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# PERMIAN CORALS OF BOLIVIA

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ABSTRACT—Permian corals of Bolivia are confined to the Lower Permian (Wolfcampian, Leonardian) Copacabana Limestone. The coral fauna of the formation in the Lake Titicaca to the central *altiplano* areas of the Department of La Paz consists of two solitary rugose coral species, two colonial rugose coral species (one each of fasciculate and cerioid), and two tabulate coral species. New taxa are *Stylastraea branisai* n. sp., *Durhamina pandolfi* n. sp., *Michelinia escobari* n. sp., and *Cladochonus carrascoi* n. sp. *Lophophyllidium striatum* (d'Orbigny, 1839), based on Bolivian specimens, is redescribed, a lectotype designated, and the range extended to North America. Although the fauna is small, its taxonomic composition shows clear affinity with faunas of similar age northward through South and Central America to Mexico and the USA Texas–Oklahoma–Midcontinent region. The Bolivian fauna thus is confirmed as belonging to the Cyathaxonid Coral Province, which is restricted to the above areas. A species of *Durhamina* previously erected for Guatemalan specimens occurs in the Copacabana Limestone of Peru and strengthens the province assignment of the formation.

## INTRODUCTION

THE PRIMARY purpose of this study is to report the diversity and stratigraphic distribution of the stony corals of the Lower Permian Copacabana Formation, Department of La Paz, Bolivia. Eleven sections were measured and intensively sampled from the Puerto Carabuco area on the east-central shore of Lake Titicaca southwards for about 150 km to the Colquencha area of the central *altiplano* (Figures 1, 2). Primary collecting emphasis was on corals but representative collections of other megain vertebrates and of fusulinids also were obtained. The results provide a detailed sampling of the corals from the formation in this area and a reconnaissance collection of other fossils. Except as noted, the specimens are deposited in the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

Field work was undertaken between August 4 and September 9, 1985, and August 4 and September 16, 1986. Part of the latter interval was devoted to investigation of the formation in Peru.

## PREVIOUS WORK

Previous work on the coral fauna of the Copacabana Limestone of Bolivia is slight. D'Orbigny (1839, 1842b) erected the only coral species based on Bolivian Permian specimens, *Turbinolia striata,* from Yaurichambi. Branisa (1965) figured eight taxa from Ancoraimes, Apillapampa, Colquencha-Vilaque, Yaurichambi, and Zudanez, referring them to ?*Clinophyllum* sp., *Favosites* sp., *Lithostrotionella* sp., ?*Lophophyllidium* sp., *Lophophyllidium* sp. B, *Macgeea* cf. *M. solitaria, Michelinia* sp., and *Soshkineophyllum* sp. Maeda, Yamagiwa, and Branisa (1973) described and figured three solitary corals from the Colquencha area as *Caninia* sp. indet., *Lophophyllidium* cf. *L. spinosum,* and *Stereostylus*? sp. indet. Yamagiwa, Maeda, Torrez, and Urdininea (1974) described and figured a transverse section of *Lophophyllidium* sp. indet. from "Parquipujio," in the village of San Pedro, west side of the Straits of Tiquina. Yamagiwa, Mukumoto, and Urdininea (1983) described and figured the ontogeny of *Stereostylus*? sp. from the Colquencha area. None

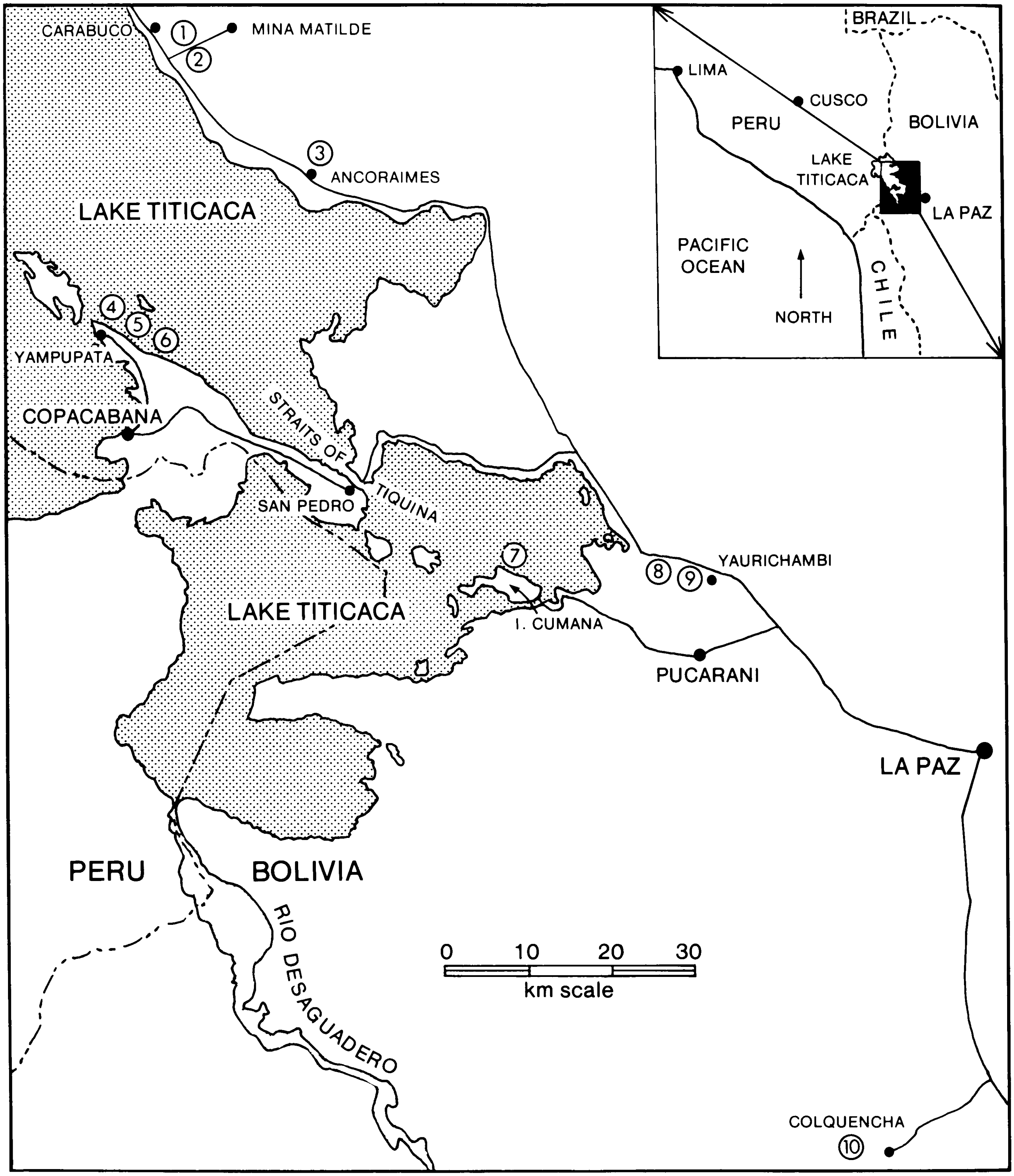


FIGURE 1—Locations (numbered circles) of stratigraphic sections measured in the Copacabana Limestone for this study: 1, Cerro Quimsa Phekhena section; 2, Matilde section; 3, Ancoraimes section; 4, Cerro Pucara section; 5, Yampupata section; 6, Cerro Cabiltosirca section; 7, Cuyavi section; 8, 9, Yaurichambi sections; 10, Colquencha section.

of these papers supplied detailed locality or stratigraphic information. The specimens of Branisa (1965) apparently are lost (L. Branisa, personal commun.).

The Copacabana Limestone extends northward from Bolivia into Peru. Several authors have reported on the corals in the formation there. Douglas (1920), Boit (1940), and Lisson and Boit (1942) listed several taxa from Viscachani, Cerro de Pasco, and Vilcambamba, respectively, all perhaps from the Copacabana Limestone. Finks (1953), in an unpublished M.A. thesis, described and figured the corals in the collections of the American Museum of Natural History from the upper Paleozoic of Peru. He reported 10 species in the Copacabana Limestone, all indicating a northward extension of the Bolivian fauna described here. Rangel (1976) figured a fasciculate corallum from Peru that may be from the Copacabana Limestone. Yamagiwa and Rangel (1978) first mentioned *Durhamina*? *andensis* from the Chaparra area of south coastal Peru and later described and figured the species (Yamagiwa and Rangel, 1979), indicating a Wolfcampian age for it. The Chaparra beds are about 250 km west of the Copacabana Limestone outcrop band and perhaps represent a different formation. The geology of the area is only sketchily known. The small collection of corals from the Chaparra area in the Museo de Historia Natural at Lima contains fasciculate corals very unlike those in the Copacabana Limestone of Bolivia.

The upper Paleozoic Peruvian corals of Meyer (1914) and in the lists of Harrison (1942, 1943) apparently are from the Middle Pennsylvanian Tarma Group.

Few workers have considered the Permian corals from elsewhere in South America. Probable Permian corals from Brazil were reported by Derby (1894) in annotated lists suggesting to this author a similarity to the Copacabana Limestone fauna. Scrutton (1971) described and figured taxa similar to those in the Copacabana Limestone from the Lower Permian (in part) Palmarito Formation of Venezuela. Hoover (1981) listed two solitary corals and a tabulate coral also from the Palmarito Formation of Venezuela.

## D'ORBIGNY'S LOCALITY AT YAURICHAMBI

Rock drumlins formed largely of the Copacabana Limestone occur in two areas near the community of Yaurichambi, Department of La Paz: 1) at the northern side of the community as two very low mounds that are rather sparsely fossiliferous and expose neither the upper nor the lower formational contacts; and 2) about two km north of the community at a much larger, twin-peaked hill named Cerro Jacha Khatawi that exposes both the upper and lower formational contacts.

D'Orbigny (1842a, 1844, 1847) mentioned this area in several of the volumes of *Voyages dans l'Amerique meridionale*. Because it is the type locality for several of his species, including a coral, it is important. Two citations pinpoint the locality that he collected only on June 12, 1833. D'Orbigny (1842): "... I came ... toward two isolated little mamelons, which I perceived near the farm of Yarbichambi: on one of them, the more southerly, elevated to more than 40 m ... I collected ... a great number of well-preserved fossils...." "Considered under the point of view of their composition, the Carboniferous terrains offer different marks ... at Yarbichambi, they are covered stratigraphically and concordantly with a very friable, quartz sandstone, red, not clayey, without fossils." (Translation by this author.)

The southern peak of Cerro Jacha Khatawi presently is known in Yaurichambi as Cerro Hiscka Khatawi, the former name being restricted to the higher northern peak. Cerro Hiscka Khatawi is somewhat higher than 40 m, exposes beds containing the species described by d'Orbigny, and has a brick-red, unfossiliferous, quartz sandstone at the top of the section. No other hill in the area has this combination of characters. Cerro Hiscka Khatawi is therefore considered here to be the locality collected by d'Orbigny.

Sakagami (1986) identified one of the much lower hills at the northern edge of the community as the d'Orbigny locality. It is too low, exposes no upper formational contact, and therefore cannot be the d'Orbigny locality.

## REGIONAL GEOLOGY

The Andes in Bolivia are divided geomorphically into the volcanic Cordillera Occidental on the west, the sedimentary basin known as the *altiplano* in the center, and the largely Paleozoic sedimentary Cordillera Oriental on the east. Exposures of the Paleozoic sedimentary rocks, including the Copacabana Limestone, also crop out as hills in the *altiplano,* around Lake Titicaca, and in the western foothills of the Cordillera Oriental. The complex geology of the Bolivian Andes has been treated extensively in the monographic studies of Ahlfeld (1946), Newell (1949), and Ahlfeld and Branisa (1960).

## STRUCTURE AND RELATIONSHIPS

The Paleozoic rocks on the *altiplano* are exposed in discontinuous bands that strike generally northwest–southeast. They are divided into irregular thrust sheets accompanied by folding and faulting. In the upper Paleozoic, thick and widespread beds of marine Devonian shales are overlain by nonmarine Carboniferous sandstones that in turn are overlain by Permian limestones and volcanics. The Permian limestones constitute the Copacabana Limestone, named for prominent exposures on the Copacabana Peninsula in southern Lake Titicaca.

The contact of the Copacabana Limestone with the underlying Carboniferous Gondwana Series sandstones is an angular unconformity in all the measured sections where it was exposed. It is best seen near Yaurichambi on the east side of Cerro Jacha Khatawi. The contact of the Copacabana Limestone with the overlying formations is variable. On the east-central shore of Lake Titicaca, it appears to be conformably overlain by the Tiquina Sandstone or in fault contact with the Cretaceous beds. The top of the formation is folded along the Copacabana Peninsula, and a contact with the Tiguina Sandstone is not observable there. The type locality for the formation unfortunately is on the peninsula on the western shore of the straits of Tiquina, a badly faulted area which is the western limb of the syncline, the axis of which is filled by the straits. The eastern limb of the syncline forms the eastern shore of the straits and is a sparsely fossiliferous, purple-colored, tuffaceous formation (Tiquina Sandstone) containing the Permian marine bivalve *Aviculopinna,* a genus also present in the Yaurichambi and Cerro Cabiltosirca sections of the Copacabana Limestone. This syncline apparently extends along strike southwards beneath the lake, reappearing at the island (sometimes peninsula) of Cumana, where the gradual and conformable contact on the eastern limb between the Copacabana Limestone and the overlying Tiquina Sandstone was placed at the base of the lowest purple sandy unit. At Yaurichambi, the Copacabana Limestone is overlain unconformably by a brick-red sandstone and a conglomerate, probably of Mesozoic or Tertiary age. Farther to the south, at Colquencha neither the base nor the top of the Copacabana Limestone in the measured section is exposed.

These represent largely the field observations of this author. A Japanese research group studying the Paleozoic and Mesozoic biostratigraphy of Bolivia has been working partly in the same areas and has published (Sakagmi et al., 1983; Sakagmi, 1984, 1986) valuable information on the Copacabana Limestone.

## STRATIGRAPHY, AGE, AND CORRELATION

The thickest section of the Copacabana Limestone (Cuyavi) is 316 m thick. The best-studied sections (near Yaurichambi)

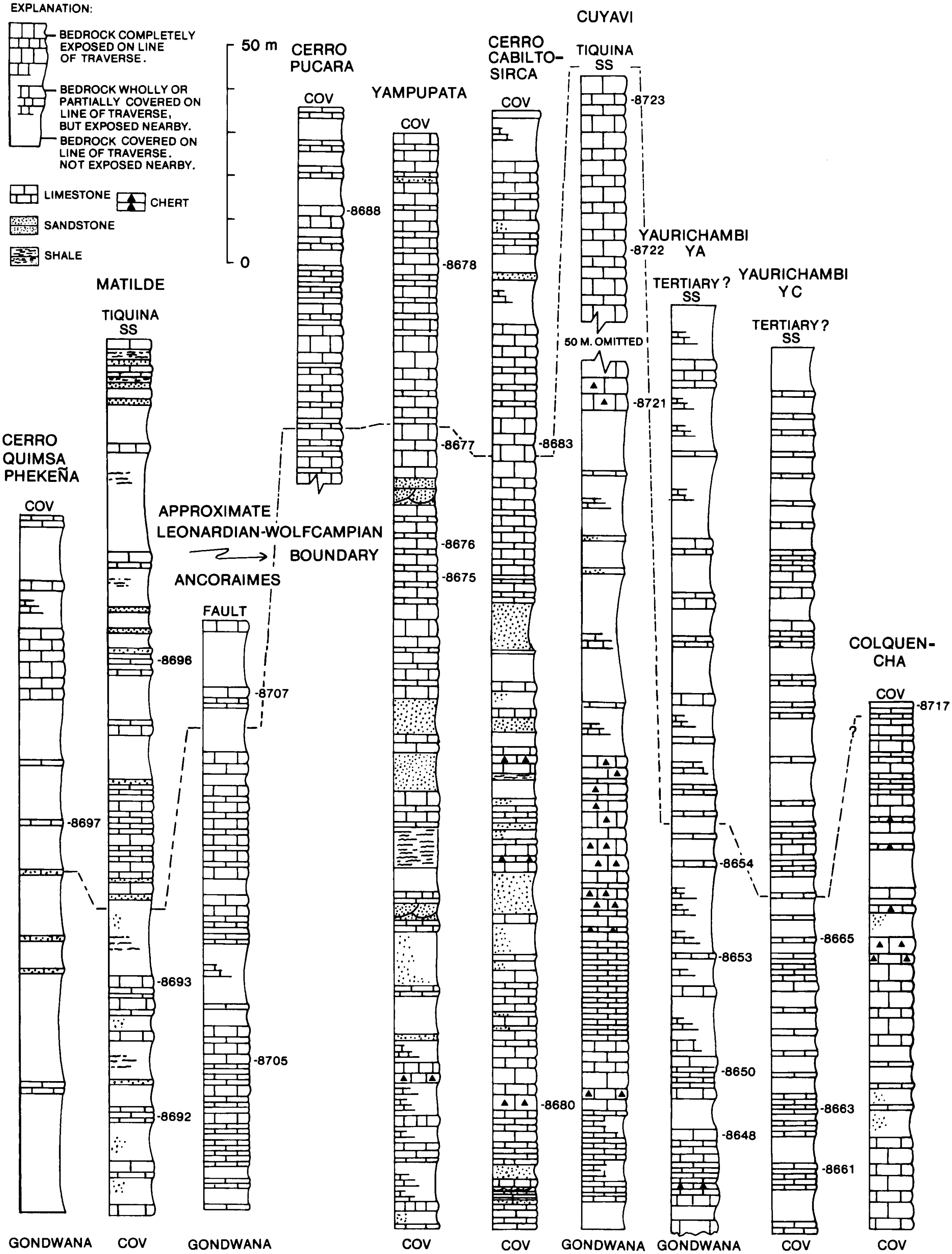


FIGURE 2—Columnar sections of the Copacabana Limestone, showing locations of coral collections.

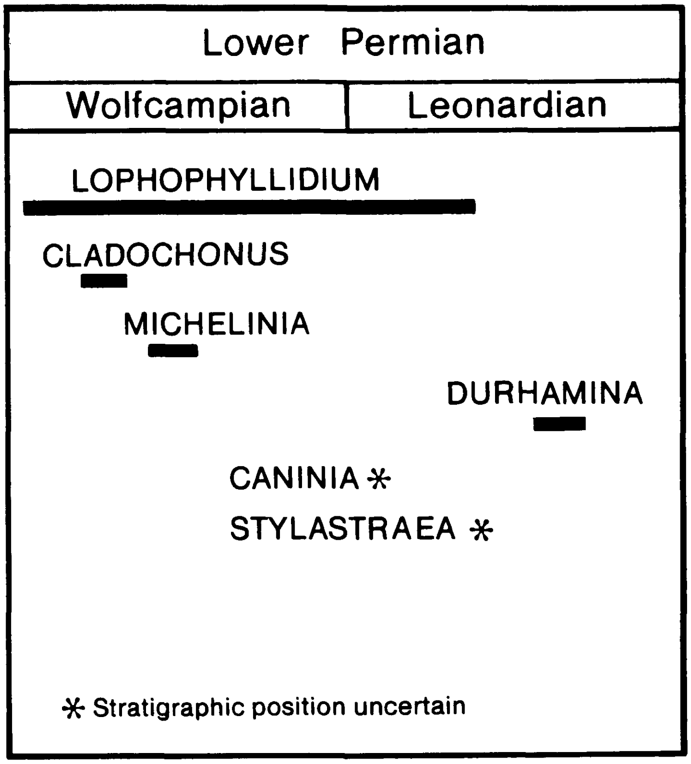


FIGURE 3—Stratigraphic ranges of coral genera in the Copacabana Limestone.

are about 213 m thick, perhaps reduced by Tertiary erosion. The other sections are faulted or folded at the tops so that complete thicknesses are unobtainable but they all suggest original thicknesses of 200–300 m. The formation is roughly cyclical. The most prominent rock units are the gray-blue bioclastic limestones, which can be followed locally along strike from section to section and also regionally correlated biostratigraphically. Several quartzose sandstones, some cross-bedded, are of potential use in lithologic correlations over wide areas. These are yellow, brown, gray, or buff. Of special interest are thin rock units weathering shades of green, some strikingly bright blue-green, and ranging in grain size from aphanitic to shale and sandstone. They occur throughout the formation, generally as benches. A sample submitted for identification to the U.S. Geological Survey, Menlo Park, was identified as of possible volcanic origin. The aphanitic beds therefore, possibly being Permian flows or sills, and perhaps some of the larger clasts also, are potential sources of absolute age dates for the formation. However, dropstones of similar color also are present in the uppermost Devonian on the Copacabana peninsula, suggesting an older upland source.

Dunbar and Newell (1946), Newell, Chronic, and Roberts (1953), and Sakagami (1986) demonstrated that sections of the Copacabana Limestone in the Lake Titicaca area could be simply correlated biostratigraphically using a variety of invertebrates, principally fusulinids, brachiopods, bryozoans, and mollusks. My observations confirm this and add the corals as another useful group.

D'Orbigny (1842) first identified the fauna as Carboniferous in age. This assignment was accepted until Dunbar and Newell (1946) described the fusulinid faunas of the Copacabana Limestone and reassigned the age to the Early Permian, an age accepted by later workers (Urdininea and Yamagiwa, 1980) on the fusulinids. However, Sakagami et al. (1981; Sakagami, 1986) extended some of their columnar sections down into the Upper Pennsylvanian without explanation. Suarez-Riglos (1984) and Suarez-Riglos, Hunicken, and Merino (1987) reported high Virgilian conodonts in the lowermost beds of the formation at Yaurichambi. Suarez-Riglos (1984) acknowledged that the critical species, *Strepognathodus elongatus* Gunnell, ranges into the Wolfcampian, but considered the presence of the fusulinid *Triticites,* which is common in the lower part of the Copacabana Limestone, as corroborative evidence for a Virgilian age. In North America, *Triticites* ranges from the Upper Pennsylvanian into the Lower Permian (Thompson, 1964). For the purposes of the present coral study, especially as abundant corals are not present in the questionable sequence, the formation is considered to be entirely Lower Permian, with the reservation that future study may verify a Virgilian assignment for some lower beds.

Field geologists should find the lowest occurrence of the large gastropod *Omphalotrochus* the most obvious of the megafossils for recognizing the middle part of the formation. It is near the base of the lowest occurrence of the fusulinid *Pseudoschwagerina. Omphalotrochus* ranges higher (Zone of *Parafusulina*) in some sections, but it is neither so abundant there nor accompanied by such a rich fauna of other invertebrates as in the basal bed.

The corals also are of potential use to field geologists. Stratigraphic and geographic ranges of genera are shown in Figures 3 and 4. The little solitary coral *Lophophyllidium* has the greatest stratigraphic range, occurring from fairly low in the formation to somewhat above the *Omphalotrochus* bed. Beds with abundant specimens can be followed along strike some distances. The solitary coral *Caninia* is rare and from an unknown stratigraphic position somewhere in the *Lophophyllidium* range. The tabulate coral *Cladochonus* is narrowly restricted to the lower range of *Lophophyllidium. Michelinia* was found by this author at about this same level but in only one section. Reports of it from other sections at unknown stratigraphic positions suggests that it is more widespread and could be useful for correlation. The fasciculate coral *Durhamina* is narrowly restricted in the Zone of *Parafusulina* near the top of the formation. Its occurrence in only one section in Bolivia limits its value as an index fossil there but it is more common in Peru. The cerioid coral *Stylastraea* has been reported from two widely separated localities with the suggestion that it occurs very high in the formation in apparent conflict with an associated *Pseudoschwagerina* that indicates a lower occurrence. However, its extreme rarity (not seen by this author anywhere in the field in either Bolivia or Peru) lessens its potential usefulness for correlation in the field.

In general, the tabulate corals occur low in the formation, within the lower part of the wide stratigraphic range of the solitary corals. The colonial rugose corals occur high in the formation, above the range of the solitary corals.

## OCCURRENCE AND COMPARISON OF RELATED PERMIAN CORAL FAUNAS

This is the first fauna of Permian corals monographed from South America. It represents a southward extension of the fauna in the Copacabana Limestone of Peru that was described in an unpublished thesis by Finks (1953). Lists and minor studies of Peruvian Permian corals by Douglas (1920), Boit (1940), Lisson and Boit (1942), Rangel (1976), Yamagiwa and Rangel (1978), and Yamagiwa and Rangel (1979) also are based on this fauna. The lists of Derby (1894) of Brazilian Permian corals and the work of Scrutton (1971) and Hoover (1981) on Venezuelan Permian corals extend this fauna to those countries. In Central

| CHECKLIST OF COPACABANA LIMESTONE LOWER PERMIAN STONY CORALS | Peru | Cerro Quimsa Phekena section | Matilde section | | | Ancoraimes section | | Cerro Pucara section | Yamapupata section | | | | Cerro Cabiltosirca section | | Cuyavi section | | | Branisa Cumana area | Yaurichambi sections | | | | | | | | | Colquencha section and nearby | | Branisa Colquencha area | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | | | | | YA | | | | YB | | YC | | | | | | |
| SPECIES \ LOCALITIES | 10629 | 8697 | 8692 | 8693 | 8696 | 8705 | 8707 | 8688 | 8675 | 8676 | 8677 | 8678 | 8680 | 8683 | 8721 | 8722 | 8723 | unknown | 8648 | 8650 | 8653 | 8654 | 8656 | 8657 | 8661 | 8663 | 8665 | 8717 | 8718 | unknown | unknown |
| Lophophyllidium striatum (d'Orbigny) | | X | | | X | X | X | | X | X | X | X | X | X | X | X | X | | X | X | X | X | | | | X | X | X | X | | |
| Caninia sp. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | X | |
| Stylastraea branisai n. sp. | | | | | | | | | | | | | | | | | | X | | | | | | | | | | | | | X |
| Durhamina chocalensis Rowett & Walper | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Durhamina pandolfi n. sp. | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | |
| Michelina escobari n. sp. | | | X | X | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Cladochonus carrascoi n. sp. | | | | | | | | | | | | | | | | | | | X | | | | X | X | X | | | | | | |

FIGURE *4*—Checklist of coral species of the Copacabana Limestone.

America, the small fauna from the Permian of Guatemala described by Rowett and Walper (1972) and from nearby Mexico described by Reyeros (1976) are extremely similar.

It is in the southern midcontinent region of the United States (Texas, Oklahoma, Kansas, and nearby areas) that this fauna is best known and seems to be richest. Hill (1981), following the use of Rowett (1975), used the name Cyathaxonid Province to describe the coral province. The dominant corals are species of *Lophophyllidium* (most species formerly assigned to *Cyathaxonia,* hence the province name) and other similar solitary corals, accompanied by less common fasciculate and cerioid rugose corals and several tabulate corals. The most significant studies are those of Moore and Jeffords (1941), Mudge and Yochelson (1962), Ross and Ross (1962, 1963), LeMone, Stevens, and Simpson (1976), and Fedorowski (1987).

Hill (1981), after Rowett (1975) extended the Cyathaxonid Coral Province through Central America into South America and Bolivia, an assignment in agreement with the present study (Figure 5). This province was confined to the Southern Hemisphere of the eastern Pacific realm during the Permian, separated by unknown barriers (coastal upwelling?) from the Durhaminid Coral Province, and subprovinces, of the eastern Pacific to the north and west. The Bolivian Permian species *Lophophyllidium striatum* is here recognized in Kansas, Oklahoma, Texas, Mexico, and Venezuela and is inferred to be present in suitable Permian formations of poorly collected intervening countries. *Stylastraea* is a rare genus in the South American and Texas Lower Permian. The Bolivian species *S. branisai* is not the same species as *Stylastraea* sp. LeMone, Stevens, and Simpson (1976) from the Lower Permian of Texas as presently classified, but the presence of so rare a genus in both faunas is significant. *Durhamina chocalensis* Rowett and Walper, originally described from the Lower Permian of Guatemala, does not occur in the Copacabana Limestone of Bolivia but was collected by this author in the formation in neighboring Peru and is included in this paper because it indicates an important correlation between the faunas of the two continents. *Durhamina pandolfi* is a new species from Bolivia and is somewhat similar to other species from Nevada in the Durhaminidae Coral Province. The genus is widespread and species are known from the Lower Permian of Texas as well as Peru and Guatemala. *Michelinia escobari* is unknown outside Bolivia and the genus is cosmopolitan, also occurring in the Texas Permian. *Caninia* is too widespread a genus, and has too many species assigned to it, to permit any provincial conclusions to be drawn from a *Caninia*(?) sp. in the Permian of Bolivia.

## PALEOECOLOGY

The fauna of the Copacabana Limestone collected in the course of this study consists of fusulinids, corals, bryozoans, brachiopods, mollusks, echinoids, crinoids, and shark teeth. There are algal pellets in some beds. This fauna indicates full marine salinity because corals, echinoids, and crinoids are unknown from other environments.

Fusulinids occur throughout the formation. Tasch (1957) believed that they inhabited open-sea depths of 5–50 feet (1.5–15 m) and Thompson (1964) cited an offshore, open-water environment. Sando (1980) used associations of corals and algae to determine depths of shallow-water corals, concluding that a maximum depth of 100 m was possible but less than 50 m more probable.

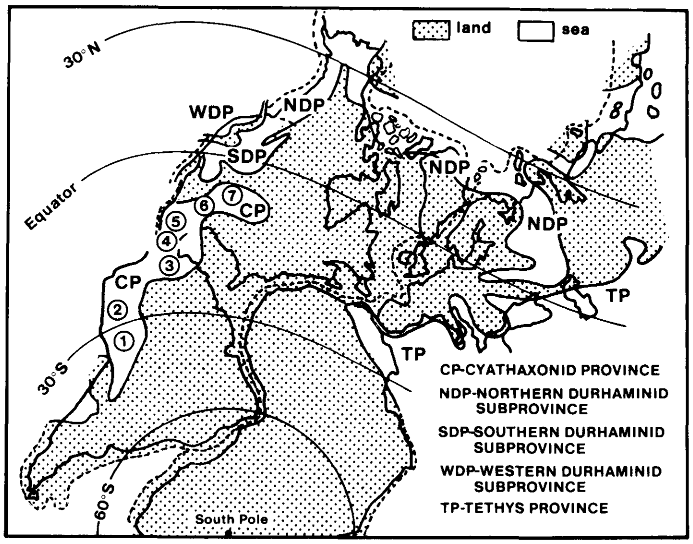


FIGURE *5*—Early Permian coral provinces and subprovinces. Numbered circles in Cyathaxonid Coral Province indicate locations of faunas mentioned in text: 1, Bolivia; 2, Peru; 3, Venezuela; 4, Guatemala; 5, Mexico; 6, Texas; 7, Kansas. Modified from Rowett (1975) and Hill (1981).

Wells (1957) thought that Paleozoic rugose corals were indicators of well-oxygenated, gently circulating marine water with annual temperature minima of 16°–21°C. Early Permian continental reconstructions show the equator as passing across North America from the California or Mexico area to the Nova Scotia or mid-Atlantic U.S.A. area. On such maps, the Copacabana Limestone is well south of the equator in subtropical or warm-temperate latitudes.

It is concluded here that the Copacabana Limestone was deposited in clear, shallow, warm to temperate marine waters with full access to the open sea.

## SYSTEMATIC MATERIALS AND METHODS

Morphological terminology and higher systematics are from Hill (1981). Locality numbers are from the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section (LACMIP). Locality descriptions are given in the Locality Register. Type specimens of *Stylastraea branisai* are in the U.S. National Museum of Natural History (USNM) and of *Lophophyllidium striatum* in the Museum National d'Histoire Naturelle, Paris (MNHN). Hypotypes of *Canina* sp. are in Chiba University, Japan (CUG), and National Science Museum, Tokyo (PA). All other specimens used for this study are deposited in LACMIP. Figured specimens not part of a type series are designated hypotypes.

## SYSTEMATIC PALEONTOLOGY

Phylum Coelenterata Frey and Leuckart, 1847
Subphylum Cnidaria Hatschek, 1888
Class Anthozoa Ehrenberg, 1834
Subclass Rugosa Milne-Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder Plerophyllina Sokolov, 1960
Family Lophophyllidae Grabau, 1928
Genus Lophophyllidium Grabau, 1928
Lophophyllidium striatum (d'Orbigny, 1839)
Figure 7

*Turbinolia striata* D'Orbigny, 1839, Pl. 6, figs. 4, 5 (see Mones, 1987 for date justification); 1842, p. 56.
*Stereostylus absitus* Jeffords, 1947, p. 56, Pl. 19, figs. 1–7, text-fig. 7.
*Lophophyllidium* sp. B. Branisa, 1965, p. 208, Pl. 72, fig. 14.
*Lophophyllidium* sp. cf. *L. wewokanum* Jeffords. Scrutton, 1971, p. 203, Pl. 1, figs. 16–18.
*Lophophyllidium* cf. *spinosum* Jeffords. Maeda, Yamagiwa, and Branisa, 1973, p. 94, Pl. 1, figs. 1, 2.
*Stereostylus*? sp. indet. Maeda, Yamagiwa, and Branisa, 1973, p. 95, Pl. 1, figs. 3, 4.
*Lophophyllidium* sp. indet. Yamagiwa, Maeda, Torrez, and Urdininea, 1974, p. 18, fig. 1.
*Lophophyllidium zaphrentoidea* (Huang). Reyeros, 1976, p. 15, Pl. 4, figs. 1, 2.
*Lophophyllidium* sp. Sakagami, 1984, p. 42, Pl. 9, fig. 5.
*Lophophyllidium* (*Lophophyllidium*) *absitum* (Jeffords). Fedorowski, 1987, p. 115, text-fig. 41.1–41.7; Pl. 10.7–10.12; Pl. 13.9–13.17.

*Diagnosis.*–A species of *Lophophyllidium* characterized by large corallite diameters, many septa, rhopaloid and differentiated septa, short minor septa, a large and lenticular columella, and N:d (number of septa : diameter of corallite) ratios of 17:4–35:21.

*External description.*—Corallites ceratoid with septal grooves (for both major and minor septa) and transverse striations; calyx deep, steep sided, with high, thin to lenticular axial boss confined to lower third of calyx; major septa differentiated; minor septa only in upper third of calyx; maximum length 41 mm (lectotype), maximum diameter 23 mm (20 × 26).

*Transverse section description.*—Corallites oval to circular, 23 mm wide at greatest diameter; septa of two orders, as many as 34 each; major septa long, generally rhopaloid, some contratingent, withdrawn from columella, cardinal septum shortened, counter septum continuous with medial plate of columella; minor septa generally very short, appearing in late ephebic stage, sporadically developed, especially in cardinal quadrants, may be embedded in stereome; columella large, lenticular to nearly circular, with long medial plate, thickened by stereome and a few septal lamellae in some corallites; corallite wall very thin, eroded in many corallites leaving expanded septal bases and peripheral stereome deposits that function as wall.

*Longitudinal section description.*—Tabulae 8–10 per cm, thin, straight to broadly domed upwards, steeply to moderately inclined inwards and upwards to columella; columella straight to broadly sinuous, moderately to very thickened, with central dark line; wall thin.

*Collections.*—Lectotype, Museum National d'Histoire Naturelle, Paris, specimen B47572 (collection d'Orbigny 1123/1). Paralectotype, Museum National d'Histoire Naturelle, Paris, specimen B47573 (collection d'Orbigny 1123/2). Both recorded as being from "Yarbichambi, Bolivia." 113 specimens from LACMIP localities 8648 (2), 8650 (1), 8653 (2), 8654 (1), 8663 (1), 8665 (7) type bed, 8675–8678 (1 each), 8680 (50), 8683 (9), 8696 (1), 8697 (1), 8705 (3), 8707 (1), 8717 (1), 8718 (9), 8721 (2), 8722 (20), 8723 (3), including LACMIP hypotypes 8010, 8011 (LACMIP loc. 8680), 8012 (LACMIP loc. 8665), 8013 (LACMIP loc. 8680), 8014 (LACMIP loc. 8718), 8015 (LACMIP loc. 8723), 8016 (LACMIP loc. 8680), 8017 (LACMIP loc. 8653), 8018 (LACMIP loc. 8723), 8019, 8051 (LACMIP loc. 8680).

*Discussion.*—Although the lectotype does not exactly match the d'Orbigny (1839, Pl. 6, fig. 4) illustration of *Turbinolia striata,* it is closer than the paralectotype. The drawing probably is of the lectotype, but somewhat idealized for aesthetic purposes. The yellow silty color of the "fossil hash" limestone matrix indicates that the d'Orbigny specimens came from the LACMIP loc. 8665 bed on the northeast side of Cerro Hiscka Khatawa (local name for the southern spur of Cerro Jacha Khatawi, see discussion above), 2 km north of the village of Yaurichambi, Department of La Paz, Bolivia. Numerous coralla identical in preservation and matrix to the lectotype and paralectotype were observed here and some collected by the author in 1985. This bed lies stratigraphically between the *Omphalotrochus* bed (below) and the *Aviculopinna* bed (above) and is high in the Zone of *Pseudoschwagerina,* Wolfcampian Series, Lower Permian. It had "YC-16" painted on the rocks, a locality number of Sakagami (1984, p. 30).

*Lophophyllidium striatum* has a maximum N:d ratio of 35:21 (Figure 6), rhopaloid and differentiated major septa, short to very minor septa, and a generally inflated columella. At some localities in the Copacabana Limestone, specimens are present at one narrow stratigraphic interval in moderately fine-grained limestone, apparently in growth position and representing members of a living population. In coarse-grained beds (e.g., LACMIP loc. 8665), specimens are worn and distributed throughout the bed with other worn and broken invertebrates, perhaps representing populations of slightly mixed ages and localities. Nevertheless, the degree of morphological variation seems to be about comparable in either situation, indicating the presence of one species.

If this philosophy was applied to the more than 50 named species from North America and conservative conclusions drawn, many of these species likely could be synonymized as implied by Webb (1984). Fedorowski (1987) adopted a moderately conservative approach to species of this genus from the upper Paleozoic of southwestern Texas and adjacent areas but even then recognized 13 species (three new) from 39 localities, of which 13 localities yielded 2–5 species each.

This author is in agreement with Fedorowski (1987, p. 100) that the species of the genus are in need of monographic treatment. A uniformitarianism approach with consideration given to the great geographic distributions of living solitary coral species on the western sides of continents might be useful. Perhaps in the Early Permian, and earlier, a single variable species of *Lophophyllidium* ranged from the midwestern United States at least as far south as present Bolivia. That species would be *L. striatum,* the oldest named species.

Comparison of *L. striatum* with most presently recognized species in the North American faunas can be readily made in Fedorowski (1987, table 8) by substituting the name *L. striatum* for *L. absitum.* The types and referred specimens placed in the latter species exhibit the morphological characters of the lectotype and some same-section, same-bed topotypes of *L. striatum.* These similarities are reflected in the above synonymy for purposes of stability and convenience. Future revisors may wish to greatly lengthen this synonymy.

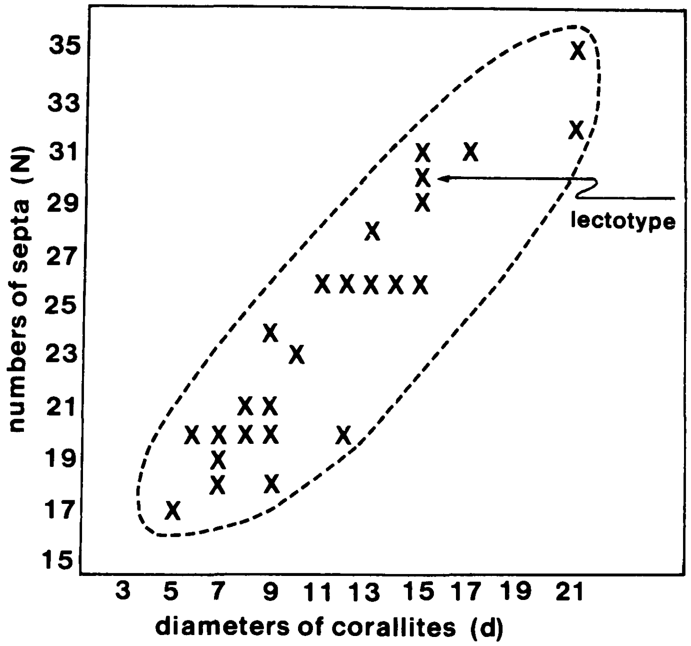


FIGURE 6—Graph showing N:d (numbers of septa: diameters of corallites) ratios of *Lophophyllidium striatum* (d'Orbigny) Copacabana Limestone specimens.

Suborder CANINIINA Wang, 1950
Family CYATHOPSIDAE Dybowski, 1873
Genus CANINIA Michelin *in* Gervais, 1840
CANINIA(?) sp.
Figure 8.1–8.4

*Caninia* sp. indet. MAEDA, YAMAGIWA, AND BRANISA, 1973, p. 95, Pl. 2, figs. 1a–1c, 2.

*Collections.*—Reg. no. CUG-C72003, Chiba University, Japan; Reg. no. PA11318, National Science Museum, Tokyo.

*Discussion.*—The specimens on which this determination was made were collected "by Leonardo Branisa from the Copacabana Group in Colquencha . . ." (Maeda, Yamagiwa, and Branisa, 1973). Further locality and stratigraphic information are unavailable. No similar coral was obtained by me from a measured section and nearby localities in the vicinity of Colquencha or from elsewhere in the formation. The coral is included here for the sake of complete representation of the fauna. The generic assignment is questioned because *Caninia,* which has a Mississippian type species, is broadly, and often inappropriately, applied to younger corals. Additional specimens are needed to determine the ontogeny and correctly assign the coral.

Suborder LITHOSTROTIONINA Spasskiy and Kachanov, 1971
Family LITHOSTROTIONIDAE d'Orbigny, 1852
Subfamily THYSANOPHYLLINAE Hill, 1981
Genus STYLASTRAEA Lonsdale, 1845
STYLASTRAEA BRANISAI n. sp.
Figures 8.5–8.8, 9.1–9.3

(?)*Lithostrotionella* sp. BRANISA, 1965, p. 208, fig. 16.

*Diagnosis.*—A species of *Stylastraea* characterized by a persistent lath-like columella, some with short septal lamellae, a wide, lonsdaleoid dissepimentarium, and some tented tabulae or tabellae.

*External description.*—Corallum cerioid, hemispheroidal; maximum observed diameter 14 cm; undoubted calices not observed; epitheca with low growth lines about 1 mm equidistant.

*Transverse section description.*—Corallites polygonal, 5–7 sided, 8–15 mm wide at greatest diameters; septa of two orders, 12–17 each; major septa 3–5 mm long, extending into tabularium 1–1.5 mm; minor septa 1.5–2.5 mm long, extending into tabularium 0.2–0.3 mm, represented by septal spines on some lonsdaleoid dissepiments, not everywhere present in tabularium; axial structure generally a lath-like or lenticular columella 0.5–2.0 mm long, generally somewhat sinuous, rarely with 1 or 2 short septal lamellae, many connected to elongate counter(?) septum; dissepimentarium as much as 4.5 mm wide, highly lonsdaleoid in largest corallites, less so or regular in smaller ones; dissepiments generally inflated and lonsdaleoid in larger corallites, some with septal spines, in smaller corallites partly lonsdaleoid or herringbone to pseudoherringbone; wall straight to slightly sinuous, 0.1–0.2 mm wide.

*Longitudinal section description.*—Dissepimentarium 1.5–4.0 mm wide, of 1–4 ranks of generally steeply dipping, various size dissepiments, only gently dipping in places; tabulae/tabellae tent-shaped around columella, flat to gently domed where columella absent, 12–15 (rarely 23) per cm; columella slightly sinuous, 0.1–0.2 mm wide.

*Collections.*—Holotype, USNM 440846; paratype, USNM 440847. Six thin sections and 31 polished sections from two coralla were studied. They are from a large collection of Bolivian Paleozoic invertebrates purchased by the USNM from Dr. Leonardo Branisa of Bolivia. The holotype corallum is labeled "8200/*Lithostrotionella*? sp./Colquencha/Beds of the nucleus/of syncline. Lw. Perm.?" The paratype corallum is labeled "*Lithostrotionella*?/*Isla Cumana*/Titicaca Lake/Lw. Perm./L.B. 1960." A *Pseudoschwagerina* on the paratype indicates Lower Permian, Wolfcampian Stage. The Copacabana Limestone, which crops out prominently in both areas, is the only likely origin. Colquencha and Cumana are shown on the index map. Isla Cumana is a peninsula when the lake is low. Casts of the holotype corallum taken before sectioning are deposited in the USNM and LACMIP.

*Discussion.*—This coral is here assigned to *Stylastraea* because it is lonsdaleoid and has a lath-like axial structure connected to one septum. The greater persistency of the axial structure and the resultant tent-shaped tabulae/tabellae differ from most Permian species of the genus but not enough to justify erection of a new genus without more specimens and better stratigraphic documentation.

Species reported from the Lower Permian of Spitsbergen by Fedorowski (1964, 1965, 1967) differ as follows. *Stylastraea toulai* (Stuckenberg, 1895), also known from Timan, lacks an axial structure and has a greater number of septa. *Stylastraea tenuiseptata* Fedorowski, 1965, has a rare axial structure that is a thin, elongate septum or a weak columella. *Stylastraea minima* Fedorowski, 1967, has smaller corallite diameters and rare columellae.

A single specimen referred to *S. inconferta* (Lonsdale, 1845) by Salter (1855) from Devon Island, Northwest Territories, Canada, was redescribed by Harker and Thorsteinsson (1960) as *Stylastraea* cf. *S. toulai* (Stuckenberg) and assigned to the Lower Permian Belcher Channel Formation. It has a greater number of septa than *S. branisai.*

*Stylastraea* sp. figured by LeMone, Stevens, and Simpson (1976, Pl. 1, figs. 3–5) from the Lower Permian Wolfcampian Stage in El Paso County, Texas, has much smaller corallite diameters and apparently no axial structure.

There are no Permian cerioid rugose corals published from Mexico or Central America. The South American record for late Paleozoic cerioid rugose corals is scanty and not well documented by existing specimens, suggesting that, although present, they are very rare. Meyer (1914, p. 627, Pl. 14, figs. 7a, 7b) described and figured a single cerioid rugose corallum from the Carboniferous at Hacienda Maco near Tarma, Peru, as *Stylastraea inconferta* Lonsdale, 1845. The figures, apparently somewhat stylized drawings, are of transverse and longitudinal sections of single corallites showing a partly lonsdaleoid dissepimentarium and no axial structure. This corallum apparently is lost. Dunbar and Newell (1946) and Newell, Chronic, and Roberts (1953) demonstrated that the very fossiliferous marine Tarma Group at Tarma is Middle Pennsylvanian, but is overlain by the Permian Mitu Group, which contains some fossiliferous marine beds. Branson (1948) cited a Permian age for Meyer's coral. Finks (1953) considered the coral to be Middle Pennsylvanian and reported "nothing like this form has been found in our [American Museum of Natural History] collections." Stevens (1982) considered that the drawing was of *Stylastraea* and suspected that the age might be Permian. Sakagami (1984) measured and collected the type section of the Pennsylvanian Tarma Group but did not indicate cerioid rugose corals in his collections from there.

This author was unable to get to Tarma in 1986 while in the field in Peru due to terrorist activities. However, the likelihood is that Meyer's coral is from the Middle Pennsylvanian Tarma Group rather than the Permian Mitu Group. Further field investigation is needed. Regardless of its stratigraphic position, *S. inconferta* of Meyer (1914) from Tarma, Peru, has no axial structure and no minor septa, as indicated by the figures, and thus is not *S. branisai,* although the corallite diameters and septal numbers appear to be comparable.

Branisa (1965, Pl. 72, fig. 16) figured a cerioid rugose coral as *Lithostrotionella* sp. from the Permian near Colquencha, Bolivia. In 1985, this author was informed by Dr. Branisa that the specimen apparently was lost but he indicated a pasture in the outcrop area of the Copacabana Limestone from which he thought it was collected as float. There was no obvious outcrop nearby from which it could have come and someone may have moved it to the pasture. After returning to the United States, it was discovered that Dr. Branisa had placed two cerioid rugose coralla from the Copacabana Limestone in the U.S. National Museum. Neither is the specimen that he figured from Colquencha. They are here designated the holotype and paratype of *S. branisai.* Sections were measured in the Copacabana Limestone at Colquencha, the holotype locality, and at Isla Cumana, the paratype locality, but no cerioid rugose corals were found in either of these localities or elsewhere in Bolivia or Peru.

Because of the rarity of cerioid rugose corals and because Dr. Branisa has collected the only ones known from the Permian of Bolivia, it is likely that his presumably lost *Lithostrotionella* sp. (Branisa, 1965, Pl. 72, fig. 16) belongs in *Stylastraea branisai.* Future work should concentrate on its stratigraphic position.

There is a record in the catalogues of the Instituto Geologico Minero y Metalurgico (INGEMET) at Lima of a cerioid rugose coral from the Copacabana Limestone in Peru but the specimen was deemed lost by the curators when inquiries were made in 1986.

*Etymology.*—The species is named for Dr. Leonardo Branisa.

Family DURHAMINIDAE Minato and Kato, 1965
Genus DURHAMINA Wilson and Langenheim, 1962
DURHAMINA CHOCALENSIS Rowett and Walper, 1972
Figure 9.4

*Durhamina chocalensis* ROWETT AND WALPER, 1972, p. 75, Pl. 1, figs. 5–12.

*Collections.*—Hypotype, LACMIP 8020. Seven thin sections and 54 polished sections from eight coralla from LACMIP locality 10629 were studied. This locality is in the Zone of *Parafusulina,* Leonardian Stage, Copacabana Limestone, Department of Cusco, Peru.

*Discussion.*—Although this species is from the Copacabana Limestone in Peru, it is included here because of the paleogeographic correlation implied at the species level. The occurrence of the type series specimens in the Lower Permian Chocal Limestone from near Huehuetenango, Guatemala, the southernmost record for the genus in North America, firmly places them in the same coral province as the Copacabana Limestone of Peru.

Rowett and Walper (1972) recorded a maximum corallite diameter "of about 13 mm." This is difficult to determine more

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FIGURE 7—*Lophophyllidium striatum* (d'Orbigny). *1, 2,* external views of lectotype, MNHN B47572, natural size, bars indicate position of transverse section; *3, 4,* transverse thin section of lectotype and ink-and-bleach drawing made from it, ×3; *5,* transverse polished section of lectotype abapical to section in Figure 7.3 showing appearance of minor septa opposite bars, ×3; *6, 7,* external views of paralectotype, MNHN B47573, natural size; *8, 9,* calicular views of etched specimens, natural size, hypotypes LACMIP 8010, 8011; *10,* transverse section, exact topotype, hypotype LACMIP 8012, ×3; *11,* longitudinal section, same specimen, ×3; *12–17,* transverse sections, hypotypes LACMIP 8013–8018, ×3; *18,* transverse and longitudinal sections of associated specimens, hypotypes LACMIP 8019 (left), 8051 (right), ×3.

FIGURE 8—*1–4, Caninia* sp. (after Maeda, Yamagiwa, and Branisa, 1973, Pl. 2). *1,* transverse section, CUG-C72003b, ×3; *2,* transverse section, PA11318, ×3; *3,* transverse section, CUG-72003a, ×2; *4,* longitudinal section, CUG-C-72002c, ×3. *5–8, Stylastraea branisai* n. sp., transverse sections, ×3. *5, 7,* holotype, USNM 44086; *6, 8,* paratype, USNM 440847.

FIGURE 9—*1–3, Stylastraea branisai* n. sp., longitudinal sections, holotype, USNM 44086. *4, Durhamina chocalensis* Rowett and Walper, transverse section, hypotype, LACMIP 8020. *5, 6, Durhamina pandolfi* n. sp., transverse sections, paratype, LACMIP 8022. All figures ×3.