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*CONOCARDIUM LANGENHEIMI* SP. N.  
(MOLLUSCA: BIVALVIA) IN THE LOWER PERMIAN SERIES  
OF THE McCLOUD LIMESTONE, NORTHERN CALIFORNIA

By EDWARD C. WILSON

LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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*CONOCARDIUM LANGENHEIMI* SP. N.  
(MOLLUSCA: BIVALVIA) IN THE LOWER PERMIAN SERIES  
OF THE McCLOUD LIMESTONE, NORTHERN CALIFORNIA

By EDWARD C. WILSON<sup>1</sup>

ABSTRACT: *Conocardium langenheimi* sp. n. (Mollusca: Bivalvia) occurs in the Wolfcampian Stage, Lower Permian Series of the McCloud Limestone in Shasta County, California. It is a large shell with a non-carinate posterior end, three pairs of perforate "shelves" within the gaping anterior end, a tube enclosed dorsally in the shell layers of each valve, unique internal hinge structures, and microstructure unlike most other bivalves. The functions of these and other characters is unknown. The entire Order Conocardidoida needs investigation to determine the significance of such characters, especially for placing the group in higher categories of classification.

INTRODUCTION

At the suggestion of R. L. Langenheim, Jr., Professor of Geology at the University of Illinois, I began a study of the paleontology of the McCloud Limestone in Shasta County, California, in the spring of 1963. Two previous papers (Wilson, 1967a, 1967b) resulted from this study and this paper is another contribution.

ACKNOWLEDGMENTS

I am grateful for opinions on the morphology and systematic position of the Conocardidoida from J. Wyatt Durham of the University of California at Berkeley, John Pojeta, Jr. of the U.S. National Museum, and Norman D. Newell of the American Museum of Natural History. Professor Durham kindly visited the type localities with me. Most of the photographs are by Lawrence S. Reynolds of the Los Angeles County Museum of Natural History.

Field work in 1963 and 1964 was financed in part by the University of California Museum of Paleontology (UCMP) and the University of California Committee on Research, both at Berkeley. The Los Angeles County Museum of Natural History (LACM) provided funds for further field work in 1968.

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## SYSTEMATIC DESCRIPTION

Phylum MOLLUSCA

Class BIVALVIA Linnaeus, 1758

Order CONOCARDIDOIDA Neumayr, 1891

Family CONOCARDIIDAE Miller, 1889

Genus *Conocardium* Bronn, 1834

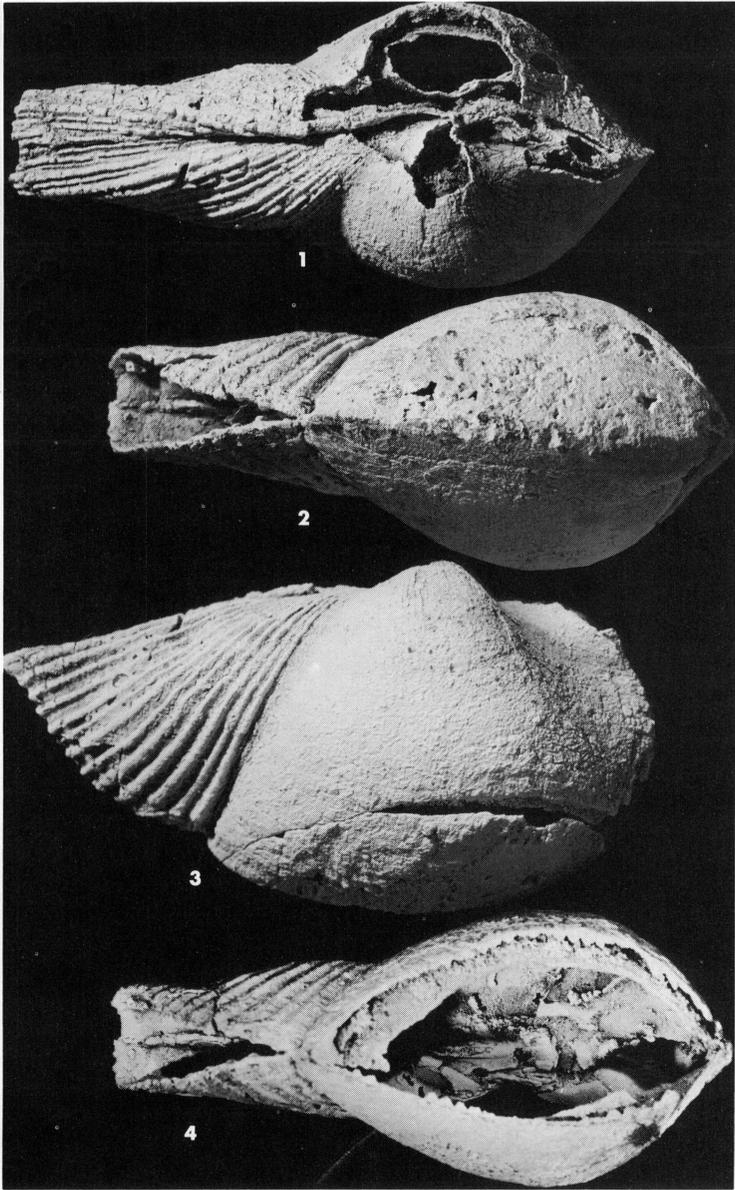
*Remarks:* Terminology has not been standardized for the unique characters of the Conocardidoidea. I have used where possible the terminology for other bivalve mollusks, although this is partially unsatisfactory. The structures called "auricles" are probably not homologous with the auricles of other bivalves. The "shelves" in the gaping anterior "auricle" are without parallel in the rest of the Bivalvia. The openings in the "shelves" and the tubes enclosed in the shells have no formal names. The kind of "teeth" on the ventral and posterior edges should probably be named. It is not even possible to use uniformitarianism to orient the shell with certainty. It may seem reasonable that dorsal and ventral are accurately delineated, but there is no such certainty about anterior and posterior. The figures and legends indicate usage of morphological terms in this paper.

*Conocardium langenheimi*, sp. n.

Fig. 1

*Description (external):* Valves equivalve, inequilateral, opisthogyrate, alate (?), not ankylosed; main body of valves inflated, rounded (not carinate posteriorly); posterior "auricle" small, sloping smoothly into main body of valves, not gaping; anterior "auricle" separated by constriction from main body of valves, large, rostrate, gaping anteriorly and ventrally, with large trigonal aperture having scalloped margins; hinge line straight, except anterior part of anterior "auricle" may dip to 25° (preservation?), occupied by groove, shallow in anterior part of anterior "auricle," deep in posterior part of anterior "auricle" and main body of shell; commissure straight on exterior of ventral parts of shells; holotype shell length 6.5 cm, height 4.3 cm, width 2.9 cm (largest specimen, LACM paratype 2443, is 4 mm. higher, but incomplete

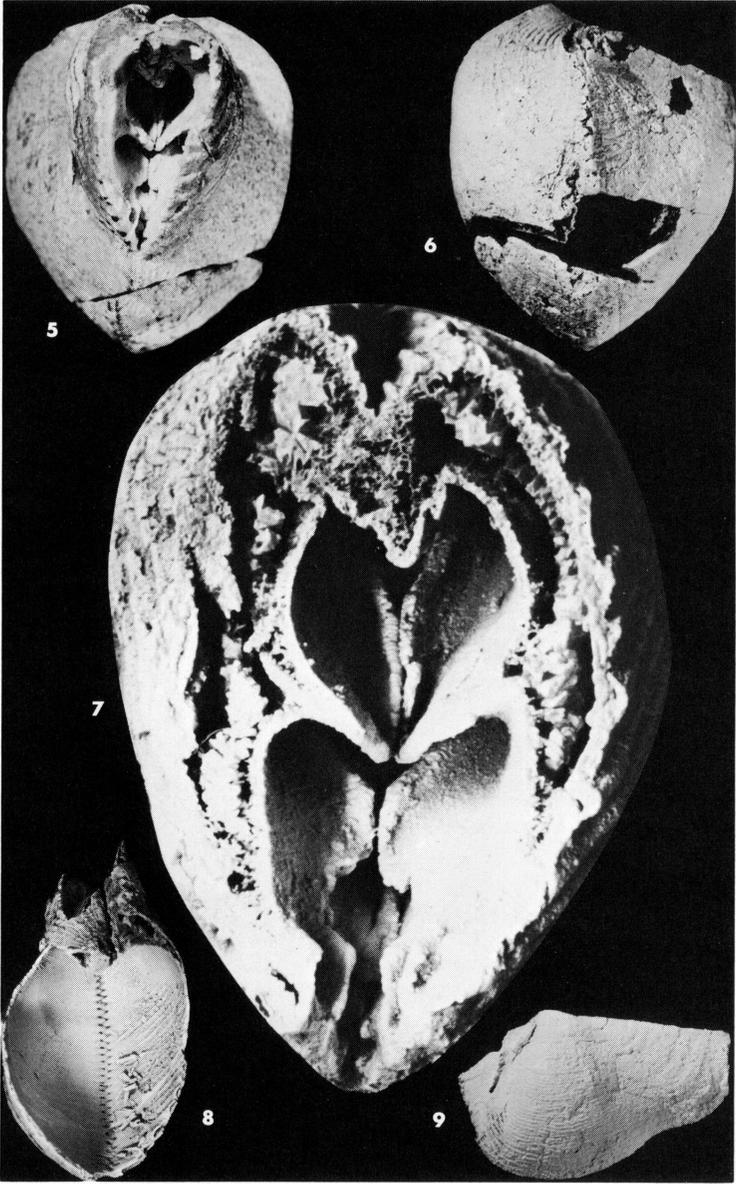
Figures 1-4. *Conocardium langenheimi* sp. n. UCMP holotype 10589, UCMP locality D-831, all figures X 1.3; (1) dorsal view, anterior "auricle" at left, posterior "auricle" at right, main body of shell inflated, openings in umbos caused by post-burial weathering, double wall caused by dissolution in HC1 of calcareous layer between silicified layers, note absence of posterior carina; (2) ventral view, showing straight exterior commissure of main body, gape of anterior auricle, internal ridge at hinge line; (3) lateral view of left valve, sculpture on main body possibly dissolved in part during etching; (4) ventral view, with piece of shell removed to show dorsal interior, dorsal ridge along hinge line of main body broken with fragments lying in right valve, note trigonal cross sections of ridges remaining in shell wall after etching.



in other dimensions); sculpture concentric or cancellate (?) on main body of valves, with about 4 evenly spaced concentric riblets in one mm., with possible traces of radial riblets; sculpture radial on "auricles" (UCMP paratype 10590, juvenile, shows some concentric), about 17 ribs on anterior "auricle" of each holotype valve, fewer on posterior "auricle" (UCMP paratype 10590, juvenile, has 9 ribs on each posterior "auricle"); ribs straight to very gently sigmoid, sloping down from hinge line at angles varying from 65° on posterior part of anterior "auricle" to 25° on anterior part, flat topped with straight to rounded sides sloping down and out at less than 45°; rib interspaces about equal to rib widths, lirate, with about 20 dorsally convex lirae in 1 mm, rarely occupied by single riblet.

*Description (internal)*: Main body of valves smooth; pallial line, muscle scars not observed; ventral and posterior commissure zig-zag, formed by series of trigonal "teeth" and intervening sockets in each valve, 3 occurring every 5 mm each side of both valves (holotype), sockets showing plainly only in section ("teeth" are surficial extensions of radial rods, trigonal in cross section, apex pointing inward, that dorsally form part of the internal shell layer); hinge line a complex ridge, low in anterior end, becoming higher posteriorly, developing horizontal distal bar (inverted T-shaped in cross section) within main body cavity of valves, where narrow trough borders each side (marking lateral limits of apparent separate hinge plate in this area), becoming lower and broader posteriorly, troughs continuing alongside into posterior "auricle," where termination not observed because of preservation; 3 pairs of complex "shelves" lining lateral interior of anterior "auricle," sloping in and up same angles as exterior ribs, each pair meeting in midline, dividing "auricle" roughly horizontally into 4 unequal areas; dorsal pair of shelves beginning about 15 mm back of "auricle" anterior edge, about 8 mm below top of "auricle," forming large heart shaped opening in cross section above "shelves," turned up along midline by lip-like ridge, sloping upward, separating along midline below

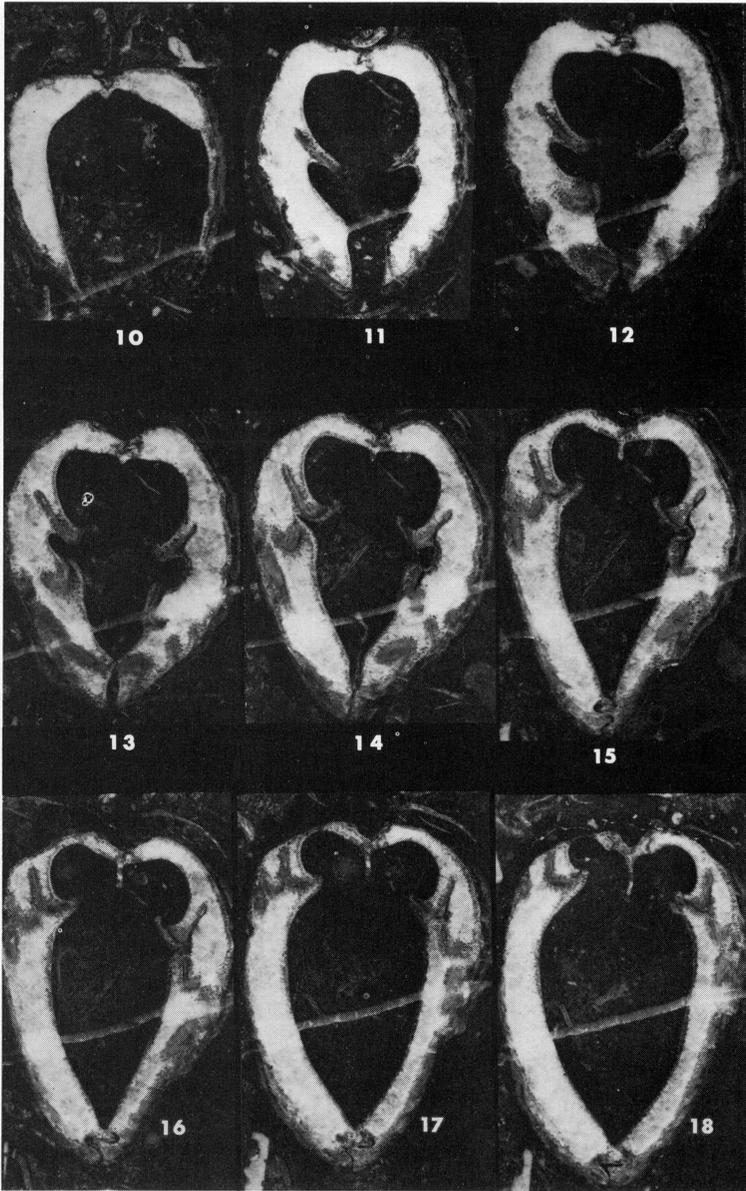
Figures 5-9. *Conocardium langenheimi* sp. n. (5) holotype, anterior view into gaping "auricle" showing 3 pairs of "shelves," X 1.3; (6) same specimen, posterior view, umbos partially weathered away, note zig-zag commissure of "auricle," straight commissure of main body, X 1.3; (7) same specimen, same view as figure 5 with part of auricle removed, missing parts of wall dissolved during etching, note exterior groove and interior ridge of hinge line with grooves bordering latter, dorsal "shelves" meeting along midline with opening into main body visible just above, middle shelves similar but extending anteriorly to form keyhole shaped opening, partly obscured small ventral "shelves" shaped like middle "shelves," X 3.6; (8) LACMNH paratype 2443, LACMNH locality 1133, fragment showing zig-zag interior ventral commissure formed of series of teeth and sockets, note left valve showing original smooth interior, right valve showing etched layer of shell wall with internal trigonal ridges which terminate ventrally as teeth, X 0.6; (9) UCMP paratype 10590, UCMP locality D-831, lateral view of right valve of juvenile specimen, note concentric sculpture on main body and anterior auricle, offset posterior "auricle," outline of anterior "auricle" varying from figure 3, X 1.4.



hinge line, leaving opening here into main part of shell, shelves continuing dorsally and posteriorly with lips incurving to form tubes passing into shell layers before leaving "auricle," tubes continuing posteriorly in shell above main body of shell, lateral to hinge line, becoming closer posteriorly and apparently dropping into external groove above hinge line, with posterior course unknown due to preservation (no apparent natural external opening observed in posterior "auricle" or hinge line); middle "shelves" also large, paralleling dorsal ones, similar in shape and slope, but extending to anterior edge of "auricle," forming key-hole shaped opening in anterior ends as well as heart-shaped opening posteriorly into main body of shell, with anterior lips as in dorsal "shelves," extending into grooves in "auricle" walls under dorsal "shelves" posteriorly, ending at posterior termination of dorsal "shelves," without continuing internal tube; ventral "shelves" small, shaped like middle "shelves."

*Description (microstructure)*: Preservation very imperfect, shell partially silicified, some layers separated by silica, some missing (erosion?) in places; shell calcium carbonate, 1.5 to 3.5 mm thick, with 3 layers throughout plus 3 highly restricted layers; exterior layer 0.33 to 1.0 mm thick, prismatic, distal crystal tips reflected ventrally, elsewhere normal to shell surface; middle layer 0.2 to 0.3 mm thick (generally replaced by silica and difficult to measure), lamellar, showing ventrally convex concentric growth lines crossed by finer radial lines, separated in places from prismatic layer by dark line (concholin?); inner layer 2 to 3 mm thick, much wider than other layers, formed of large calcium carbonate crystals (apparently recrystallized), showing residual (?) growth lines in some areas, etching in dilute hydrochloric acid in main body of shell into trigonal ridges (see above), evidence of which not observed in polished or thin sections; myostracum (?) in 3 bands in each valve, extending from opposed axial edges of "shelves" to umbos, straight to V-shaped in

Figures 10-18. *Conocardium langenheimi* sp. n. UCMP paratype 10591, UCMP locality D-831, specimen ground down from anterior to posterior to show successive cross sections, all figures X 2.2; (10) section near anterior of anterior "auricle," note great shell thickening (left) from thin anterior edge (right); (11) dorsal "shelves" begin to form, note rod like myostracum (?) protruding from "shelves," internal scalloped outline of outer shell layers; (12) three pairs of "shelves" forming, note deepening grooves between dorsal and middle "shelves"; (13) three pairs of "shelves" formed here, each with associated myostracum (?); (14) upper "shelves" move dorsally, curl inwards, middle "shelves" pass into two grooves, lower "shelves" have disappeared, internal dorsal ridge along hinge line begins to lengthen; (15) dorsal "shelves" move dorsally, other "shelves" disappear (groove extending from middle "shelf" on right still present), rods of myostracum (?) move dorsally in shell wall, teeth and sockets appear ventrally marking ventral beginning of main body of valves; (16) dorsal ridge lengthens, pre-burial erosion noticeable on dorsal edge of valve at left; (17) dorsal ridge lengthens; (18) dorsal ridge lengthens, dorsal edge of eroded valve thins, dorsal "shelves" move higher, accompanied by their myostracum (?) rods and those from two lower "shelves."



cross section (varies), about 0.2 mm thick, apparently exposed at "shelf" edges (indicates muscles joining opposing "shelves"?), showing concentric and radial lines as in middle layer.

*Name:* This species is named for R. L. Langenheim, Jr. in recognition of his contributions to our knowledge of the paleontology and stratigraphy of North America and for his inspiration and training of many students in this work.

*Type specimens:* Holotype UCMP 10589, paratypes UCMP 10590-10591, paratype LACM 2443, all UCMP locality D-831 (=LACM locality 1133); paratype UCMP 10592, UCMP locality D-819.

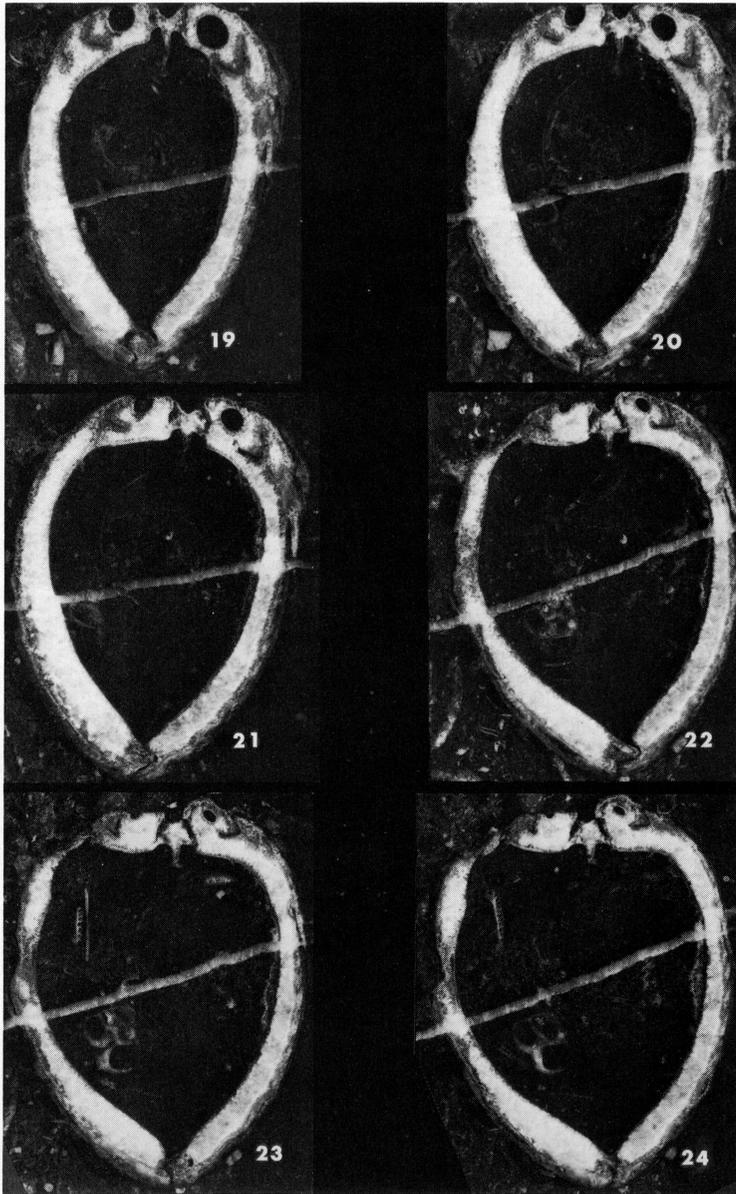
*Localities:* UCMP locality D-819. 1140 feet stratigraphically above the lowest exposure of the McCloud Limestone on the first spur south of the eastern end of the McCloud River bridge as shown in the northwest  $\frac{1}{4}$  of the southwest  $\frac{1}{4}$  of section 32, township 35 north, range 3 west of the United States Geological Survey topographic quadrangle (15 minutes, 1957) of Bollobokka Mountain, Shasta County, California. Series of one foot high ledges of limestone, fine to medium grained, black to medium gray, weathering medium to light gray; little chert; many silicified fossils, including large caninoid corals, *Conocardium*, *Omphalotrochus*, fusulinids.

UCMP locality D-831 (= LACM locality 1133). Estimated 200 yards south of locality D-819 along strike and about 15 feet higher in the section. Narrow bench of thin-bedded, black, silty limestone below a sheer massive cliff. Abundant syringoporid corals, very large solitary rugose corals, fusulinids, bryozoans, *Conocardium*.

*Age:* The fusulinids have the most refined stratigraphic ranges of the fossils found with *Conocardium langenheimi*. Two species were identified: *Pseudofusulina soluta* Skinner and Wilde, 1965 and *Triticites mulleri* Skinner and Wilde, 1965, both having type localities in the McCloud Limestone nearby the *Conocardium* localities. Skinner and Wilde (1965, pl. 4) considered the former fusulinid to indicate definite Permian age (the genus is a Wolfcampian index fossil) and the latter to be of either Pennsylvanian (Virgilian) or Per-

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Figures 19-24. *Conocardium langenheimi* sp. n. Continuation of sections of same specimen as figures 10-18, same magnification; (19) dorsal "shelves" have incurved and passed into tubes in shell wall, marking dorsal beginning of main body of valves, myostracum (?) rods now wholly within shell wall, dorsal ridge greatly lengthened and now having horizontal distal end (not clear in this photograph but see fig. 34), possibly developing into separate plate along hinge line, with lateral grooves internally, midline groove externally, tube at left opened by erosion; (20) dorsal tubes narrow, note ventral teeth showing how ventral commissure can be exteriorly straight yet interior zig-zag, also shows shell not ankylosed; (21) dorsal tubes narrow, dorsal ridge shortens; (22) dorsal tubes narrow and move toward midline, dorsal ridge shortens; (23) dorsal tubes narrow, valve at left badly eroded; (24) dorsal tubes smaller, dorsal ridge shorter, dorsal part of valves move ventrally, deepening external groove.



mian (Wolfcampian) age. It seems clear, therefore, that the interval of the McCloud Limestone from which *C. langenheimi* was collected is definitely occupied by Lower Permian Series, Wolfcampian Stage rocks.

*Diagnosis:* *C. langenheimi* can be separated readily from most other species because it lacks a carina on the posterior part of the main body of the shell. It is also larger than most species and the anterior "auricle" is proportionately longer in relation to the rest of the shell than in many other species.

*Discussion:* *C. langenheimi* resembles closely only *C. uralicum* (Verneuil, in Murchison, Verneuil, and Keyserling, 1845, p. 301, pl. 20, figs. 11a, 11b) from Upper Carboniferous rocks of the Ural Mountains. Both species lack posterior carinae and have elongate anterior "auricles." However, *C. uralicum* is smaller (length 36 mm) and has an anterior "auricle" that is much more elongate in proportion to its height than that of *C. langenheimi*. Internal structures and shell microstructure of *C. uralicum* are unknown as yet.

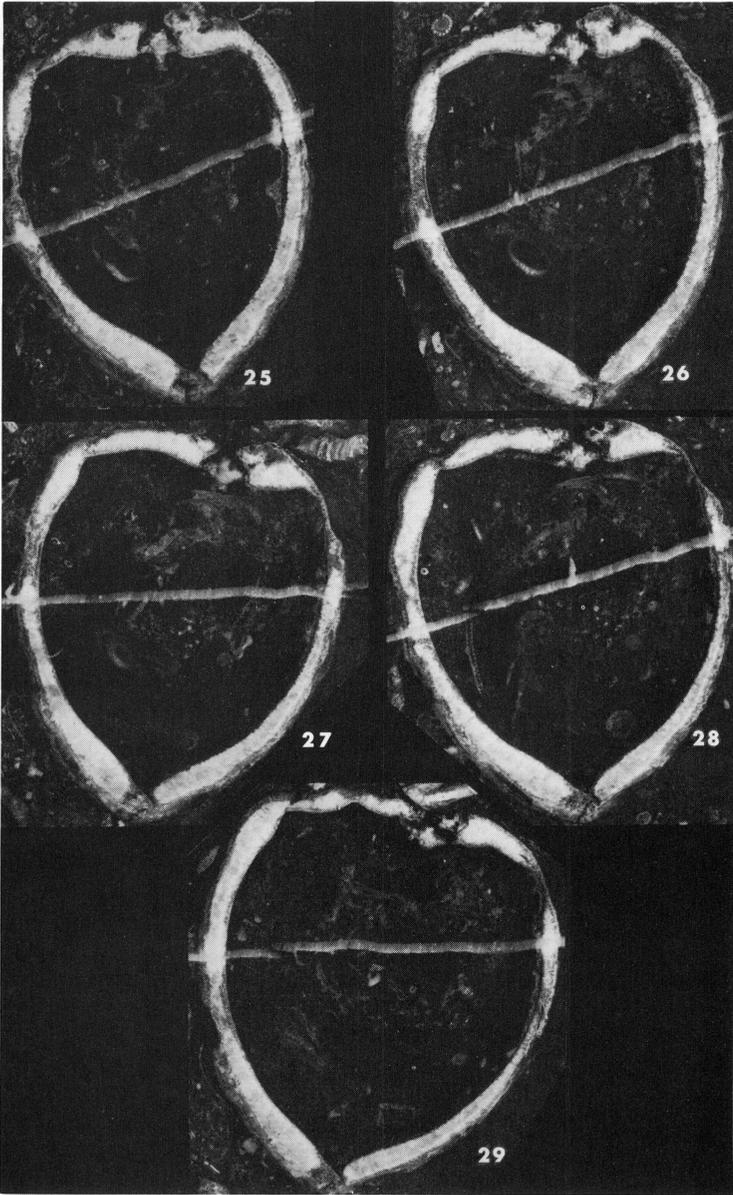
The microstructure of *C. langenheimi* apparently lacks "roofed-over pits" like those figured by Pannella and MacClintock (1968, pl. 8, fig. 5) in *C. sp.* from Upper Pennsylvanian rocks of Oklahoma. The "outer complex-prismatic shell layer" shown by Pannella, MacClintock, and Thompson (1968, fig. 1A) of *C. herculeum* Konick from Lower Carboniferous rocks of Belgium resembles a similarly positioned layer in *C. langenheimi*, but lacks the reflected tips that are present in the latter species.

The presence of complex internal structures in *Conocardium* was early reported by Hind (1900, p. 451, pl. 51, fig. 11a) in some detail, although he apparently worked from specimens somewhat worn internally. Curiously, no further refined work on them seems to have been published, although Decha-seaux (1952, p. 319, fig. 162a) and Branson, LaRoque, and Newell (1969, p. 859, fig. G1) cursorily discussed and figured some internal characters. Future workers should examine the internal structure of specimens of *Conocardium* with great care.

I have tried to find clues that would help determine the habitat and functional morphology of *C. langenheimi*. The associated fossils show that the salinity of the water must have been whatever was normal for the open oceans in Permian time. Permian near-shore faunas with restricted access to the sea in western North America generally lacked corals and fusulinids, both of which

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Figures 25-29. *Conocardium langenheimi* sp. n. Continuation of sections of same specimen as figures 10-24, same magnification; (25) dorsal ridge shorter but horizontal expansions of distal end still present, dorsal tube openings smaller (not seen in valve at left), some of dorsal part of valve at right shows erosion; (26) dorsal tube moves inward and downward, dorsal ridge shortens, distal expansions disappear, erosion of both valves and distortion of valve at left apparent; (27) continuation of movements seen in figure 26; (28) continuation, myostracum (?) rod (dark chevron) shows beside eroded tube in valve at right; (29) dorsal tubes move ventrally, hinge line plate broadens.

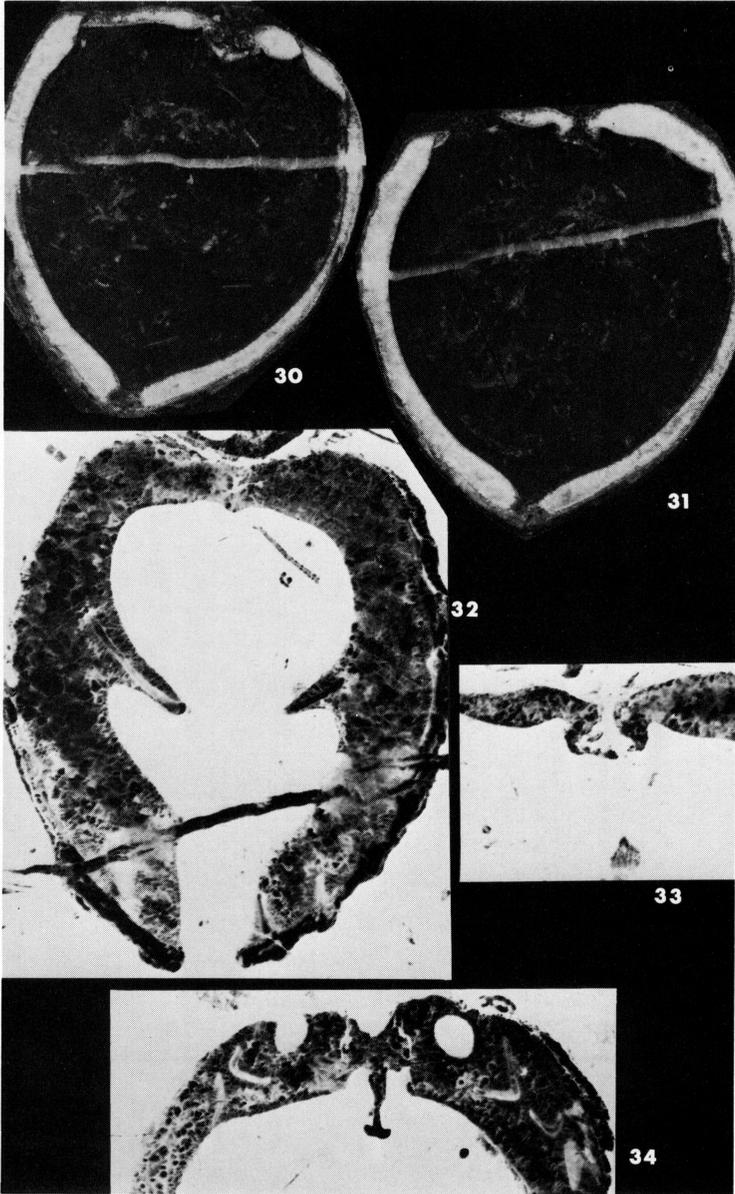


are abundant at the *C. langenheimi* localities. The shell itself is sturdy, especially the thick walled anterior "auricle," which suggests exposure to some strong current or wave action. Seemingly eroded parts of some of the specimens indicates that they may have been moved by currents from their original habitats. However, some fine silty layers in the limestone indicate that sedimentation was generally not rapid. None of the specimens shows evidence of having been buried in a burrow, which seems to me the most likely habitat by analogy with Recent bivalves of the most similar external form, size, and sturdiness (Pholadidae). Branson (1969, p. 860, figs. 3a, 3b, in Branson, LaRoque, and Newell) figured, but did not discuss, a restoration of a *Conocardium* apparently occupying a burrow, but having the anterior "auricle" innermost, which is unlike the Pholadidae. Nicol (1970, p. 70) also compared *Conocardium* with Recent bivalves, but reached the different conclusion that it "was attached by a short, stout byssus . . ." All the specimens of *C. langenheimi* appeared to be lying randomly on surfaces parallel to the bedding planes. They are all tightly closed pairs, which is unlike other Bivalvia, if one assumes because of the eroded areas that they were buried after death.

Reconstruction of the soft part morphology of *C. langenheimi* will not be simple. I have been unable to create a satisfactory model for incurrent and excurrent siphons. The complex form of the "shelves" indicates that some extremely specialized soft part morphology was present. The apparent absence of muscle scars in the anterior end may be explained by the existence of muscles between the edges of opposing "shelves," as suggested by the myostracum (?) exposed there. One would expect posterior muscles also, which seemingly are not represented by muscle scars or a posterior myostracum. Perhaps the function of the unique hinge line structures and the ventral and posterior "teeth" rendered posterior muscles unnecessary. The internal ridge along the hinge line looks greatly like a support, but one wonders for what, since the other bivalves seem to function well without such a rigid support for the ctenidia, alimentary canal, or other systems. It is tempting to postulate a

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Figures 30-34. *Conocardium langenheimi* sp. n. (30) continuation of sections of same specimen as figures 10-29, same magnification, dorsal tubes drop into exterior grooves bordering hinge line, dorsal ridge disappears; (31) same specimen, same magnification, dorsal tubes not present (preservation?), external grooves coalesce, with narrowed opening above, hole in shell at left caused by erosion, shell not preserved posterior to this section and nature of structures there unknown; (32) thin section made from polished section shown in fig. 11, note especially exposed end of myostracum (?) at edge of "shelf" at left and indeterminate nature of hinge articulation, X 3.2; (33) thin section made from polished section shown in fig. 31, showing nature of hinge and apparent absence of dorsal tubes seen in figs. 19-30, X 3.2; (34) thin section made from polished section shown in fig. 21, showing dorsal tubes, myostracum (?) layers, elongate internal hinge line ridge with horizontal distal bar, exterior ligament (?) groove, and apparent separate nature of plate along hinge line, X 3.2.



function such as brood chambers to the tubes in the dorsal parts of the valves, but, again, close analogies in living bivalves seem absent. Some of the grooves in the shell suggest ciliated tracts, but there is no certainty about this.

#### CONCLUSIONS

*C. langenheimi* is a member of the Conocardidoida, which is externally like the Bivalvia, has a world wide distribution, and ranges from Ordovician through Permian (Triassic?) rocks. The degree of complexity shown by the shell microstructure definitely appears to be molluscan. The paired valves suggest that the Order belongs in the Class Bivalvia, however the internal morphology and shell microstructure is unlike others in that class. If typical of the order, these suggest need for a reconsideration of the systematic position at the class or higher level.

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