b very thin; AII with two very broad shallow grooves on ventral side. Pallial sinus, deep, extending across the posterior portion of the shell, nearly horizontal.

Lectotype.—ANSP cat. no. 4441 (plaster cast UCLA cat. no. 36289).

Paralectotype.—ANSP cat. no. 4441a (plaster cast UCLA cat. no. 48513).

Holotype of *C. tenuissima.*—ANSP cat. no. 4361 (plaster cast UCLA cat. no. 28775), Martinez, Contra Costa Co., Calif.

Hypotypes.—UCLA cat. no. 6849, UCLA loc. 3312, Martinez; UCLA cat. no. 48515, UCLA loc. 3313, Deer Valley; UCLA cat. no. 48516, UCLA loc. 6001, Martinez; UCBMP cat. no. 14117 (plaster cast UCLA cat. no. 48514), UCB loc. 2609, Martinez.

Type locality.—"Texas Flat," but on basis of matrix, preservation and occurrence of this species: Martinez, Contra Costa Co., Calif.

Age.—Maestrichtian.

Remarks.—The holotype and only specimen of *C. tenuissima* (Gabb) is in a nearly black, limey sandstone matrix. The fossils in this rock are stained green. I have not collected such material nor have I seen any similar material with accurate locality data, but the recognition of a specimen of *Biplica miniplicata* Popenoe in one of Gabb's fragments of this matrix indicates a Maestrichtian age. The specimen of *C. tenuissima* is, furthermore, a good match for similar size specimens of *C. ashburnerii.* Stewart (1930, p. 213) complains that the supposed course of the pallial sinus has been outlined in pen or pencil, and he believed that Gabb misidentified the pallial sinus. The line of the pallial sinus shows up clearly on plaster casts of the holotype, and is very nearly as Gabb drew it, perhaps a little deeper. It resembles that of *C. ashburnerii.*

Cymbophora ashburnerii is most similar to

C. stantoni (Arnold) from which it differs in its more convex posterior outline and greater inflation of the valves. *C. ashburnerii* has a more advanced hinge with lateral AI more strongly colaminar, cardinal 3a more petaloid, and the resilifer larger. All "*C. ashburnerii*" from beds older than Maestrichtian have proved to be victims of mistaken identity. Most specimens of this species have been found north of Mt. Diablo in Deer Valley and the vicinity of Martinez, Contra Costa Co., Calif. UCLA Department of Geology collections have four incomplete specimens that are probably this species from UCLA loc. 4140, Jalama Creek, Santa Barbara Co., Calif., and from UCLA loc. 3815, Lang Ranch, Simi Hills, Ventura Co., Calif. The fauna from the Jalama Formation is considered to be younger than the *Metaplacenticeras pacificum* zone (Dailey and Popenoe, 1966, p. 1). The Cretaceous strata of the Lang Ranch overlie the *Metaplacenticeras pacificum* beds and contain *Pachydiscus* (*Neodesmoceras*) *catarinae* (Anderson and Hanna) (Popenoe, 1954, p. 17) and are possibly of early Maestrichtian age (Matsumoto, 1960, p. 69).

Like *C. stantoni*, *C. ashburnerii* is most common in a matrix of medium-grained sandstone.

CYMBOPHORA SUCIENSIS (Whiteaves)

Pl. 1, figs. 14–15; Pl. 2, figs. 12–13; Pl. 3, figs. 18–20; Text-fig. 2C; Table 3

Mactra (*Cymbophora*?) *Warrenana* Meek & Hayden, WHITEAVES, 1879, p. 142, Pl. 17, fig. 9; Pl. 19, fig. 3, 3a. Not *Mactra warrenana* Meek & Hayden.

Laevicardium Suciense Whiteaves, 1879, p. 154, Pl. 18, fig. 2.

Cymbophora Ashburneri (Gabb), small, nearly smooth variety, WHITEAVES, 1903, p. 374.

Description.—Shell of less than average size for the genus, relatively thick for its size, inflated, approaching an equilateral triangle in outline. Beaks prominent; anterior margin well-rounded; ventral margin regularly curved with a slight angulation as it meets the posterior margin at the posterior angulation; posterior margin barely curved angling gently into the slightly curved, sloping, posterodorsal margin, posterior angulation high, strong, bluntly rounded. Surface of flank polished, with fine growth lines and well-marked, usually impressed growth checks; selenis bounded by clearly defined, impressed line, ornamented with regular concentric ribs fanning from beneath the beak and extending to the line bounding the selenis; marginward area of corcelet ornamented with regular concentric ribs fanning from the beak to the posterior side of the broad unribbed but rough posterior angulation.

Resilifer with a raised ventral margin, not extending to the edge of the hinge plate. Hinge of right valve with 3a close to and nearly parallel to valve margin, 3b slightly longer than 3a, as long as the width of the hinge plate and longer than the resilifer; laterals sturdy, AI and PI ornamented by coarse granulations over upper ⅔rds of the dorsal surface of the tooth, AI with a nearly vertical cusp in dorsal side and a small posterior nubbin, AIII half as long as AI and paralleling the anterior end of AI. Hinge of left valve with inverted V of 2b nearly filled, 4b very thin; AII short and stout with two broad nearly vertical cusps on ventral side and a small nubbin on the posterior tip, the posterior ⅕th of the tooth differentiated by lack of ornamentation and being thinner, PII roughly twice as long as AII. Pallial sinus ascending, extending across approximately ¾ths of the posterior portion of the shell.

Holotype.—CGS cat. no. 5713 (plaster cast UCLA cat. no. 32206).

Hypotypes.—UCLA cat. nos. 6846–6847, UCLA loc. 3643, Chico Creek; UCLA cat. no. 6848, UCLA loc. 3648, Chico Creek; UCLA cat. no. 48517, UCLA loc. 3637, Chico Creek; UCLA cat. no. 48518, UCLA loc. 3641, Chico Creek; UCLA cat. no. 48519, CIT loc. 1183, Chico Creek; UCLA cat. no. 48520–48521, CIT loc. 1400, Sucia Island.

Type locality.—Sucia Island, San Juan Co., Washington.

Age.—Campanian, *Submortoniceras chicoense* and *Hoplitoplacenticeras vancouverense* zones.

Remarks.—Whiteaves' (1879) figures, pl. 19, fig. 3, 3a, are of the common smooth form which is very abundant at Sucia Island. He complains that the artist made the sculpture too prominent in pl. 17, fig. 9, but there are specimens from both Sucia Island and Chico Creek which otherwise agree with this form except that they are regularly concentrically sculptured by well-developed, round-topped ribs whose width is about equal to that of the interspaces.

Identification of this form as *C. suciensis* depends upon a plaster cast made by B. J. Botte of the Canadian Geological Survey of specimen, CGS cat. no. 5713. This cast was sent to me as the plastoholotype of *Laevicardium suciense* Whiteaves and is roughly similar to his Plate 18, fig. 2, but if CGS cat. no. 5713 served as the model for the drawing,

TABLE 3—Measurements in mm of *Cymbophora suciensis* (Whiteaves)

Cat. no.	H	L	T	H/L	T/L	S	S/L	RH	RW	RW/RH	Remarks
6846	16	18	5	.89	.28			1.6	1	.63	
6847	22	25	9	.88	.36			2	1.3	.65	
6848	18	22	6	.82	.27	9	.41				crushed
32206	20	22	7	.91	.33						
48517	21	23	7	.91	.3	12	.52				
48518	18	21	5	.86	.24						
48519	20	25	6	.8	.24						
48520	20	25	7	.8	.28						
48521	25	29	7	.86	.24						a large specimen

H=height of valve; L=length of valve; T=thickness of valve; S=length of pallial sinus; RH=height of resilifer; RW=width of resilifer.

either the artist did some reconstruction or the specimen has been broken subsequently. The plastoholotype is clearly the plump smooth mactrid so abundant in collections from Sucia Island and the upper part of the Chico Formation on Chico Creek. Did Whiteaves have a different specimen in hand when he described *Laevicardium Suciense*, one that was later misplaced? UCLA has one specimen of a cardiid from Sucia Island (CIT loc. 1396). It is of similar shape to "*L.*" *suciense* but about two-thirds the size of the plastoholotype. This cardiid has clearly marked radial ribs on the posterior slope, a feature not indicated in Pl. 18, fig. 2 nor mentioned in Whiteaves' description.

Whiteaves lists eight localities from which he had the "small nearly smooth variety of *Cymbophora ashburnerii*." As nearly as I can tell from Whiteaves' descriptions, these localities correspond in age to Usher's (1952) Late Campanian and Early Maestrichtian. Usher does not mention the occurrence of *Cymbophora* at all and I have not seen collections from Whiteaves' localities other than Sucia Island. *C. suciensis* (Whiteaves) certainly occurs there in the *Hoplitoplacenticeras vancouverense* zone of the Cedar District Formation which is considered by Jeletzky (*in* Muller and Jeletzky, 1970, p. 55) to be of early Late Campanian age. *C. suciensis* is abundant in the Chico Formation on Chico Creek in beds which contain *Submortoniceras chicoense* (Trask) and is present but less abundantly so in *Submortoniceras chicoense* beds of Butte Creek and Pentz.

Specimens of *C. suciensis* are also found at CAS loc. 2365, which is described by Hanna and Church (CAS locality book) as a cobble in an Eocene conglomerate cropping out in sec. 13, T. 23 S., R. 16 E., two miles north of the ranch house at Big Tar Canyon Gap. The locality description is difficult to equate with the Garza Peak quadrangle map as at no point is section 13 two miles north from Big Tar Canyon and the only ranch house, "Sargaser Ranch," is in sec. 18 due east. Neither Stewart (1946) nor Vokes (1939) mention Cretaceous fossils in the basal Eocene, and Stewart (1946, p. 90) suggests that a fossiliferous boulder

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EXPLANATION OF PLATE 2

Left valves of *Cymbophora* spp., all natural size.

FIGS. *1–3*—*Cymbophora ashburnerii* (Gabb). *1,* Pallial sinus, plaster cast (UCLA 28775) of holotype (ANSP 4361) of *C. tenuissima* (Gabb). *2,* paralectotype (ANSP 4441a), photo by T. Susuki. *3,* Pallial sinus, hypotype (UCLA 6849).

4—*Cymbophora stantoni* (Arnold), hypotype (UCLA 48503).

5–6—*Cymbophora buttensis* Anderson. *5,* hypotype (USNM 187735). *6,* Pallial sinus, hypotype (USNM 187736).

7–8—*Cymbophora triangulata* (Waring). *7,* hypotype (UCLA 40664=CIT 3450). *8,* Pallial sinus, hypotype (UCLA 48525).

9—*Cymbophora popenoei* n. sp., paratype (UCLA 48492).

10—*Cymbophora gabbiana* (Anderson), holotype (CAS 1), photo by T. Susuki.

11—*Cymbophora bella* n. sp., holotype (UCLA 48533).

12–13—*Cymbophora suciensis* (Whiteaves). *12,* Pallial sinus, hypotype (UCLA 48517). *13,* hypotype (UCLA 48521).