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MORPHOLOGY AND MODE OF LIFE OF THE LATE CRETACEOUS RUDIST, *CORALLIOCHAMA ORCUTTI* WHITE (MOLLUSCA: BIVALVIA)

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ABSTRACT—Beds of Late Campanian to Early Maestrichtian age in the Rosario Formation exposed at Punta Banda, Baja California, Mexico, contain extensive biostromal deposits of the rudist bivalve *Coralliochama orcutti* White, 1885. Spiral growth during early ontogeny of the attached valve produced a stable base for later upward growth. Spat attachment occurred even on steeply inclined substrate surfaces, and active sedimentation necessitated rapid upward growth of individuals to avoid suffocation. Lateral attachment between individuals was common.

The form of the valves and details of dentition and internal morphology are extremely variable due to the gregarious habit of most individuals. Stunted specimens of the conical attached valve apparently resulted from cementation to a steeply inclined substrate surface.

The most complete specimen of White's 16 syntypes is designated lectotype and the remaining specimens are designated paralectotypes.

Coralliochama flouriei Damestoy, 1965, based on a single specimen from Punta Banda, is considered to be a junior synonym of *C. orcutti*.

INTRODUCTION

THE rudist bivalve *Coralliochama orcutti* White, 1885, was described from specimens collected at Punta Banda, Baja California, Mexico, and Gualala, Mendocino County, California. White visited Gualala with G. F. Becker (Becker, 1885) and specimens from Punta Banda were sent to him by C. R. Orcutt, but he did not designate a type locality. However, Punta Banda (Text-fig. 1) is probably the locality for all of White's syntypes, because specimens of the quality illustrated by White are not known to occur in the Gualala beds, the species was named after Orcutt, and several of the syntypes are labelled as coming from Punta Banda.

Coralliochama orcutti has received very little attention since its description by White. Except for a few cases (Moore, 1968; Perkins, 1969), published illustrations are copies of White's original figures. The drawings given by White adequately illustrate the external morphology of both valves, but he apparently had only one specimen that showed any internal features, and that for only part of one free valve. Early in the present study, the range of morphologic variation was found to be greater than that indicated by White (1885). The purposes of this study are to describe the morphology of *C. orcutti* and to infer its mode of life from these features.

The manuscript was read by Dr. William H. Easton, University of Southern California, Dr. Edward C. Wilson, Natural History Museum of Los Angeles, Dr. Erle G. Kauffman, U.S. National Museum of Natural History, and Dr. Alan H. Coogan, Kent State University; their helpful comments are gratefully acknowledged. Dr. Wilson and Dr. Arnold Ross, San Diego Natural History Museum, loaned specimens for examination. Dr. Porter M. Kier and Mr. Frederick J. Collier arranged for loan of the type specimens of *C. orcutti* from the U.S. National Museum of Natural History. Dr. Gary Rosenberg, University of California at Los Angeles, assisted in collecting specimens at Punta Banda.

The following abbreviations are used in the text and in figure captions: LACM, Natural History Museum of Los Angeles; SDSC, San Diego State College; USC, University of Southern California; USNM, United States National Museum of Natural History.

TAXONOMIC REVIEW OF DESCRIBED *CORALLIOCHAMA* SPECIES

Seven species have been placed in *Coralliochama*. Muellerried (1932) reviewed the six species known to that time and concluded that only three of them were correctly included in *Coralliochama*: *C. orcutti* White, 1885, *C. gboehmi* Böse, 1906, and *C.* n. sp. Muellerried, 1931. The latter two species are known only from eastern Mexico. An additional species,

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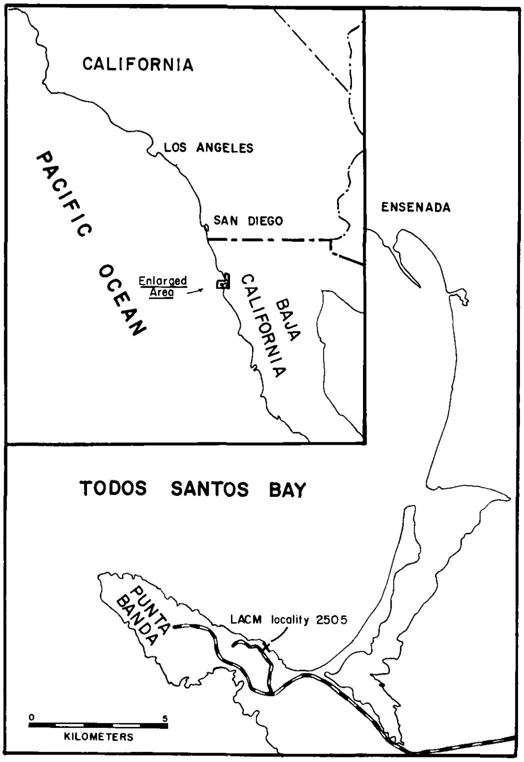
C. flouriei Damestoy, 1965, was described from Punta Banda. *Coralliochama flouriei* is known from a single specimen given to Damestoy by G. Flourie, who visited Punta Banda, and it is obviously an extensively eroded young adult of *C. orcutti* and thus a junior synonym. Damestoy's specimen is characterized by an abruptly truncated apex on the conical attached valve, and by details of its dentition as seen in a cross-section made approximately along the plane of commissure. However, truncation of the attached valve illustrated by Damestoy appears to be due to breakage rather than to natural growth, as is often the case with specimens of *C. orcutti.* The dentition shown by Damestoy does not differ from that described here for *C. orcutti.*

MATERIAL

White (1885) based his description of *Coralliochama orcutti* on 16 specimens (USNM 12698), of which 12 are reasonably complete valves or whole specimens and 4 are small fragments. Seven specimens have been cut and polished, usually on the attached valves. No additional sections were made for this study. White illustrated 9 specimens and gave a diagrammatic sketch of a cross-section of an attached valve. Twelve of White's specimens have no locality data with them, but 4 of the labels list the locality as Todos Santos Bay, of which Punta Banda forms the southern boundary (Text-fig. 1). Because all specimens bear the same lot number and are in a similar state of preservation, I assume that they were all collected at Punta Banda. White also noted the presence of this species at Gualala in northern California, but specimens from that area are known to be poorly preserved.

White referred to all of his specimens as cotypes (syntypes). He did not designate a holotype or paratypes, nor have subsequent workers done so. The most complete specimen indicated by White (1885, Pl. 2, fig. 1) in his description is here designated the lectotype (Pl. 2, figs. 3,4; USNM 186661), and the remaining 15 specimens in his type series are designated paralectotypes. The 4 paralectotypes newly figured here are assigned USNM catalog numbers 186662 to 186665, and the remaining unfigured paralectotypes retain their original USNM catalog number of 12698. The handwritten label accompanying the lectotype reads "Cotype. 12698. *Coralliochama orcutti* White, Up. Cretaceous (Chico), Todos Santos Bay, Low. Cal., Id. by C. A. White."

I have examined collections of *C. orcutti* at the University of Southern California, the Natural History Museum of Los Angeles, the San Diego Museum of Natural History, and San Diego State College, and collected at several localities along the coast at Punta Banda.



TEXT-FIG. *1*—Location of the Punta Banda area.

GEOLOGIC SETTING

Specimens of *C. orcutti* used in this study were collected at Punta Banda from the Rosario Formation. These beds, as mapped by Lindgren (1888) were reported to extend along the north side of Punta Banda for about 3 miles, and inland for one mile. Since then they have been visited by many collectors. At the exposure designated LACM 2505, the sea-cliff is about 70 feet (21 meters) high and shows the beds dipping north at 10° to 20°. The molluscan fauna at Punta Banda (Anderson and Hanna, 1935; Saul, 1970) and the foraminiferal fauna of correlative beds to the north (Sliter, 1968) indicate a Late Campanian to Early Maestrichtian age for the *Coralliochama* beds.

Coralliochama orcutti is the only rudist bivalve known at Punta Banda. Although this species is said to occur throughout several hundred feet of strata (Anderson and Hanna, 1935), it is found most abundantly in one bed 1.5 to 2 meters thick, in which the rudist shells form the bulk of the deposit. This bed consists of gray, fine- to coarse-grained, angular, micaceous sandstone, whose permeability has allowed ground water to cement shells and matrix into an indurated mass. Above and below this cemented layer are siltier and less permeable beds in which *C. orcutti* and other mollusks are generally well-preserved. These finer sediments are predominantly brown sandy siltstone, but range from claystone to medium- and coarse-grained sandstone, and are not indurated by calcite. Cobbles and boulders of volcanic rocks up to 25 cm in diameter occur throughout the exposed section.

COLLECTING LOCALITIES

Specimens collected by me and described in this report were found at locality LACM 2505 (Text-fig. 1), in the sea-cliff along the north side of Punta Banda, about 1660 m south and 4290 m east of the summit of Banda Peak on Punta Banda (U.S. Hydrographic Office chart 5184). Additional numbered localities given in the plate captions were visited by other collectors, and the only locality information known for any of them is a general reference to the Cretaceous beds on the north side of Punta Banda.

ORIENTATION

It is often difficult to determine which are the right and left valves in rudists, especially for those species in which both valves are uncoiled and conical (Perkins, 1969). However, the asymmetrical valves of *C. orcutti* do contain indications of their true orientation. The beaks of most modern bivalves are directed anteriorly, and if this relation holds true for *Coralliochama* then the coiled free valve is the left and the conical attached valve is the right. Similarly, the siphons of modern bivalves are located at the posterior end of the body. If the positions of the siphonal passages of *C. orcutti* have been correctly interpreted in this paper, then their placement supports the inference that the attached valve is right and the free valve is left. The dentition is not always a reliable guide to orientation, as in some rudists and modern Chamidae either the free or attached valve bears the typically left- or right-valve dentition pattern (Yonge, 1967; Perkins, 1969). As interpreted here, the morphology of *C. orcutti* supports the inference (Perkins, 1969) that attachment was by the right valve in the Caprinidae. However, the criteria used here are not entirely reliable, because rudists as a group are not yet well-understood, and the conclusions here are only tentative. The terms "anterior" and "posterior" are used here assuming attachment to the substrate by the right valve.

SHELL STRUCTURE

The shell of *C. orcutti* consists of a prismatic outer layer and a cellular inner layer (Pl. 1, fig. 17, Pl. 2, fig. 16). On the largest specimen at hand (an attached valve, Pl. 1, fig. 7), the greatest thickness of the outer layer is 4.6 mm, and of the inner layer 41.0 mm, measured across the posterior margin. The innermost rank of tubules making up the inner shell layer have their walls coalesced to form the smooth lining of the body cavity. White (1885) mistook these coalesced tubule walls for a "porcellaneous" inner shell layer, but Chubb (1971) has noted that rudists have only two calcareous shell layers. In some of White's polished sections, the prismatic layer appears to be further divided into a darker outer portion and a lighter and thinner inner portion. The thick inner layer is made up of thin-walled polygonal tubules that extend in the direction of growth and are partitioned by closely-spaced tabulae that are concave toward the commissure. In transverse section, the tubules in the inner part of the tubular layer are nearly equidimensional, although they become radially elongate toward the outer part of the tubular layer and eventually form radial plates with pyriform interspaces. The radial plates are more obvious in the free valve, although they are present in the attached valve.

The cellular construction of the valves produces an unusually (for bivalves) strong, light shell per unit calcium carbonate used. The porous construction also probably allowed rapid shell growth (Perkins, 1969), which would have been advantageous in an environment of rapid sedimentation and intense biotic competition for space.

SYSTEMATIC PALEONTOLOGY

Order HIPPURITOIDA Newell, 1965

Superfamily HIPPURITACEA Gray, 1848

Family CAPRINIDAE d'Orbigny, 1850

Genus CORALLIOCHAMA White, 1885

CORALLIOCHAMA ORCUTTI White, 1885

Coralliochama orcutti WHITE, 1885, p. 10–12, Pl. 1, figs. 1–5, Pl. 2, fig. 1, Pl. 3, figs. 1–2, Pl. 4, figs. 1–4; BÖSE, 1906, p. 25, 56; PALMER, 1928,

p. 20, 53; Muellerried, 1931, p. 177; 1932, p. 171–175, 177, Text-figs. 1–6; Anderson and Hanna, 1935, p. 31; Weaver, 1944, p. 16; Anderson, 1958, p. 125–126; Moore, 1968, p. 20, Pl. 8; Dechaseaux and Perkins, 1969, p. 793, Figs. E258, 2a-c; Saul, 1970, p. 79, Figs. 17–22.

Coralliochama flouriei Damestoy, 1965, p. 209–211, Figs. 1–4.

Morphology first described and illustrated by White (1885). Interior features poorly known on free valve, unknown on attached valve; my own collection contains 6 attached valves, 11 free valves, with interiors prepared.

Attached valve.—Typically elongate, conical, attached at its apex, radial and concentric sculpture present. Radial sculpture of two kinds: closely spaced striations occur regularly over whole valve; coarser ridges mainly occur on dorsal shell surface (Pl. 1, fig. 13); striations described by White (1885), coarser sculpture occurs only on one specimen. Concentric sculpture of growth lines ranging from minute striae to coarse undulations (Pl. 1, fig. 7); coarser concentric sculpture usually occurs on dorsal side of valve, rarely elsewhere.

Ligament in each valve contained within narrow cavity formed by inflection of prismatic outer shell layer into cellular inner layer (Pl. 1, fig. 9); on exterior of attached valve, position of ligamental cavity marked by posterodorsal groove running along valve from apex to commissure (Pl. 1, fig. 7); on attached valve hinge-plate, marginal inflection may extend to posterior tooth and be elevated above general level of hinge-plate (Pl. 1, fig. 9); ligamental groove and inflection seen even on small growth stages (Pl. 2, fig. 1). Ligament of small cross-sectional area, probably of little value in opening valves, may have served mainly to hold dorsal margins of valves together (Perkins, 1969). Valve opening may have been accomplished mainly by expansion of soft parts such as foot, as described for hippuritid and radiolitid rudists (Dechaseaux, 1969).

Two attached valves in present collection (Pl. 1, figs. 9–12, 15, 16) radically different from any described previously, their conical shapes greatly shortened compared to typical specimens; width across commissure is greater than depth of valve in one specimen (Pl. 1, figs. 9, 11, 15). Apex of more complete specimen also arched dorsally, as if individual were attached to steeply-inclined surface and first had to grow horizontally before growing upward (Pl. 1, fig. 15). Sculpture of these two individuals similar to that of typical specimens. Significance of these stunted specimens is discussed later.

Shell cavity of conical attached valve relatively large, extends into apex undivided by tabulae; only feature within cavity is radial ridge, located below tooth (Pl. 1, fig. 9) and extending entire length of cavity; ridge may have served for attachment of adductor muscles (Perkins, 1969); walls of shell cavity smooth.

Dentition of attached valve typical for a caprinid rudist (Perkins, 1969), consisting of single broad tooth flanked by anterior and posterior sockets (Pl. 1, figs. 2, 6); relative sizes of teeth and sockets vary considerably, some specimens with moderately elevated tooth flanked by small, shallow sockets (Pl. 1, figs. 2, 3), others with massive, strongly projecting tooth and large, deeply impressed sockets on either side (Pl. 1, figs. 6, 7, 8).

Anterior and posterior walls of attached valve usually very thick, posterior wall being the thicker one; largest individual in present collection has posterior wall 4.3 cm thick, anterior wall 3.0 cm thick at commissure (Pl. 1, fig. 6). Anterior and posterior portions of hinge-plate have rough surfaces produced by exposed ends of pallial canals of inner shell layer; medial part of posterior hinge surface elevated, acting as buttress for posterior tooth (Pl. 1, fig. 8). Ventral wall is thinnest part of attached valve, commonly crushed by compaction of enclosing sediments after horizontal burial. Mid-dorsal margin of attached valve bears shallow, eroded notch to accommodate umbo of free valve, necessary for even slightest opening movement of free valve, because notch in attached valve is completely filled by umbo of free valve in a whole specimen (Pl. 2, fig. 2); free valve possibly was lifted straight up, eliminating need for tilting when opening.

Dentition of stunted attached valves mentioned earlier differs in several details from that of typical specimens; posterior tooth is broken in each specimen, but they were obviously not broad and massive (Pl. 1, figs. 9, 10); tooth reduced to narrow ridge along posterior margin of shell cavity; anterior socket of one specimen narrow and slit-like, that of other specimen rounded, which are common variations in typical specimens; posterior sockets of stunted valves located more dorsally than in other specimens, and posterior socket in larger specimen is very broad and deep for size of valve, indicating correspondingly large tooth on missing free valve.

Although the hinges of the two stunted specimens appear to be aberrant, even typical specimens of *C. orcutti* show a wide range of variation in nearly every morphologic feature.

If more specimens were available for examination, the stunted specimens probably would be included in the normal morphologic range of the species. The cause of the stunting may have been related to the microhabitat of each individual. The arching of the umbonal area of the more complete specimen may, as stated above, indicate growth on a steeply inclined surface. If this was so, then the long axis of the attached valve would have been necessarily angled slightly away from the inclined substrate to provide space for the unhindered opening of the free valve (the umbo of which faced the vertical substrate). However, if the proportions of the attached valve had been typically elongate, continued growth would have eventually resulted in high torsional stress at the apical attachment, and the individual might have broken free. The short, broad attached valves of the stunted individuals would have kept the center of gravity as close as possible to the apex, preventing overstressing the apical region. In order to contain the increasing bulk of the soft parts, the stunted specimens developed broader shells rather than longer ones. The observed differences in hinge structure from typical *C. orcutti* may be related to the speculated differences in microhabitat. The notation by Palmer (1928, p. 53) that in rare cases the free valve of *C. orcutti* is larger than the attached valve may refer to specimens such as those described here.

Free valve.—Specimens in present collection comprise growth series of individuals ranging in height from 11 mm to 79 mm (Pl. 2, figs. 5, 6, 9–15, 17–19); interior of free valve previously known from single incomplete specimen (White, 1885).

Proportions of free valve vary so much that either height or length may be greatest dimension. Earliest-formed portion of umbo generally concealed by later growth, most adult valves have slightly more than one visible whorl; umbones vary in relative height from greatly

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EXPLANATION OF PLATE 1

Specimens of *Coralliochama orcutti* collected at Punta Banda, Mexico. All specimens from LACM locality 2505 unless stated otherwise.

FIG. *1*—Enlargement of part of fig. 5, showing continuity of shell material between adjacent individuals in life positions; ×1.2.

2—Interior view of specimen shown in fig. 3; ×0.4; t, tooth; s, socket.

3—Dorsal view of attached valve, showing prominent posterior tooth on left. Ridge of shell material along posterior side of specimen indicates former attachment to a neighboring rudist; ×0.4.

4—View of part of fig. 5, showing apices of two attached valves abutting on a third individual. The three specimens would be cemented together if the outer shell layers of the specimens were intact; ×0.8.

5—Cluster of specimens, showing attached valves of four individuals cemented together. This is underside of cluster as it was in life. Note the recumbent attitude of the individuals; ×0.25.

6—Interior view of specimen shown in fig. 7; ×0.25. t, tooth; s, socket.

7—Dorsal view of attached valve. Ligamental groove extends along exterior of valve near prominent posterior tooth. Broad indentations of apex on anterior side indicates former attachment to substrate. SDSC 1608; ×0.25.

8—Posterior view of specimen shown in fig. 7. Possible siphonal groove (g) is an indentation between posterior tooth (t) and the elevated postero-ventral portion of hinge plate (b); ×0.25.

9—Interior view of specimen shown in fig. 11. Note broad posterior socket (lower left), slit-like anterior socket, and posterior tooth reduced to a ridge. Adductor muscle insertion ridge (r) projects into shell cavity at the posterior tooth. Inflection of the ligamental groove (l) is clearly seen on postero-dorsal margin; ×0.55.

10—Interior view of specimen shown in fig. 12; ×0.55; t, tooth; s, socket.

11—Dorsal view of stunted attached valve, showing abrupt apical termination; ×0.55.

12—Ventral view of stunted attached valve, showing posterior tooth reduced to an elevated ridge along dorsal margin of shell cavity; ×0.55.

13—Dorsal view of incomplete attached valve, showing radial sculpture. SDSC 1608; ×0.4.

14—Interior view of specimens shown in fig. 18; ×0.33.

15—Posterior view of specimen shown in fig. 11. The apex is directed dorsally, indicating former attachment on a vertical substrate surface; ×0.55.

16—Posterior view of specimen shown in fig. 12, from which the apex is missing; ×0.55.

17—Polished section of an attached valve. Paralectotype. USNM 186665; ×0.6.

18—Cluster of three attached valves that are cemented together in life positions; USC 1466; ×0.33.


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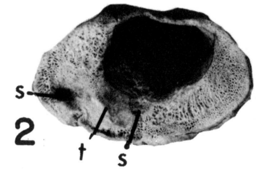

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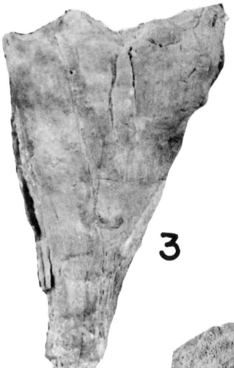
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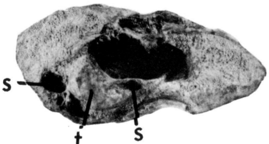

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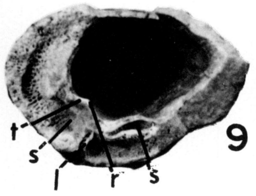

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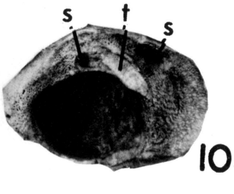

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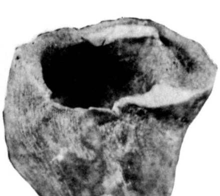
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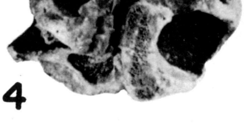
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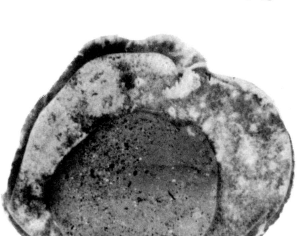
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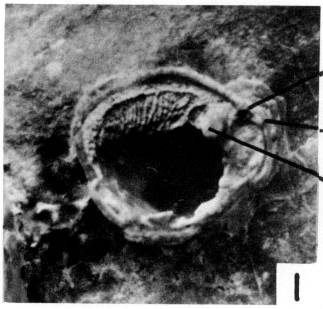

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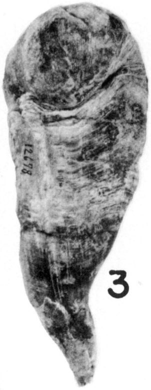

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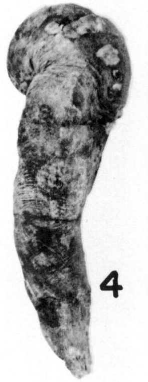

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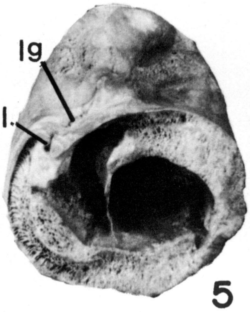

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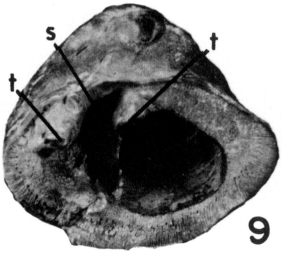

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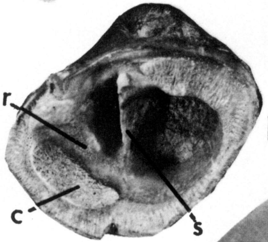

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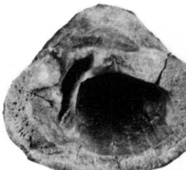

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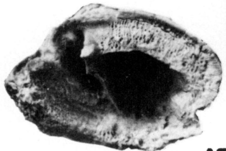

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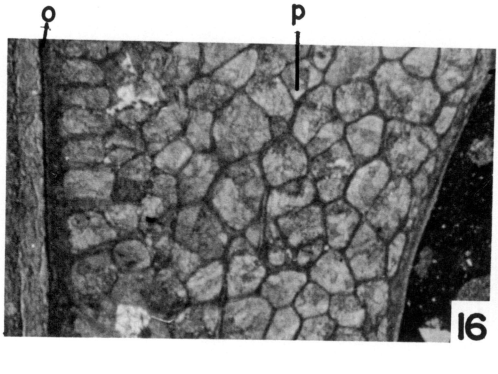

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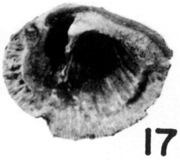

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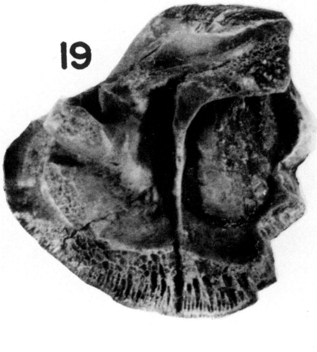

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elevated (Pl. 2, fig. 13) to rather low (Pl. 2, fig. 11); convexity increases with age of individual, valves of equal size not necessarily equally convex (Pl. 2, figs. 6, 10); outline of free valve generally trigonal, juveniles generally longer than high.

Outer shell layer of free valve bears closely and irregularly spaced concentric rugae (Pl. 2, fig. 12) that are prominent on adult portion of shell. Minute incremental growth lines number about 15 per millimeter, may be diurnal growth increments; "multitude of very fine radiating lines" (about 40 per millimeter) described by White (1885, p. 11) on free valve is indistinct.

Margin of free valve broad (up to 14mm), except dorsally, exposing ends of tabulate canals in inner shell layer; margin thickness varies among individuals of equal size, but relatively broad (up to 3 mm) even in smallest juvenile specimen (Pl. 2, fig. 1). Medial portion of broad posterior margin of adults is interrupted by elongate callus (Pl. 2, fig. 11) that is not prominent in juveniles and not seen in smallest free valve. In life position, callus would have rested on broad posteroventral portion of hinge plate of attached valve; raised ventral margin of callus fits into shallow depression on attached valve; callus may have aided in maintaining valve alignment when valves were closed, thus removing some stress from hinge teeth.

Free valve bears two prominent teeth located at posterior and median parts of hinge area (White, 1885, Pl. 1, fig. 3). Posterior tooth massive, with rounded termination, usually more prominent of the two, although median tooth may be larger; juveniles show marked outward inclination of posterior tooth, which may project beyond adjacent shell margin. Median tooth directly below umbo or slightly posterior to it, generally less massive in appearance than posterior tooth, may have bifid termination in adults.

Septum extends from posteroventral edge of anterior tooth to ventral shell wall in all growth stages; septum becomes progressively less elevated as it approaches ventral wall and intersects ventral rim in one specimen (Pl. 2, fig. 19); median tooth well-defined from cardinal end of septum. Septum divides free valve into two cavities, of which anterior one is larger; walls of anterior cavity show no evidence of muscle scars; posterior cavity mostly occupied in life by massive tooth of attached valve. An irregularly shaped area of shell wall extending from posterior tooth to distal end

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EXPLANATION OF PLATE 2

Specimens of *Coralliochama orcutti* collected at Punta Banda, Mexico. All specimens from LACM locality 2505 unless stated otherwise.

FIG. *1*—Enlargement of juvenile attached valve shown attached to adult specimen in fig. 2; ×2; t, tooth; l, ligamental inflection; u, umbo.

2—Adult specimen bearing attached remains of four juvenile attached valves. Umbo of the adult free valve fits into a notch worn into the dorsal margin of the attached valve. LACM 1445; ×0.4.

3—Dorsal view of lectotype. USNM 186661; ×0.25.

4—Anterior view of lectotype. USNM 186661; ×0.25.

5—Interior view of free valve; ×0.5; l, ligamental inflection; lg, ligamental groove.

6—Posterior view of specimen shown in fig. 5. Note relatively strong convexity of valve; ×0.5.

7—Dorsal view of complete individual. Paralectotype. USNM 186664; ×0.5.

8—Dorsal view of complete individual, showing relatively abrupt tapering of attached valve. Paralectotype. USNM 186663; ×0.5.

9—Interior view of free valve, with prominent central and posterior teeth and median septum; ×0.5; t, tooth; s, socket.

10—Posterior view of specimen shown in fig. 9. Note relatively weak convexity of valve and prominence of teeth; ×0.5.

11—Interior view of free valve, showing large postero-ventral callus (c) that may have aided in maintaining alignment of valves; ×0.5; s, septum; r, roughened area.

12—Exterior of free valve, showing concentric sculpture. Microscopic concentric growth lines are not visible; ×0.55.

13–15, 17, 18—Interiors of adult and juvenile free valves; 13, ×0.5; 14, ×0.55; 15, ×0.65; 17, ×0.9; 18, ×1.5.

16—Enlarged cross-section of ventral shell wall of attached valve. Note radial arrangement of pallial canals at outer shell wall; × 10; o, outer shell wall; p, pallial canals; i, inner shell wall.

19—Interior of young adult free valve. Paralectotype. USNM 186662; ×1.

of septum is thickened and roughened by exposed ends of pallial canals; area is present in all growth stages, but function is unknown. Adductor muscles were probably inserted on septum, as it aligns with muscle-insertion ridge of attached valve.

Ligamental inflection located on dorsal margin above posterior tooth; corresponding groove on exterior shell surface is shallow (Pl. 2, fig. 5). Shallow groove across margin of one free valve from distal end of septum is shown by White (1885, Pl. 1, fig. 3), but is not present on other specimens; examination of White's specimen (Pl. 2, fig. 19) shows groove is unrelated to shell structure. Also on White's free-valve specimen and on others is a shallow groove across margin between posterior tooth and posteroventral callus; this may be a siphonal canal; on one attached valve (Pl. 1, figs. 6,8) is a corresponding groove between the tooth and the elevated posteroventral portion of the hinge plate. These grooves only traverse the inner parts of the valve margins, so the animal could not have extruded its siphons without opening its valves. However, these passages would have been exposed to the sea with only a slight parting of the valves, so the animal could have respired in comparative safety.

MODE OF LIFE

The accumulation of *C. orcutti* and other mollusks at Punta Banda is often informally referred to as a reef. However, there is no evidence that the prolific mass of rudists here formed the mound-like structure characteristic of true reefs. The most abundantly fossiliferous bed at Punta Banda is 1.5 to 2 meters thick, tabular in shape, has sharp contacts with beds above and below it, and terminates gradually along strike. The rudist beds also contain a small associated fauna (Saul, 1970), in contrast to the variety and abundance of life forms associated with true rough-water coral reef deposits (Lowenstam, 1950). In a stratigraphic sense, the *Coralliochama* beds are better referred to as a biostrome rather than as a bioherm or reef. A population of rudists consisted of an irregular patch of living and dead individuals, some cemented to their neighbors and others solitary. Assuming that the shells were geotropic, the relatively straight attached valves of most specimens indicate that they grew upright, although some were recumbent (Pl. 1, fig. 3).

In the Punta Banda beds the rudists show chaotic orientation. Most of the specimens are broken and worn, and single valves are common, although many specimens are still articulated. The outer shell layer is absent from many specimens and may have been removed by abrasion that occurred mainly after death. The only oriented specimens collected at Punta Banda are those in two blocks (Pl. 1, figs. 5,14,18), but only their orientation relative to each other is preserved, as the blocks were not found in place. The disarray in which the rudists appear may be due solely to post-mortem mixing by currents and by wave action during storms. However, if most individuals were supported upright by attenuated lower valves attached at their narrow umbones, they probably would have been broken from their attachments commonly by storm waves, currents and the work of other organisms both before and after death. The basic instability of the living position thus would account for the disarray in which the shells occur.

The generally fine sediments enclosing the fossils attest to the low-energy environment that prevailed during their accumulation. If most of the individuals in a population of *C. orcutti* stood upright on the sea floor, clastic debris would have been trapped in the spaces between neighboring shells. Cobbles and boulders that occur commonly among the fossils indicate that the rudists were in a high-energy environment from time to time. The associated molluscan fauna and plant debris (Anderson and Hanna, 1935; Saul, 1970) suggests a shallow-water environment for the *Coralliochama* beds. The population preserved at Punta Banda was probably living below mean wave base in a shallow-water, low energy environment, but was affected periodically by storm waves or currents. The accumulation of rudists was close enough to a high-energy shoreline to receive a continual influx of terrestrial debris. The extent to which individuals were given added support by sediment trapped around the growing shells is not known.

The elongate attached valve of *C. orcutti* may have been necessary for survival in the area of fine sedimentation in which the species lived. As Kauffman (1969) recently noted, the tall, conical attached valves of Cretaceous rudists elevated the feeding and respiratory margin above the surrounding substrate to prevent clogging and suffocation. This feature was probably of critical importance to an organism surrounded by predominantly soft substrate. The recumbent specimens shown in Plate 1, figure 5 indicate that some individuals could tolerate sediment fouling. These individuals grew parallel to the substrate for half the length of the attached valve before bending to grow upright. If these individuals lived in a local area of low sedimentation, their orientation would not be evidence for sediment-fouling tolerance.

The elongate attached valve would have been less important to survival if the surrounding sediment were trapped and bound by algae or other plants. This phenomenon has been described for Recent carbonate sediments in the Bahamas by Scoffin (1970). In addition, clastic sedimentation may have been less pertinent to the growth of the shell if it were intermittent and periodic. However, there is no layering or lamination in the Punta Banda beds to indicate anything other than continuous sedimentation. The attached mode of life of *C. orcutti,* plus the greatly elongate attached valve of this species and most other caprinid rudists, also suggests a causal relationship between sedimentation and shell form.

The strongly arched, convex free valve may also have aided survival. The flat or concave free valves known in many other rudists (Kauffman, 1969) could have served as sediment traps in rapidly accumulating deposits, whereas the rounded free valves of *C. orcutti* would shed sediment easily. The limited gape possible because of the closeness of the umbones (if the valves did not open by vertical elevation; Pl. 2, fig. 2) also inhibited entry of sediment particles into the mantle cavity. Thus, the external morphology of this species is well-adapted to the presumed sedimentary conditions under which it lived.

Specimens of *C. orcutti* were said by White (1885) either to grow separately or in clusters, although he did not describe or illustrate a cluster of these clams or describe the attachment of an individual to the substrate. White's syntypes consist only of solitary individuals. Specimens collected or assembled during the present study show some individuals were attached to one another. In several instances the outer shell layers of adjacent individuals are cemented together (Pl. 1, fig. 1). The illustration of the grouping in Plate 1, figure 5 shows the underside of the specimen as they were in life. Each of the upper valves is situated so that it opened on the side away from that shown in the photograph.

Where two individuals were cemented together and grew approximately parallel with each other (Pl. 1, fig. 18), evidence of their attachment would persist even after the individuals were separated by post-mortem processes. This is because an irregular ridge of shell material on each attached valve traces the line of contact where the two rudists were formerly cemented togther. This feature is seen on two attached valves of the present collection (Pl. 1, figs. 3,7). However, these ridges are not common features, because the outer shell layer often is missing from specimens due to abrasion and solution. Another possible explanation for the lack of more such calcite ridges on rudists is that an individual could live successfully without being propped-up by its neighbors. The abundance of specimens seen in outcrop with an intact outer shell layer but lacking such ridges implies that individuals of *C. orcutti* may have lived in close proximity, but were not necessarily cemented together.

Former attachment of individuals is also indicated where the base of one rudist is distorted to conform to the shape of its previous attachment site on another rudist or the substrate (Pl. 1, fig. 7). Also, where the outer shell layers have been partially stripped away from closely adjacent valves by post-mortem processes, it is apparent that the rudists were cemented together when the shell layers were intact (Pl. 1, fig. 4).

Four juveniles (Pl. 2, fig. 2) attached to a single adult specimen show how early growth of the attached valve took place. The best-preserved valve (Pl. 2, fig. 1) is 14 mm in length and 4.4 mm in depth. These specimens clearly show spiral growth during early ontogeny of the attached valve. The spiral growth is parallel to the plane of commissure and directs the apex of the valve anteriorly. Spiral growth at this stage aided survival, as it produced a relatively broad, stable base for future upward growth. The spiral growth phase probably did not last long, because individuals quickly reached the size where they began to develop the characteristic conical attached valve and elevate their feeding and respiratory margins above the potentially suffocating substrate. Eroded remnants of two or more juveniles are shown attached to another adult by White (1885, Pl. 3, fig. 1). One adult specimen at hand retains the spiral growth stage of its attached valve (Pl. 1, fig. 5, upper right).

I have observed *C. orcutti* attached only to others of its kind, and have found no mention of specimens attached to rocks or to other organisms. However, attachment to foreign objects must have taken place. The great weight and top-heavy proportions of an individual would have made existence on an unconsolidated substrate unlikely. Attachment to a hard bottom and upward growth was necessary to maintain the feeding and respiratory margin above the fine substrate. In the first stages of establishing a population at a new location or the expanding of an existing population, attachment of the pioneer individuals probably would have been on scattered cobbles and boulders. Once a successful first generation had matured and reproduced, the following generation could use the shells of its predecessors as convenient attachment sites.

There are several possible reasons for many of the specimens seen at the outcrop being articulated. As described above, the ligament has such a small cross-sectional area that it probably was ineffectual in opening the valves and served mainly to hold the dorsal valve margins together. If valve opening was accomplished primarily by expansion of the soft parts (Dechaseaux, 1969), there would have been no opening pressure on the valves after death. In addition, the roughened margins of each valve, produced by the exposed ends of the cellular inner shell layer, might also have tended to keep the valves together after death. If most specimens grew relatively erect, the considerable weight of the free valve would have helped to prevent it from being easily dislodged in the predominantly low-energy environment. It is also possible that some of the individuals were buried alive by shifting sediments, perhaps during storms. This would have preserved individuals in their life orientations.

SUMMARY

1.—The *Coralliochama orcutti* beds at Punta Banda are biostromal deposits formed below mean wave base in a shallow-water, mostly low-energy environment. They show no evidence of ever having formed free-standing reef structures.

2.—Attachment among individuals did not occur necessarily, but was common. All individuals were cemented to a hard substrate, beginning in early ontogeny.

3.—Spiral growth during early ontogeny of the attached valve produced a broad, stable base for later upward growth and allowed proper orientation of the individual no matter what the initial inclination of the juvenile or substrate.

4.—Tooth morphology in each valve is extremely variable.

5.—Two stunted attached valves are probably an adaptation to cementation on a steeply inclined substrate.

6.—A raised callus on the postero-lateral portion of the free valve served as an accessory tooth to aid valve alignment.

7.—A narrow groove traversing the ventral margin of the free valve in one of the original illustrations (specimen figured herein, Pl. 2, fig. 19) is shown to be an artifact, and is not present in other free valves.

8.—The holotype of *C. flouriei,* also described from Punta Banda, is interpreted as a young adult of *C. orcutti.*

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