



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

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; $\times 2$; 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; $\times 0.4$.
- 3—Dorsal view of lectotype. USNM 186661; $\times 0.25$.
- 4—Anterior view of lectotype. USNM 186661; $\times 0.25$.
- 5—Interior view of free valve; $\times 0.5$; l, ligamental inflection; lg, ligamental groove.
- 6—Posterior view of specimen shown in fig. 5. Note relatively strong convexity of valve; $\times 0.5$.
- 7—Dorsal view of complete individual. Paralectotype. USNM 186664; $\times 0.5$.
- 8—Dorsal view of complete individual, showing relatively abrupt tapering of attached valve. Paralectotype. USNM 186663; $\times 0.5$.
- 9—Interior view of free valve, with prominent central and posterior teeth and median septum; $\times 0.5$; t, tooth; s, socket.
- 10—Posterior view of specimen shown in fig. 9. Note relatively weak convexity of valve and prominence of teeth; $\times 0.5$.
- 11—Interior view of free valve, showing large postero-ventral callus (c) that may have aided in maintaining alignment of valves; $\times 0.5$; s, septum; r, roughened area.
- 12—Exterior of free valve, showing concentric sculpture. Microscopic concentric growth lines are not visible; $\times 0.55$.
- 13–15, 17, 18—Interiors of adult and juvenile free valves; 13, $\times 0.5$; 14, $\times 0.55$; 15, $\times 0.65$; 17, $\times 0.9$; 18, $\times 1.5$.
- 16—Enlarged cross-section of ventral shell wall of attached valve. Note radial arrangement of pallial canals at outer shell wall; $\times 10$; o, outer shell wall; p, pallial canals; i, inner shell wall.
- 19—Interior of young adult free valve. Paralectotype. USNM 186662; $\times 1$.

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 pro-

cesses. 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 together. 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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