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TROPICAL MARINE MOLLUSK ASSEMBLAGES FROM THE PLEISTOCENE OF OAXACA, SOUTHERN MEXICO

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Abstract. The Colotepec Formation crops out along the southern Pacific coast of Oaxaca, Mexico. This unit harbors a notable diversity of mollusks from the Pleistocene, mainly taxa of Bivalvia and Gastropoda. The malacological assemblage of both localities consists of 53 taxa of Bivalvia and 71 of Gastropoda; all of them are currently distributed in the southern part of Mexico. Also, specimens of rhodoliths, echinoids, and crustaceans were identified. All the identified taxa inhabit shallow and warm tropical waters, and some are from coastal lagoons. Both localities share 16 taxa of Bivalvia and 11 of Gastropoda. The assemblages are considered para-autochthonous. Most taxa inhabit subtidal environments, on both hard and soft substrates. Bivalves with thick shells display a variety of associated sclerobionts, including bivalves, gastropods, sponges, serpulids, and bryozoans. The ichnodiversity comprises *Thalassinoides*, *Psilolichnus*, and *Ophiomorpha nodosa*. According to the rate of subsidence, the maximal age of the Pleistocene sequences may range from 248,000 to 112,000 years BP (Marine Isotope Stage 8 to Marine Isotope Stage 5). The information on the Pleistocene assemblages provides valuable evidence for conservation strategies for modern taxa. Despite their paleontological value, the localities are at risk of natural hazards and anthropogenic pressures.

Key words. Colotepec Formation. Marine mollusks. Pleistocene.

Resumen. ENSAMBLES TROPICALES DE MOLUSCOS MARINOS DEL PLEISTOCENO DE OAXACA, SUR DE MÉXICO. La Formación Colotepec aflora a lo largo de la costa de Oaxaca, en el Pacífico sur de México. Esta unidad resguarda una diversidad notable de moluscos del Pleistoceno, principalmente taxones de Bivalvia y Gastropoda. El conjunto malacológico de ambas localidades consiste en 53 taxones de Bivalvia y 71 de Gastropoda, todos ellos distribuidos actualmente en el sur de México. También se identificaron ejemplares de rodolitos, equinoideos y crustáceos. Todas las especies de moluscos viven en aguas tropicales someras y cálidas; algunas son características de lagunas costeras. Ambas localidades comparten 16 taxones de Bivalvia y 11 de Gastropoda. Los ensambles se consideran parautóctonos. La mayoría de los taxones habitan en ambientes submareales, tanto en sustrato duro como suave. Los bivalvos con conchas gruesas muestran una variedad de esclerobiontes asociados, incluidos bivalvos, gasterópodos, esponjas, serpúlidos y briozoarios. La icnodiversidad incluye a *Thalassinoides*, *Psilolichnus* y *Ophiomorpha nodosa.* De acuerdo con la tasa de subsidencia, la edad máxima de las secuencias del Pleistoceno puede abarcar desde los 248.000 a 112.000 años AP (Estadio Isotópico Marino 8 a Estadio Isotópico Marino 5). La información de los ensambles del Pleistoceno ofrece evidencia valiosa para establecer estrategias de conservación de los taxones modernos. A pesar de su valor paleontológico, las localidades se encuentran en riesgo por amenazas naturales y presiones antropogénicas.

Palabras clave. Formación Colotepec. Moluscos marinos. Pleistoceno.

LATE PLEISTOCENE coastal deposits are relatively common worldwide (*e.g.*, Cantalamessa & Di Celma, 2004; González-Acebrón *et al.*, 2016; Ninis *et al.*, 2022). They represent a valuable source of information on the evolution of coastal environments and their paleobiotas during the glacial-interglacial episodes of the Pleistocene. In North America, the record comprises several localities along the coast of California (*e.g.*, Kern, 1977), Baja California peninsula (*e.g.*, Woods, 1980; Ortlieb, 1981; DeDiego-Forbis *et al.*, 2004), and along the Zihuatanejo terrane, including the coastlines of the states of Michoacan and Guerrero (Centeno-García *et al.*, 2003).

The studies concerning Mexican marine Late Pleistocene biotas have more tradition in the northern area of the Mexican Pacific coast (*e.g.*, Stump, 1975; Valentine, 1980; Pedrin Aviles *et al.*, 1987; DeDiego-Forbis *et al.*, 2004) than in the southern part of the country. The Colotepec Formation of Late Pleistocene age is the only lithological marine unit recognized in the south of the Mexican Pacific. The formation crops out near Puerto Escondido city, located on the coast of Oaxaca (Palmer 1928a, 1928b; Palmer & Hertlein, 1936). Even though there are reports of a Pliocene-Pleistocene fauna near Salina Cruz city, located in

the eastern part of the coastal region (Durham *et al.*, 1981), the only Quaternary formal record is from the Colotepec Formation. Previous paleontological studies of the Colotepec Formation enlisted fossil species of Anthozoa, Echinodermata, Bivalvia, and Gastropoda (Palmer, 1928b; Palmer & Hertlein, 1936). Erfa and Geister (1976) reported structures similar to mangrove roots in an undetermined location of the Colotepec Formation, at 30 meters above sea level, outside of Puerto Escondido city.

There are several patches of the Colotepec Formation within the city. Two of the major fossiliferous outcrops are exposed in Punta Colorada and Playa Coral beaches; both stand out for their fossiliferous biota. Preliminary observations noted that both assemblages of both deposits differ in the species composition. Based on the possibility of merging the evidence of fossils and trace fossils to support an integral study of the paleoenvironmental conditions, the aims of this study are 1) to report the taxa of Bivalvia and Gastropoda in the faunal assemblage and the ichnoassemblage from both localities, 2) to infer paleoenvironmental conditions of the deposit, 3) to compare the species diversity between localities, 4) to propose some considerations based on Conservation Paleobiology related to the modern assemblages of molluscan species in the study area, and 5) to discuss considerations regarding the conservation status of the localities to avoid the permanent loss of the fossiliferous deposits.

MATERIAL AND METHODS

Study area

The Pacific coastal region of southern Mexico extends across the tectonic boundary of an active convergent margin, characterized by the subduction of the Cocos and Rivera plates beneath the North American plate (Ramírez-Herrera & Urrutia-Fucugauchi, 1999). The state of Oaxaca is in the southeastern part of the Mexican Pacific coast. The coastal region of Oaxaca is a dynamic area because of its position in front of the Middle American Trench (**MAT**). The MAT is a continuous feature of the southern Pacific margin of Mexico and Central America over more than 3,000 km (Ramírez-Herrera *et al.*, 2011). It extends from the Tres Marias islands off western Mexico to the Cocos ridge southwest of Costa Rica (Fisher, 1961). The MAT is considered the most important tectonic feature on the Pacific coast of southern Mexico (Yamamoto *et al.*, 2013) because of its significance in the geomorphologic evolution of the area (Fig. 1).

Puerto Escondido is a coastal city located in the southern region of the Mexican Pacific region (Chiappa-Carrara *et al.*, 2019). This area has a very narrow continental shelf along the Cocos plate, which slides beneath the North American plate at a rate of about seven centimeters per year (Chiappa-Carrara *et al.*, 2019). Several marine and fluvial terraces are situated on the Oaxaca coast along *ca.* 40 km, from Puerto Escondido city eastward. These marine terraces have a well-preserved and steep sea cliff. The active river incision and well-preserved sea cliffs on these terraces suggest active tectonic uplift in this area (Ramírez-Herrera *et al.*, 2011).

The fossiliferous deposits of the Colotepec Formation are settled into two marine terraces. The localities are situated on the Punta Colorada (Fig. 2.1) and Playa Coral (Fig. 2.2) beaches. Both sites are notable because of their exposure and accessibility, well known by local people and tourists. The deposits face the menaces of erosion by water and wind, landslides, sporadic hurricanes, pollution, and human buildings. Also, local artisans and sellers have extracted fossil specimens.

Geologic Setting

The geological features of the study area have been described since the 1920s and 1930s. Palmer (1926, 1928a) described several Quaternary outcrops of the coastal region of Oaxaca in two papers. He referred to several outcrops as "Upper Pleistocene beds occur in more or less connected patches from the Potrero River west along the coast beyond Puerto Escondido, a distance of nearly 30 miles" (Palmer, 1926, p. 727). Palmer (1926) recognized the Pleistocene deposits as "flat lying or has locally a low dip coastward, and rests on the schists and granodiorite. It has a maximum thickness of about 60 feet, and the highest elevation recorded is 75 feet" (Palmer, 1926, p. 727-728). Later, the Colotepec Formation as formally erected as "… made up mostly of a soft gray or buff sandstone, although locally it is hard and flinty" (Palmer and Hertlein, 1936, p. 35); the type locality was designated about 16 km west of the mouth of the Colotepec River (Palmer and Hertlein, 1936).

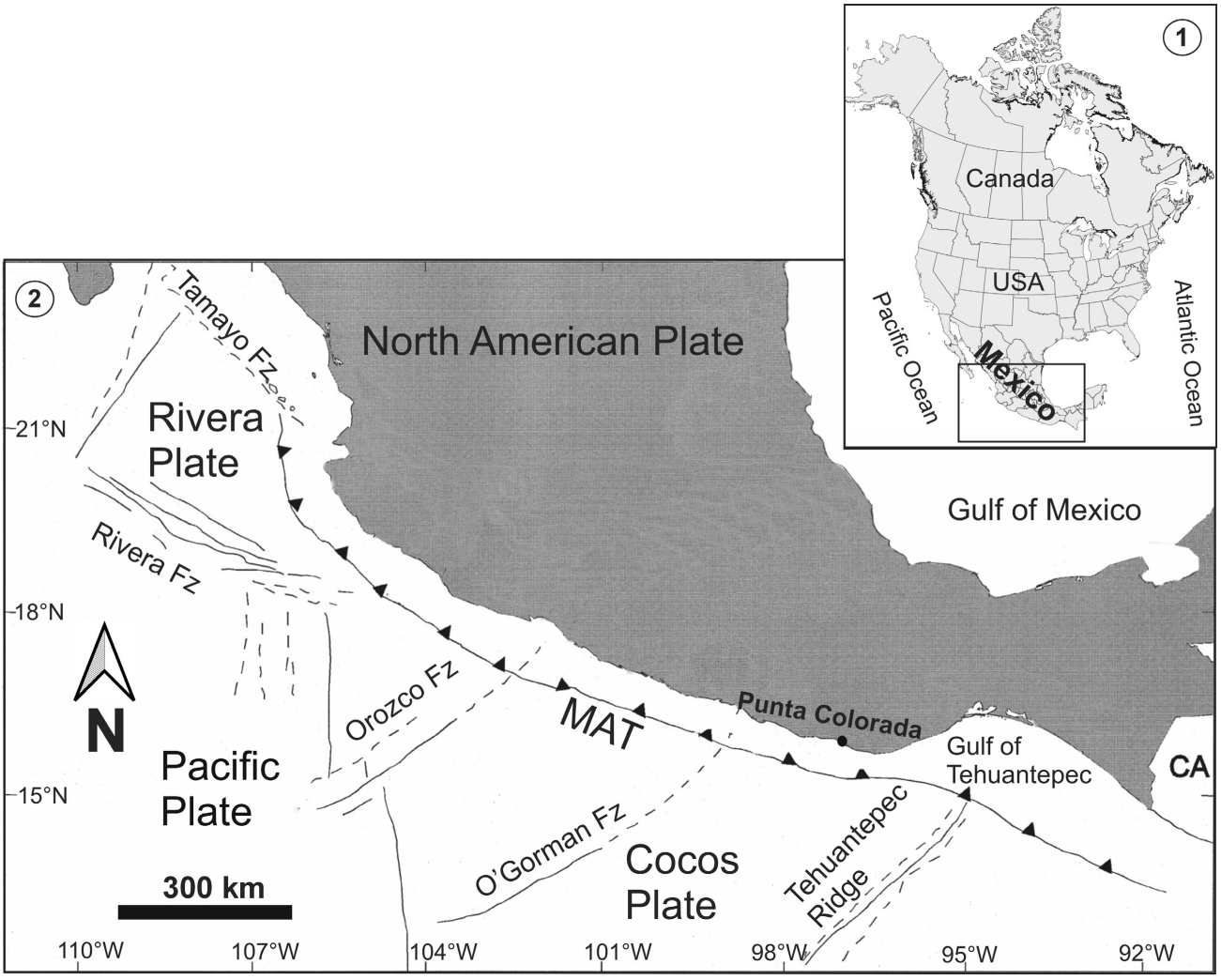

Figure 1. 1, location of Mexico within the North American subcontinent. The area within the rectangle corresponds to central and southern Mexico. **2,** main morphotectonic features of the Mexican coastal region of the Pacific Ocean. Only the locality of Punta Colorada is marked because of the scale and the nearness of the Playa Coral locality (Modified from Ramírez-Herrera and Urrutia-Fucugauchi, 1999). Abbreviations: **CA,** Central America; **Fz**, fault zone; **MAT,** Middle American Trench.

The outcrops of the Colotepec Formation have been eroded or destroyed over time, mainly due to urban land expansion and hurricanes. A distance of around 2 km separates the fossiliferous deposits in the proximity of Punta Colorada and Playa Coral beaches. Despite this nearness, there is no lateral continuity of the strata. The basal part of both terraces unconformably overlies rocks of the Xolapa Complex, which range in age from the Permian to the Oligocene (Ducea *et al.*, 2004). Close to the fossil localities, a sample of the Xolapa Complex gave a more specific age of 29.6 Ma U-Pb (Figueroa-Guadarrama *et al.*, 2017; Peña-Alonso *et al.*, 2021).

The sedimentological sequence in the Punta Colorada

Figure 2. General views of the studied outcrops in the southern Pacific of Mexico. **1,** view of the Punta Colorada locality; **2,** view of the Playa Coral locality.

locality measures four meters, approximately (Almazán-Vázquez & Briseño-Sotelo, 2013). There are three well-differentiated beds, which discordantly overlie the Xolapa Complex. The first bed is a conglomerate constituted by well-rounded clasts derived from the Xolapa Complex, with a diameter from one to 120 mm. In the upper part of the conglomerate, there are coarsely cemented mollusk shells, and fragments of them replacing the clasts. The second bed consists of fossiliferous fine-grained sandstone; small- and medium-sized invertebrate fossils (1–3 to 100 mm) have been deposited at this level. The third main bed is mainly composed of beach deposits, with laminated sandstone. In the upper part of the sequence, there is a massive level of sandstone. The contact between the massive bed and the beach sediments is interpreted as a hiatus because of the drastic change in the conditions of the two levels (Fig. 3.1).

The outcrops of the Playa Coral locality are highly eroded by water runoff. Nowadays, many parts of the terrace are covered by vegetation, because the erosion deposited sediment and generated the burial of some levels. The sequence is composed of several layers of sand and gravel, lying discordantly with the rocks of the Xolapa Complex. From the bottom to the top, the sequence comprises nine strata: 1) coarse sand, 2) gravels, 3) medium to coarse sand, 4) coarse sand, 5) gneiss gravel, 6) medium to coarse sand, 7) fine sand, 8) sand with gravel, and 9) coarse sand. The thickness of the sequence is approximately 28 m (Almazán-Vázquez & Briseño-Sotelo, 2013). The fossils and trace fossils appear in the medium to coarse sand levels (Fig. 3.2).

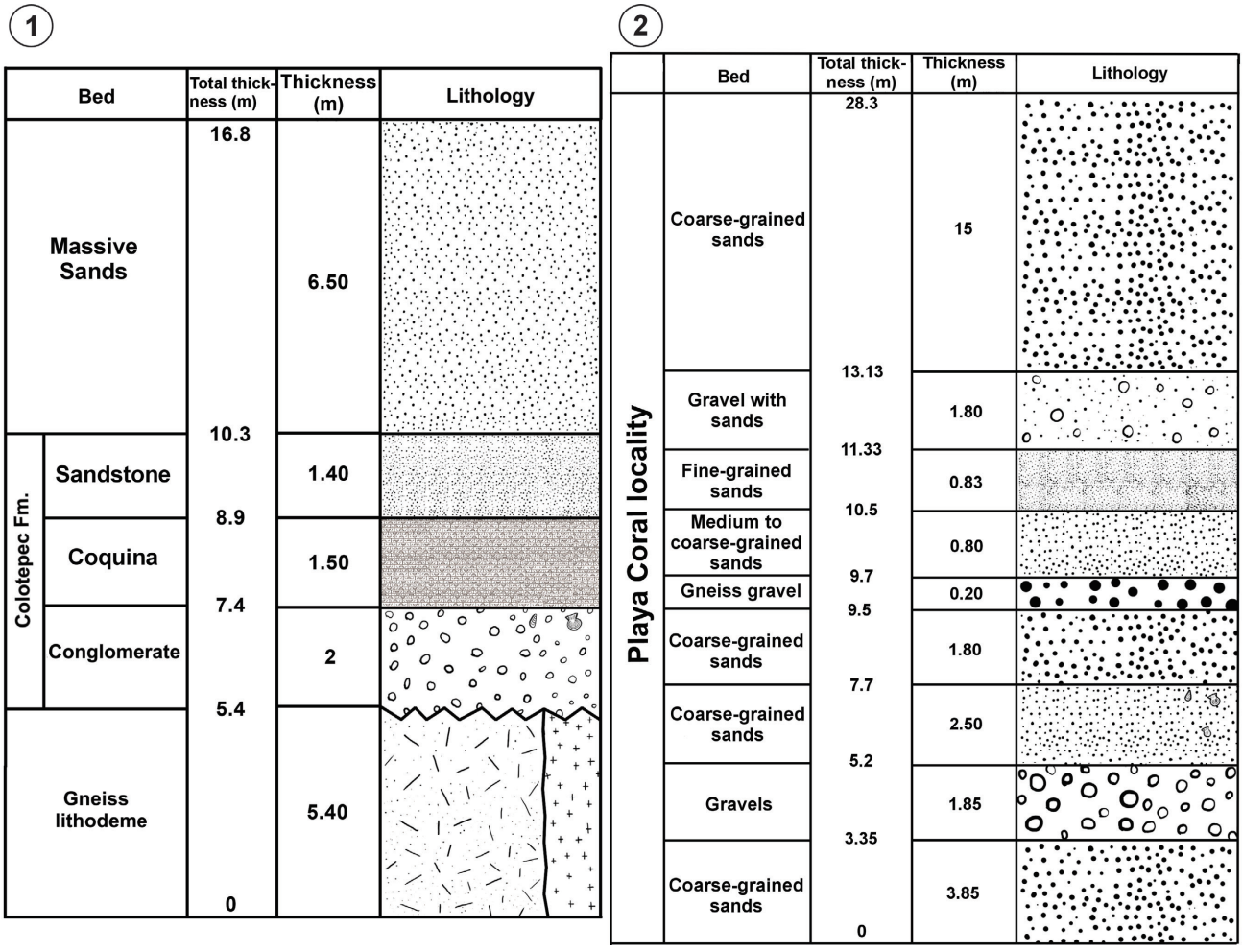

Figure 3. 1, lithologic composition of Punta Colorada locality; **2,** lithologic composition of Playa Coral locality (modified from Almazán Vázquez & Briseño Sotelo, 2013).

Methods

Students and researchers from the Universidad del Mar collected and photographed the fossil material in several field trips (2005 to 2023); the selected specimens were adults, leaving juvenile and sub-adult stages in the strata. Field observations on fossil assemblages consider their distribution in sediment, diversity, and taphonomic features.

In the laboratory, the specimens were cleaned using mechanical procedures. In some cases, the fossils were separated from the rock matrix using dissection needles or air scribes.

The molluscan specimens were identified to the lowest possible taxonomic level based on Keen (1971) and Coan and Valentich-Scott (2012). The scientific names were updated with Molluscabase (MolluscaBase eds., 2024). The list of the species was organized according to the criteria of Bouchet *et al.* (2017) at the family level for gastropods and bivalves with Coan and Valentich-Scott (2012).

The information on the habitat and the geographical distribution of the taxa was compiled from several bibliographic references (*e.g.*, Keen, 1971; Keen & Coan, 1974; Zamorano *et al.*, 2008; Coan & Valentich-Scott, 2012; MolluscaBase eds., 2024). Also, the species distribution was compared with the records in the catalogue of the Colección de Moluscos del Museo de Historia Natural de la Universidad del Mar (CMNHNUMAR, 2024), housed in the Puerto Angel campus. The collection is registered as OAX-CC-246-2011 in the Secretaría de Medio Ambiente y Recursos Naturales (**SEMARNAT**, by its acronym in Spanish).

Trace fossils were measured and photographed in the localities. Only two specimens were collected. All were identified at a minimum ichnotaxonomical level. The information on the related environments was compiled in bibliographic references.

The Whittaker diversity index was used to calculate the Beta diversity comparison of the two fossil assemblages. The analysis was performed with the Past 4 software (Hammer *et al.*, 2001).

All the collected specimens were deposited in the Colección de Invertebrados Fósiles, Laboratorio de Paleobiología, Campus Puerto Escondido, Universidad del Mar. Also, the specimens and the fossiliferous localities have been registered in the Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos of Instituto Nacional de Antropología e Historia. The fossil specimens of mollusks have been registered under the acronym **UMLP** (by its acronym in Spanish, Universidad del Mar, Laboratorio de Paleobiología). Also, the ichnological specimens have been registered under the acronym **UMPLIC** (by its acronym in Spanish, Universidad del Mar, Laboratorio de Paleobiología, Icnología).

RESULTS

The compilation of the identified taxa of Gastropoda and Bivalvia, their identification, the presence in one or both localities, and their habitat preferences are reported in the Supplementary Online Information 1. Some well-preserved specimens are illustrated in Figures 4 and 5.

Species richness

The assemblage comprises 53 taxa of Bivalvia (51 at species level and two at genus level) and 71 of Gastropoda (69 at species level, one at genus level, and one in open nomenclature). The assemblage of Punta Colorada locality includes 35 taxa of Bivalvia and 54 of Gastropoda. Meanwhile, the assemblage of Playa Coral locality consists of 34 taxa of bivalves and 29 of gastropods (Supplementary Online Information 1). Both localities share 16 taxa of Bivalvia and 11 of Gastropoda.

The Whittaker diversity index between the assemblages of Punta Colorada and Playa Coral is 0.6315.

Also, additional collected taxa in both localities include unidentified rhodoliths and fragments of crustaceans and corals. Specimens of the barnacle *Paraconcavus pacificus* and spines of the echinoderm *Eucidaris thouarsii* were identified.

Taphonomic features

The assemblage is composed of juvenile, sub-adult, and mature specimens in both localities. Their presence in the strata is according to their hydraulic equivalence. The small to medium-sized specimens (including juvenile and sub-adult specimens of mollusks) were deposited in the fine and medium-grained beds in both localities (Figs. 6.1–6.2). Specimens with thicker shells, like oysters and *Spondylus*, were the predominant species in the conglomerate in Punta Colorada locality (Fig. 6.3).

Moreover, in both localities, the specimens lack a specific spatial orientation. None of the specimens were found in their life position.

Almost all the specimens have been fragmented. The majority of them have a completeness of up to 85%, allowing their taxonomic identification. The unbroken specimens measure less than 15 mm. All the bivalves were disarticulated; however, many thin valves of bivalves (as *Tagelus longisiniatus*) were almost unbroken in some levels of the Punta Colorada locality (Fig. 6.2).

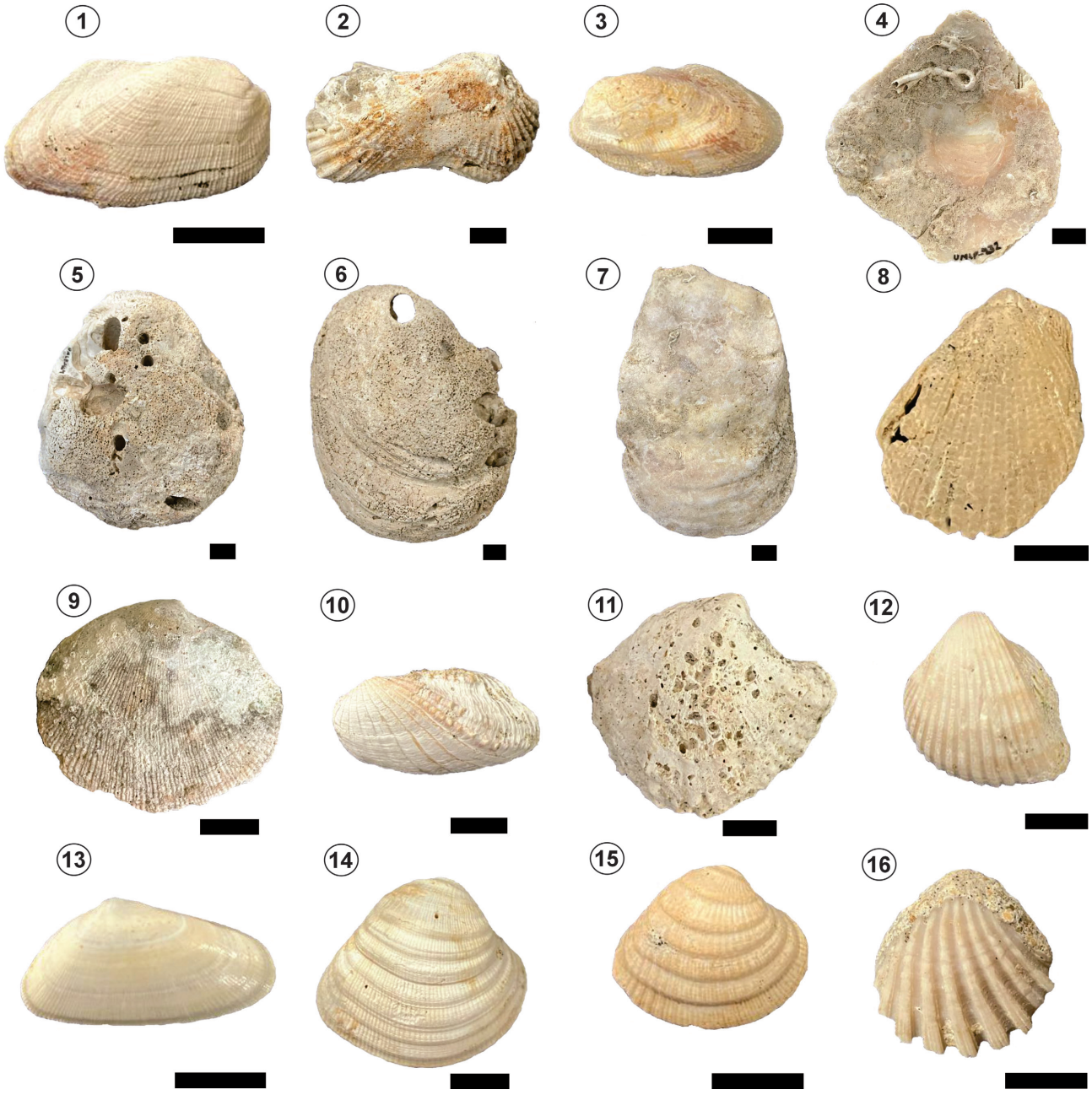

Figure 4. Some specimens of Bivalvia and their identification in the Laboratorio de Paleobiología, Universidad del Mar. **1,** ***Arca pacifica*** (**UMLP**-0066); **2,** ***Acar rostae*** (**UMLP**-0063); **3,** ***Calloarca alternata*** (**UMLP**-0128); **4,** ***Ostrea*** sp., internal valve with a serpulid tube (**UMLP**-0432); **5,** ***Ostrea*** sp., external valve with ***Entobia*** isp. and ***Gastrochaenolites*** sp. (**UMLP**-464); **6,** ***Striostrea*** sp. external valve with ***Entobia*** isp. and ***Gastrochaenolites*** isp. (**UMLP**-0445); **7,** ***Striostrea*** sp., external valve with serpulid tubes (**UMLP**-0453); **8,** ***Lima tetrica*** (**UMLP**-0087); **9,** ***Codakia distinguenda*** (**UMLP**-0490); **10,** ***Carditamera affinis*** (**UMLP**-0069); **11,** ***Cardites laticostatus*** (**UMLP**-0288); **12,** ***Americardia planicostata*** (**UMLP**-0066); **13,** ***Donax gracilis*** (**UMLP**-0081); **14,** ***Tivela delessertii*** (**UMLP**-0186); **15,** ***Chione subimbricata*** (**UMLP**-0076); **16,** ***Chione tumens*** (**UMLP**-0077). Scale bars equal 10 mm.

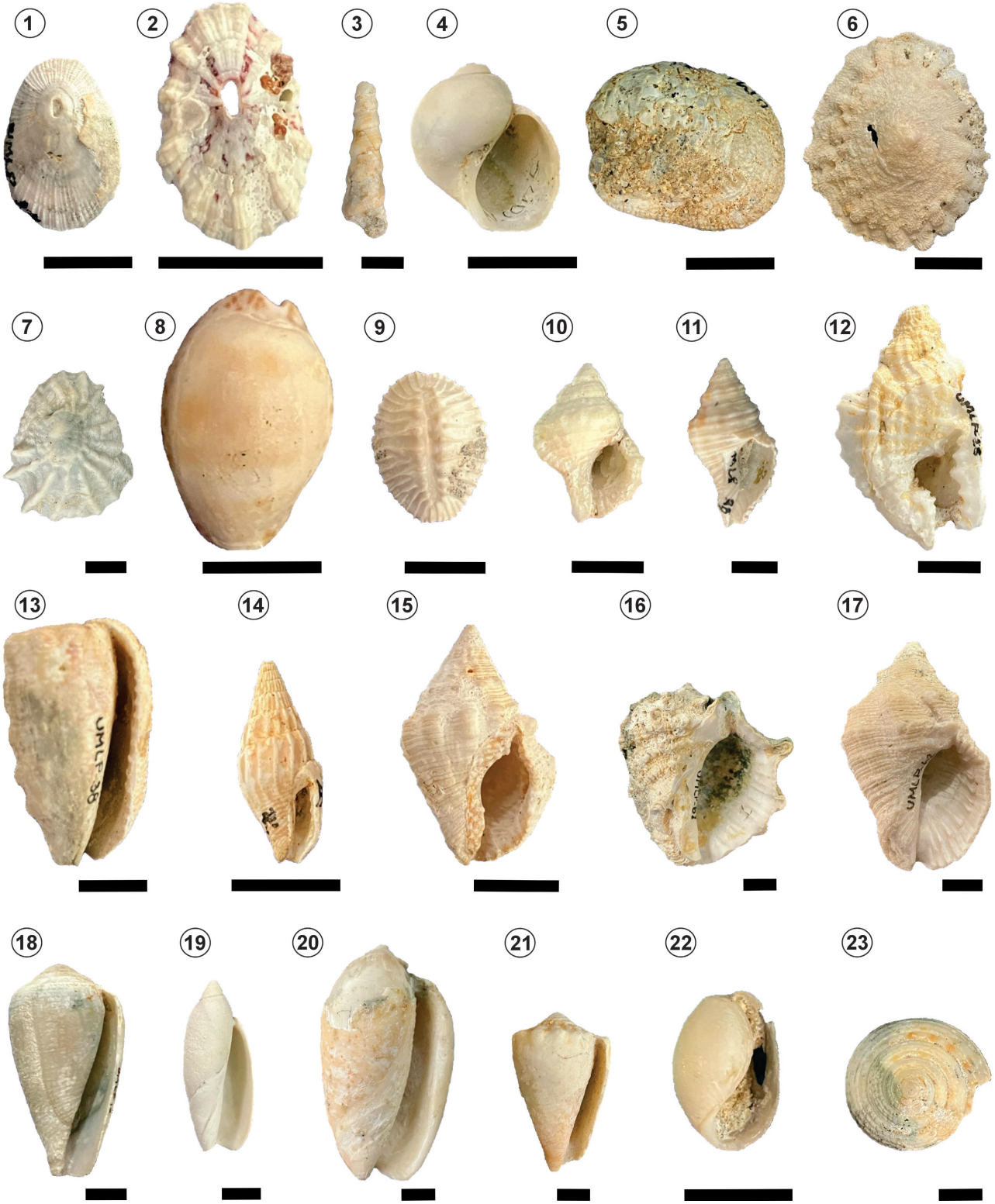

Figure 5. Some specimens of Gastropoda and their identification in the Laboratorio de Paleobiología, Universidad del Mar. **1,** ***Diodora inaequalis*** (**UMLP**-0027); **2,** ***Fissurella decemcostata*** (**UMLP**-0029); **3,** ***Caviturritela leucostoma*** (**UMLP**-0053); **4,** ***Natica caneloensis*** (**UMLP**-0040); **5,** ***Bostrycapulus aculeatus*** (**UMLP**-0021); **6,** ***Crucibullum scutellatum*** (**UMLP**-0023); **7,** ***Crucibulum spinosum*** (**UMLP**-0024); **8,** ***Pseudozonaria arabicula*** (**UMLP**-0035); **9,** ***Pusula radians*** (**UMLP**-0052),; **10,** ***Bursa rugosa*** (**UMLP**-008); **11,** ***Monoplex keenae*** (**UMLP**-0025); **12,** ***Distorsio constricta constricta*** (**UMLP**-0028); **13,** ***Morum tuberculosum*** (**UMLP**-0038); **14,** ***Strombina bonita*** (**UMLP**-0048); **15,** ***Gemophos sanguinolentus*** (**UMLP**-0013); **16,** ***Neorapana muricata*** (**UMLP**-0061); **17,** ***Stramonita biserialis*** (**UMLP**-0062); **18,** ***Agaronia propatula*** (**UMLP**-001); **19,** ***Agaronia testacea*** (**UMLP**-0002); **20,** ***Oliva incrassata*** (**UMLP**-0044); **21,** ***Conus brunneus*** (**UMLP**-0017); **22,** ***Bulla gouldiana*** (**UMLP**-007); **23,** ***Architectonica nobilis*** (**UMLP**-0006). Scale bars equal 10 mm.

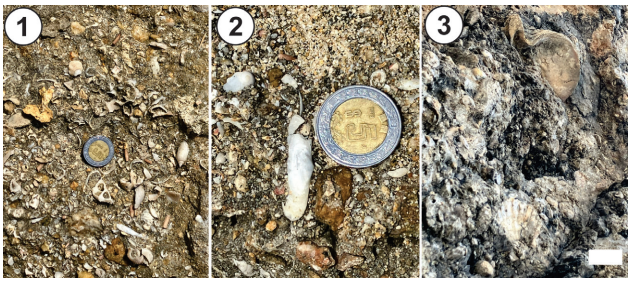

Figure 6. 1, small and medium-sized fossils in sandstone level; **2,** ***Tagelus longisinuatus***; **3,** ostreids in conglomerate and sandstone level. Diameter of the coin equals 25.5 mm. Scale bar equals 5 cm.

In both localities, some thicker specimens (*e.g.*, ostreids, *Chama*, *Spondylus*) show signs of abrasion on their surface ornamentation (Fig. 6.3). Besides, these shells have several associated bioerosive organisms, including bivalves, sponges, serpulids, bryozoans, and gastropods (Guerrero-Arenas *et al.*, 2021).

Habitat preferences

The molluscan species of the assemblage have been reported from shallow and tropical waters (Supplementary Online Information 1). The non-molluscan species (*Paraconcavus pacificus* and *Eucidaris thouarssii*) also inhabit tropical shallow waters nowadays. Their geographic distribution includes the coast of southern Mexico (Barrientos-Luján, oral communication).

The identified taxa have a variety of environmental settings, from coastal lagoons to subtidal areas. Most of the species in both localities inhabit subtidal environments: 81% in Punta Colorada locality and 88% in Playa Coral locality (Supplementary Online Information 1). Regarding the preference of subtidal taxa in Punta Colorada locality, 43 taxa dwell in soft substrate, and 34 taxa live on hard substrate. Concerning the subtidal taxa in Playa Coral locality, 24 taxa inhabit soft substrate, and 30 taxa live on hard substrate (Supplementary Online Information 1).

Some taxa from Punta Colorada could be associated with tropical lagoon systems, like the species *Mytella strigata* and *Tagelus longisinuatus* (Zamorano *et al.*, 2010).

In the Punta Colorada locality, some species inhabit coralline areas, like *Jenneria pustulata*, *Zetecopsis zeteki*, and *Gemophos sanguinolentus* (Zamorano *et al.*, 2006; Barrientos-Luján, 2009; Barrientos-Luján *et al.*, 2017, 2022). On the other hand, *Anachis scalarina* and *Barbatia reeveana* (Zamorano *et al.*, 2006) are reported from Playa Coral locality. However, the shells of these species are not abundant. The specimens do not show evidence of being transported over long distances. So, it is probable that both deposits are in proximity to coralline habitats.

Ichnofossiliferous richness

The diversity of trace fossils in both localities is low. They appear mostly in the sandstone levels in the Punta Colorada locality. Most of the specimens were found in fallen blocks. Therefore, their positions along the stratigraphic column are not completely accurate. The identified ichnogenera were *Thalassinoides* and *Psilolichnus* (Fig. 7.1), attributable to crustaceans (Nesbitt and Campbell, 2006; Pervesler & Uchman, 2009).

A notable variety of ichnofossils in the Punta Colorada locality is recorded in hard substrates. Bivalves are capable of boring lithified sandstones (Kelly & Bromley, 1984; Carmona *et al.*, 2013). Several specimens identified as *Gastrochaenolites*, a club-shaped boring in a hard substrate, were identified in clasts and fallen blocks (Fig. 7.2). A unique specimen from Playa Coral locality is a cast of one *Ophiomorpha nodosa* tunnel burrowed by *Botula cylista* (UMLP-0500) (Fig. 7.3). Also, another hard substrate was exploited by different kinds of sclerobionts (see next section).

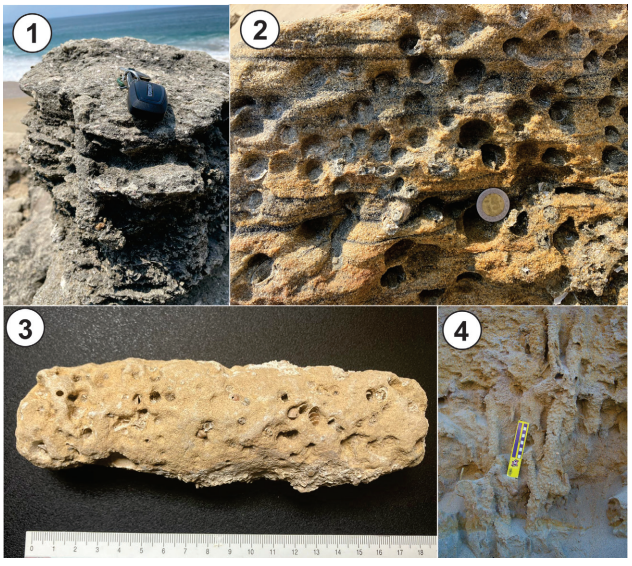

Figure 7. 1, ***Psilolichnus*** isp. cast in the upper level of Punta Colorada locality; **2**, ***Gastrochaenolites*** isp. in a fallen block of sandstone in Punta Colorada locality; **3,** a cast of ***Ophiomorpha nodosa*** (**UMPLIC**-1153) buried by ***Botula cylista***, from Playa Coral locality; **4,** casts of ***Ophiomorpha nodosa*** *in situ*, in Playa Coral locality.

The ichnofossiliferous richness in the Playa Coral locality includes only two ichnotaxa. Five years ago, beneath the fossiliferous deposits, a sand level contained abundant *Ophiomorpha nodosa* specimens (Fig. 7.4). The proposed producers of the tunnels are thalassinidean crustaceans (de Gibert *et al.*, 2006), specifically ghost shrimp (Pereyra, 2021). Nowadays, several landslides bury the level. Besides the *Ophiomorpha* tunnels, there were a few specimens of *Psilonichnus* in the lower part of the stratigraphic sequence.

Sclerobionts

Many sclerobionts have been reported previously in specimens from the Playa Coral locality. The diversity comprises serpulids, clionid sponges, bryozoans, and mollusks (Guerrero-Arenas *et al.*, 2021). Several fragments and incomplete thicker shells of Punta Colorada locality show the same reported sclerobionts as in the Playa coral locality: encrusting (bryozoans and serpulids) and borer organisms (clinoid sponges, bivalves, and polychaetes) (Guerrero-Arenas *et al.*, 2021) (Supplementary Online Information 2; Fig. 8.1). They have been settled in the interior and the exterior sides of the shells. Most of the shells were identified as ostreids.

Additional sclerobionts have been identified in both localities. The boring bivalve *Leisolenus hastasius* (UMLP-0499) was recovered from a *Striostrea prismatica* specimen (UMLP-0498) from Punta Colorada locality, and another individual (UMLP-0284) was recovered inside a *Chama* from Playa Coral locality. Specimens of the attached gastropoda *Dendropoma* sp. were found in the interior and exterior sides of bivalve shells of Playa Coral locality (Fig. 8.2). Several individuals of *Chama* sp. were attached to a fragmented Ostreidae (UMLP-0428).

Figure 8. 1, borings produced by bivalves in the outer side of an ostreid specimen; **2,** several individuals of the gastropod ***Dendropoma*** sp. attached to the internal side of the valve of a ***Codakia distinguenda*** specimen (**UMLP**-490).

DISCUSSION

Age and correlation of the localities

Punta Colorada and Playa Coral deposits have been considered as not synchronous, given the difference in lithology, the lack of continuity of the sedimentological strata, and the differences in the richness of the fossil assemblages.

Regarding the species in the localities, all the taxa are registered in recent communities. Some taxa, like *Acar gradata*, *Calloarca alternata*, *Saccostrea palmula*, or *Periglypta multicostata* have been recorded since the Pleistocene in the Pacific coastal area. Even some species, such as *Arca pacifica* and *Barbatia reeveana*, have older records dating back to the Pliocene on the Pacific Ocean coast (Supplementary Online Information 1). There is no biostratigraphical evidence that could help to limit the temporal range of the sedimentological deposits.

The absolute age of both deposits remains undetermined, as preliminary analyses of C-14 were not successful, since the fossils were older than 40 kyr. However, relative ages were inferred using the uplift rate of the study area. According to information from drill site 493 of Leg 66 of the DSDP (the nearest drill site to the marine terraces, on the continental platform of the Pacific coast), the uplift rate of the continental edge could be estimated as 125 m/my (McMillen & Bachman, 1982). The base of the Pleistocene sequence in the marine terraces of Punta Colorada locality is the conglomerate level, at 14 meters above sea level (**masl**). Therefore, the maximum calculated age for the Punta Colorada locality is 112,000 years. Regarding the Playa Coral locality, the base of the sequence is 31 masl. Therefore, the maximum age of this deposit is around 248,000 years.

Considering the uplift rate, the sediments of the Punta Colorada locality might have been deposited during the Late Pleistocene, specifically during the Marine Isotope Age 5 (MIS 5), which spanned from 130 to 71 kyr (Tawil-Morsink *et al.*, 2022). This period corresponds with the most recent Last Glacial-Interglacial (**LG-I**) cycle, which started at *ca.* 120 kyr BP and culminated at around *ca.* 20 kyr BP (Helmens, 2014). On the other hand, the proposed age of 248,000 years for the deposit of Playa Coral corresponds to the Middle Pleistocene. Specifically, the MIS 8 (Middle Saalian), which occurs within a relatively weak larger glacial-inter-

glacial cycle, between 320 to 243 kyr BP, approximately (Hughes *et al.*, 2020). At 243 kyr, Termination III occurs (Pillans & Gibbard, 2012).

These relative ages have been proposed, considering the minimal influence of tectonism in the area. The Pacific coastal area is characterized by complex tectonic activity (*e.g.*, Keppie & Morán-Zenteno, 2005; Ramírez-Herrera *et al.*, 2011; Yamamoto *et al.*, 2013). Along the Pacific coast, differential uplift processes have been reported through time (Ramírez-Herrera *et al.*, 2011). Nevertheless, the relative ages should be interpreted with caution until further dating analyses are conducted.

Paleoenvironmental conditions

The faunal assemblage represents a metacommunity, since the time averaging of intertidal and nearshore environments is established in the order of 10^1 to 10^3 years (Flessa, 2001). The assemblage is classified as parautochthonous, consisting of autochthonous specimens that have undergone some degree of reworking but have not been transported out of their original life habitat (Kidwell *et al.*, 1986). The variety of habitat preferences reinforces the condition of parautochthony of the assemblage (Supplementary Online Information 1).

The conditions of the environmental energy were variable in both deposits. The shells of bivalves and gastropods show a variety of different taphonomic signals. In the Punta Colorada locality, levels where thin shells are almost unbroken could reveal low-energy conditions (like the lagoonal systems). The conglomerate levels, characterized by clasts, were associated with high-energy conditions (Selley, 2000). Along the stratigraphic sequence, the sediment grain size ranges from fine to medium, indicating the low- to medium-energy conditions.

In Playa Coral, the sequence has predominantly fine- to medium-grained sand. The energy conditions were similar to some levels of the Punta Colorada locality, where the sediment grain size ranges from fine to medium, evincing the low- to medium-energy conditions (Selley, 2000).

Both localities have a low diversity of marine trace fossils. The ichnotaxa of Punta Colorada locality have been associated with transitional marine/terrestrial environments (Knaust *et al.*, 2012), while the ichnotaxa of Playa Coral are common in sedimentary rocks deposited in shallow and marginal marine environments (Frey *et al.*, 1978; de Gibert *et al.*, 2006). Because of their wider record in several environments, the ichnotaxa do not indicate a specific environment.

Colonization of opportunistic sclerobionts

The presence and variety of sclerobionts are probably linked to the predominance of soft substrates, as evidenced by the dominance of sandy levels along the stratigraphic sequence. In environments with soft, muddy, or sandy seafloors, the availability of hard substrates may be crucial for the survival of boring and encrusting organisms (Belaústegui *et al.*, 2017).

Sclerobionts are found on both the interior and exterior sides of the shells. When sclerobionts are present on the interior side, it indicates a post-mortem colonization (Rodland *et al.*, 2004). Sclerobionts on the exterior side could settle either while the host organisms were alive or after their death.

The hard substrates, such as shells, fallen blocks of sandstone, and consolidated casts of *Ophiomorpha nodosa*, provide microhabitats for sclerobionts, functioning as benthic islands (*sensu* Tapanila & Ebbestad, 2008). The presence of these benthic islands reinforces the hypothesis that sessile invertebrates utilized any available hard substrates in conditions where soft substrates were more abundant (Kauffman, 1978, 1982; Tapanila & Ebbestad, 2008) in both localities.

Apparently, the sclerobiont assemblages in both deposits appear to show a preference for thicker bivalve shells, since they are more abundant and diverse in this type of shell. In modern sclerobiont studies, preferences have been linked to shell size, external ornamentation, calcitic mineralogy, and bacterial biofilms (Ochi Agostini *et al.*, 2017). Additional studies on Pleistocene sclerobionts could help determine whether these factors played a relevant role in the colonization patterns of the preference for thicker shells.

Geographic Distribution

In general, all the identified species of fossil assemblages currently inhabit the southern Pacific coast of Oaxaca (Supplementary Online Information 1). The distribution of the taxa is within the Panamic Province

(Coan & Valentich-Scott, 2012), which extends from the Cedros Island-Punta Eugenia area on the Pacific coast of the Baja California Peninsula to Punta Aguja, Piura, Peru. This region is also known as the Tropical Eastern Pacific Ocean (Coan & Valentich-Scott, 2012).

Eleven species are considered endemic to Mexico: *Carditamera affinis*, *Chione tumens*, *Epicodakia clarionensis*, *Calliostoma aequisculptum*, *Conus scalaris*, *Crucibulum monticulus*, *Fissurella decemcostata*, *F. nigrocincta*, *F. rubropicta*, *F. spongiosa*, and *Thylaeodus indentatus* (González, 1993). The species could be considered paleoendemic (Noguera-Urbano, 2017) due to its fossil record and appears to be geographically restricted to the Mexican Pacific coastal area.

Turnover of communities

Fossils can provide data on locality and community composition through geologic time (Ludt & Rocha, 2014). So, it is possible to establish the species turnover to measure the difference in species composition between assemblages (Koleff *et al.*, 2003).

The beta diversity between the assemblages of Punta Colorada and Playa Coral is moderate (0.6315), meaning they are not so similar, suggesting that the studied fossil assemblages differ in species composition. All the species identified from the Pleistocene still inhabit the Oaxacan coast habitats today (Supplementary Online Information 1). The difference in species composition could be related to the diachrony of both fossil assemblages, given that climatic conditions varied along the Pleistocene, as the species identified in the studied localities inhabit similar coastal environments.

Considerations for the conservation of modern malacological assemblages

The potential of the marine fossil record in the study of the dynamics and history of modern marine assemblages has been discussed by several authors (*e.g.*, Kowalewski *et al.*, 2023; Tomašových *et al.*, 2023, and the references therein). Information from geohistorical records could contribute to tracking climate change from the Pleistocene to the present, and its impact on modern communities and ecosystems. The use of geohistorical records in conservation strategies is addressed by Conservation Paleobiology. This discipline applies the theories and analytical tools of paleontology to the solution of problems concerning the conservation of biodiversity (Dietl *et al.*, 2015).

The fossil record of Punta Colorada and Playa Coral localities may contribute to proposing effective strategies of conservation and management of the extant marine fauna along the coast of Oaxaca. The fossil assemblages of Punta Colorada and Playa Coral localities may provide insight into the young fossil record of some modern species. For example, the gastropods *Plicopurpura columellaris* and *Nerita scabricosta* inhabit the modern rocky intertidal zone from the study area (Keen, 1971). They are appreciated for their beauty and used by artisans and local people. Neither species has been recorded in the fossiliferous deposits, suggesting that they may have a young fossil record. This information highlights the importance of conservation efforts, particularly for *P. columellaris*, which is exploited as a producer of an appreciated purple textile dye (López-Chávez *et al.*, 2016; Barrientos-Luján *et al.*, 2022).

Only one gastropod recorded in the fossil assemblage faces a critical conservation status, according to the Mexican Official Norm NOM-059-SEMARNAT-2010 (NOM-059). *Cruciculum scutellatum* is subject to special protection (Secretaría de Medio Ambiente y Recursos Naturales, 2010). This category refers to species that could be threatened by factors that negatively affect their viability. So, there is a need to promote their recovery and conservation, or the recovery and conservation of populations of their associated species.

Regarding the geographic distribution of the recorded species, they have been inhabiting the coastal area of Oaxaca from the Pleistocene to the present. No local extinctions of species were recorded in the Pleistocene, since the species have persisted through time in the study area. The molluscan species persist over time, even in the Pleistocene periods of climatic change, suggesting resilience to disturbances (Cant *et al.*, 2023). This resilience is a critical factor for modern biotas, which face anthropogenic and climatic threats. However, it is unknown if the recent molluscan assemblages could be resilient to the rise in temperature. Since they are ectotherm organisms, global warming is a real menace with several possible consequences in the communities, as has been reported in numerous parts of the world (Assan *et al.*, 2020; Albano *et al.*, 2021). The other

possibility is that they may be able to develop the adaptive capacity to tolerate climate change (Ross *et al.*, 2023).

Considerations for the conservation of the marine terraces and their fossil biota

As mentioned earlier, marine terraces are vulnerable to various natural and anthropogenic hazards. In the Puerto Escondido area, the main factors include natural events such as earthquakes, hurricanes, and storms, as well as the degree of vulnerability of the local settlements (Lavell, 2006; Narváez *et al.*, 2009).

One significant threat to these terraces is the heavy rainfall caused by storms and hurricanes. Puerto Escondido has experienced several events, with recorded rainfall reaching up to 1160.65 mm, like the one in August 2010 (Morales-Barrera *et al.*, 2021). The water saturated the rocks and soils, triggering gravitational processes that resulted in landslides.

Another risk factor is the seismic activity, driven by the subduction of the Cocos Plate beneath the North American Plate. Historically, numerous earthquakes have affected the coastal region, with cities such as Puerto Escondido, Pochutla, Puerto Angel, Huatulco, and Loxicha among the most affected (Morales-Barrera *et al.*, 2021).

Marine terraces with fossiliferous outcrops experience significant landslides along their steep slopes. These landslides have partially destroyed Playa Coral strata, and nowadays, the outcrops remain buried under vegetation (Fig. 9.1). Additionally, several constructions have been developed on the terrace edges, despite recommendations against building in such areas (Morales-Barrera *et al.*, 2021).

Figure 9. 1, the strata from the Playa Coral locality are currently buried by landslide processes and covered by local vegetation; **2,** several fallen blocks characterize the Punta Colorada locality and are constantly eroded by wave action.

Currently, there are no constructions on the Punta Colorada locality terrace, but the area is unsuitable for buildings or civil works due to several fallen blocks, highlighting its susceptibility to natural hazards (Fig. 9.2). The future permanence of the marine terraces in Punta Colorada is at risk due to the ongoing construction of a massive urban complex on the terrace (Pérez-Alfonso, 2024), although it is neither practical nor safe to build in the terraces.

Preserving fossiliferous localities requires the adoption of several approaches to protect, manage, and document these sites. In this regard, some authors have advocated the use of digital tools for documentation (Bratton *et al.*, 2013) or promoting societal values related to geomorphological structures (Zgłobicki *et al.*, 2015). The potential loss of paleontological heritage in Punta Colorada and Playa Coral localities means the loss of information about Pleistocene marine populations in southern Mexico, as well as the opportunity to understand their dynamics.

CONCLUSIONS

The Pleistocene Colotepec Formation crops out on the outskirts of Puerto Escondido City. It consists of a basal conglomerate overlain by sandstone and bears a diverse marine fauna. The invertebrate assemblage of the Pleistocene Punta Colorada locality comprises 35 taxa of Bivalvia and 54 taxa of Gastropoda. The assemblage from the Pleistocene Playa Coral locality consists of 34 taxa of Bivalvia and 29 taxa of Gastropoda.

The identified species of fossil assemblages currently inhabit the southern Pacific Ocean and are part of the Panamic Province.

The habitat preferences of the identified taxa suggest a tropical shallow subtidal environment. Sedimentology suggests that water energy varies in both deposits along the stratigraphic sequence. The presence of sclerobionts on various shells suggests that soft substrates predominate in the studied localities.

Based on the uplift rate of the study area, the maximum calculated age for the Punta Colorada deposit is 112,000 years (Late Pleistocene), and that of the Playa Coral locality is around 248,000 years (Middle Pleistocene).

The species turnover between the Punta Colorada locality and Playa Coral locality is moderate (0.6315), which could be related to the diachrony of both fossil assemblages and the variety of climatic conditions along the Pleistocene, since the identified species inhabit similar coastal environments.

The marine terraces of Puerto Escondido are vulnerable to diverse natural and anthropogenic hazards; thus, the fossiliferous strata in Playa Coral and Punta Colorada are at risk.

The deposits of the Colotepec Formation represent one of the few records of the marine faunas in the southern Pacific during a period of climatic changes. Its conservation in the long term is crucial to understanding the ecological and environmental dynamics of this unique region.

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Credit authorship contribution statement

RGA: writing, validation, supervision, methodology, investigation, formal analysis, data curation, conceptualization. NABL: writing, supervision, methodology, investigation, formal analysis, data curation. EJH: writing, methodology, investigation, formal analysis. JAG: methodology, investigation, formal analysis, and data curation. FBV: formal analysis and data curation.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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