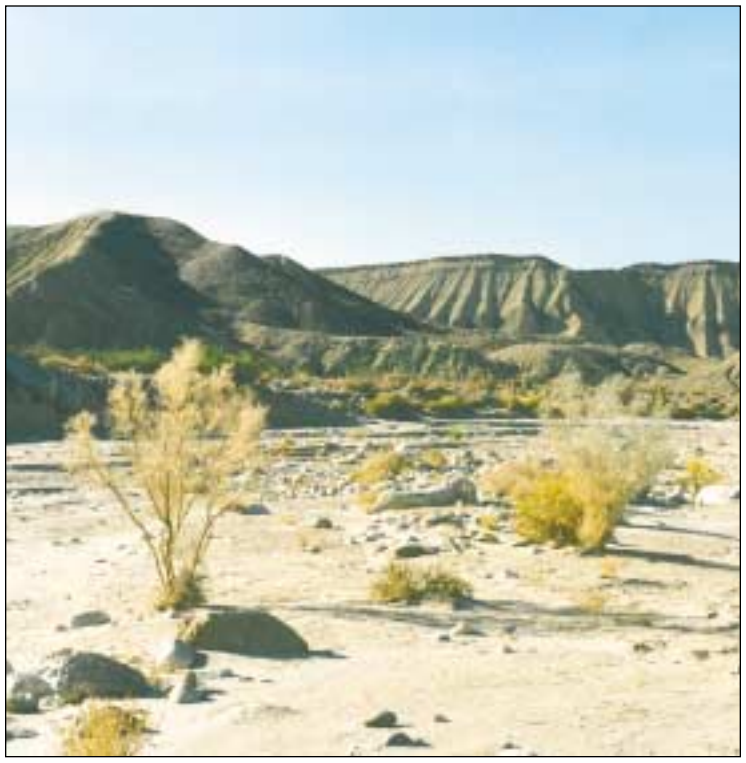
3 Invertebrates of the Imperial Sea



One could not ignore a granite monolith in the path of the waves. Such a rock, breaking the rushing waters, would have an effect on animal distribution radiating in circles like a dropped stone in a pool.

John Steinbeck and Edward F. Ricketts, in *Sea of Cortez*, 1941

Thomas A. Deméré
N. Scott Rugh

Invertebrates of the Imperial Sea

Tilted Shell Beds in the Deguynos Formation, Painted Gorge Area. (Photograph by Tom Deméré)

Introduction

The fossil marine invertebrate assemblages recovered from sedimentary rocks of the late Miocene Imperial Group (see Deméré, this volume, *The Imperial Sea*) have, for many years, attracted the attention of professional and avocational paleontologists, as well as casual collectors. Perhaps it is the stark contrast between the dry and rugged desert setting and the tropical looking, "petrified" shells that makes the Imperial Group fossils so appealing. In any event, the fossils from this rock unit are locally abundant and provide an excellent opportunity to study the life of the ancestral Gulf of California.

The last time that marine waters flooded this part of southern California was during the early part of the Pliocene Epoch four to five million years ago. Ironically, it was the Colorado River with its tremendous volume of water and high sediment load that spelled the death of the northern portion of the ancestral Gulf of California (see Deméré, this volume; Dorsey, this volume, *Stratigraphy, Tectonics, and Basin Evolution in the Anza-Borrego Desert Region*). However, during the late Miocene and early Pliocene, before this portion of the proto-Gulf dried up, its waters supported diverse assemblages of marine invertebrates including an impressive variety of corals, molluscs (clams and snails), crustaceans (barnacles, crabs, and shrimp), and echinoderms (sand dollars, sea urchins, and sea stars).

Although many of these fossils represent species that still live today in the Gulf of California, a surprising number also represent species or genera surviving only in the Caribbean Sea. This strong Caribbean component is a historical artifact of a time when the equatorial eastern Pacific Ocean, the western Gulf of Mexico, and the Caribbean Sea were all linked to form an unbroken tropical region – the Tertiary Caribbean faunal province. At this time during the

late Miocene and early Pliocene, the Isthmus of Panama did not exist and, instead, the Central American Seaway occupied the region of Panama and Costa Rica (Figure 3.1). Surface ocean currents of the eastern Pacific (Equatorial Countercurrent) and Caribbean (Caribbean Current) presumably flowed west to east and east to west, respectively, through the Central American Seaway and provided a means for dispersing larvae of various groups of marine invertebrates. Countercurrents flowing north along the west coast of Mexico, in turn allowed dispersal of Tertiary Caribbean species into the proto-Gulf and vice versa (see Deméré, this volume).

Figure 3.1
Central American Seaway During the Late Miocene. The gold depicts the North and South American continents before they were joined forming the Isthmus of Panama about 3.5 million years ago (see McDonald, this volume, *Anza-Borrego and the Great American Biotic Interchange*).

A thick sequence of sedimentary rocks accumulated during this time period in the region of the modern day Imperial Valley. Geologists call these rocks the Imperial Group and have subdivided them into an older series of coarse-grained sandstones and conglomerates called the Latrania Formation, and an upper series of claystones and fine-grained sandstones called the Deguynos Formation (see Dorsey, this volume). The Latrania Formation was deposited during the late Miocene, prior to the beginning of deposition of delta sediments of the ancestral Colorado River. The fine-grained delta deposits of the Deguynos Formation overlie the sandstones of the Latrania Formation.

Mode of preservation is an important aspect of the invertebrate fossils from the Imperial Group, with the majority of specimens represented not as intact original crystalline shell material, but as hardened sandstone molds preserving either the internal or external form of the shell. The original mineralogy of the shells and/or tests of the fossils is largely responsible for determining their mode of preservation. Fossil remains consisting of original shell/test material typically represent organisms with a higher percentage of $MgCO_3$ (magnesium carbonate) in their shells/tests. Organisms that fall into this group include oysters, spiny oysters, scallops, barnacles, and sand dollars. In contrast, shells/tests constructed with little or no $MgCO_3$ are more likely to be leached away by percolating ground waters and/or under the harsh physical and chemical conditions of the desert region. The result is that the original shell/test material is selectively removed leaving a void in the hardened sandstone.
If a fossil specimen is the impression of the outside of the shell it is called an *external mold*. If instead the fossil is an impression of the inside of the shell it is called an *internal mold* (Figure 3.2). The German word “steinkern” is often used for three-dimensional internal molds, such as the internal sandstone mold formed within a snail shell or articulated pair of clam shells.

This chapter presents an overview of the more common Imperial Group marine invertebrates (corals, molluscs, and echinoderms) and discusses their temporal, environmental, and geographic distributions. Other groups of invertebrates (e.g., sponges, bryozoans, brachiopods, foraminifers, and crustaceans), although reported from the Imperial Group (Appendix, Table 2), are not common fossils and will not be treated herein. Thus, this chapter is not meant as a comprehensive treatment of Anza-Borrego's invertebrate fossils but will provide a foundation for a future monograph of this marvelous fauna. It is hoped, however, that the reader will come to realize some measure of the diversity of life forms that once flourished in the lost Miocene and Pliocene seas of the proto-Gulf of California.

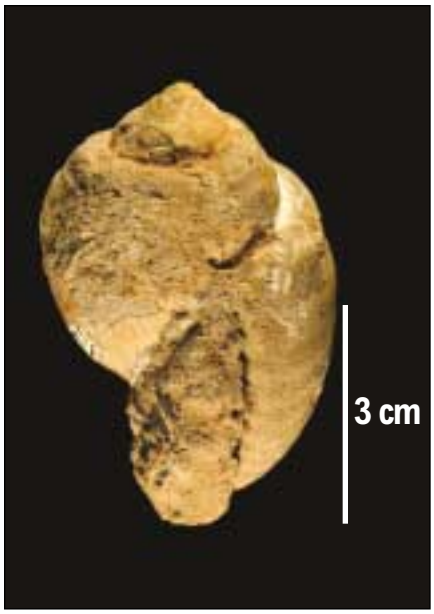


Figure 3.2
Malea ringens.
An example of a fossil gastropod preserved as an internal mold, or steinkern (SDSNH 12234). (Photograph by Barbara Marrs)

Figure 3.3
Solenosteira sp.
An example of a fossil gastropod preserved with original crystalline shell material (ABDSP 1327). (Photograph by Barbara Marrs)

Cnidaria (corals)

The Imperial Group fossil coral assemblage consists of seven to nine colonial species representing both encrusting and branching forms. All belong to the Order Scleractinia or stony corals, which today are important reef builders in tropical seas. The majority of these corals are known for their symbiotic relationship with photosynthetic zooxanthellae (unicellular yellow-brown algae) that live within the body tissues of the coral.

Typically, the Imperial Group coral specimens occur as fragmentary coral heads (coralla) that were transported by ocean currents to a common site of deposition and concentrated together to form dense fossil shell beds. There are, however, rare instances where specimens are preserved in life position as *in situ* coral heads or small patch reefs still firmly attached to the ancient sea floor bedrock. The vast majority of confirmed records of Imperial fossil corals have come from the Latrania Formation, with only a single species reported from the Deguynos Formation. Among the genera known from the Latrania Formation (Vaughan, 1917), only one, *Porites*, is represented by a species that still lives today in the Pacific Ocean region. All of the other genera are either extinct today or have been extirpated (localized extinction) from the region since at least the early Pleistocene. In the latter case, the fossil taxa are primarily represented by species living today only in the western Atlantic Ocean and adjacent regions (i.e., Caribbean Sea).

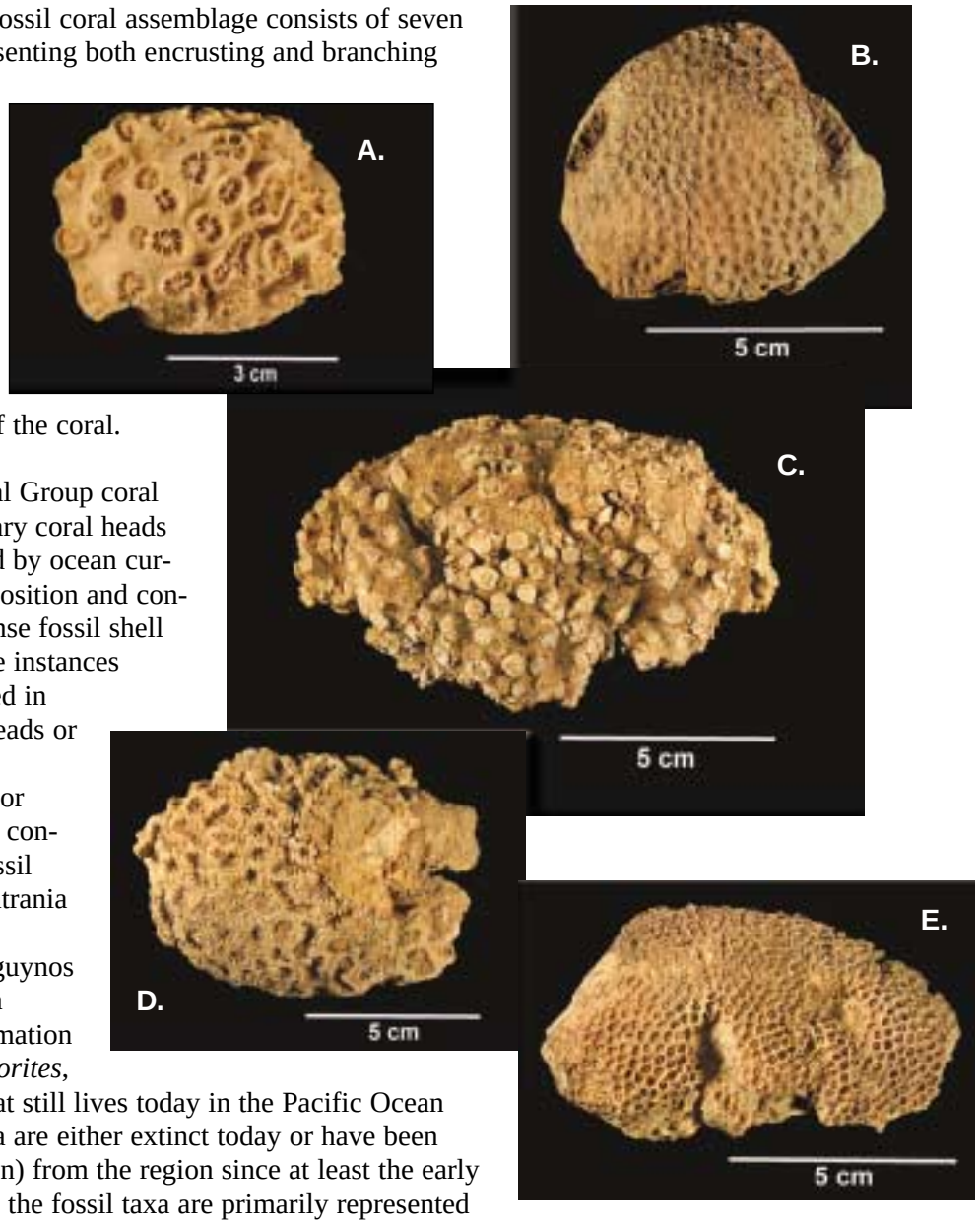


Figure 3.4
Examples of Fossil Corals from the Imperial Group.
A. *Dichocoenia merriami* (SDSNH 11953),
B. *Siderastrea mendenhalli* (SDSNH 11964),
C. *Astrangia haimei* (ABDSP 1325),
D. cf. *Meandrina* sp. (SDSNH 11935), and
E. *Solenastrea fairbanksi* (SDSNH 11966).
(Photographs by Barbara Marrs)

Meandrinidae (brain and flower corals)

There are four species of meandrinid corals from the Latrania Formation. Perhaps the most beautiful of the Imperial fossil corals, *Dichocoenia merriami* (Figure 3.4A) is relatively rare and characterized by large irregular corallites (skeleton of individual polyp) up to

10 mm (0.4 in) across and distinctly separated from neighboring calices by complex winding valleys. The fossil species is similar to the extant *D. stokesi* from the Caribbean Sea. A related fossil species from the Latrania Formation, *Meandrina bowersi* is a small extinct brain coral similar to the extant *D. labyrinthiformis* from the Caribbean Sea. In brain corals the individual corallites are fused into long meandering skeletal rows resembling wrinkles of a human brain. The Latrania Formation species of *Meandrina* (Figure 3.4D) has coarse septa (radially positioned walls within a corallite) and irregular, elongate corallites measuring up to 15 mm (0.6 in) in length.

Eusmilia carrizensis is an extinct species of branching coral originally named from the Imperial fossil beds of the Coyote Mountains. Specimens of this species are relatively rare and often consist of single branches with paired, terminal corallites 13-17 mm (0.5-0.7 in) in size. Septa are discontinuous and there is no central columella (central crystalline column within a corallite). The Latrania Formation fossil species resembles *E. fastigiata* from the Caribbean Sea.

Siderastreidae (starlet corals)

Siderastrea mendenhalli (Figure 3.4B) is a relatively common fossil coral from the Latrania Formation with massive coralla up to 300 mm (12 in) across; although most are much smaller. This coral is distinguished by its closely crowded polygonal corallites (4-7 mm in diameter; 0.2-0.5 in), which often are deformed because of their tight packing. The septa in each corallite are very thin and form a delicate star-like pattern. Although Vaughan (1917) named two fossil species of *Siderastrea* and one variety from the Imperial fossil beds, most workers today only recognize the one species, *S. mendenhalli.* This extinct species is similar to the extant *S. siderea* from the Caribbean Sea.

Rhizangiidae (cup corals)

The Deguynos Formation typically is devoid of fossil coral specimens, a pattern apparently reflecting the more turbid nature of the deltaic portion of the Imperial Group deposits. However, there is one species of coral, *Astrangia haimei* (Figure 3.4C), which has been reported from the Deguynos Formation as exposed in the East Mesa area of the Anza-Borrego Desert State Park. This coral is distinguished by its separate and elongate, cylindrical corallites, which typically extend above the main mass of the corallum.

The occurrence of this more typically temperate genus of stony coral in the Pliocene portion of the Imperial Sea indicates that paleoenvironmental conditions for the Deguynos Formation were different from those of the Latrania Formation. Today, most members of this family lack symbiotic zooxanthellae perhaps indicating that their tolerance for lower light levels is greater than for the true zooxanthellate corals, which occur in the clear water sandstone facies of the Latrania Formation.

Faviidae (star corals)

Solenastrea fairbanksi (Figure 3.4E) is by far the most common fossil coral from the Latrania Formation. Specimens typically occur as large fragmentary coral heads up to 400 mm (16 in) across with distinctly separate polygonal corallites only 2-3 mm (0.1 in) in diameter. Specimens often occur with corallites covering all exposed surfaces, indicating that the coralla were periodically dislodged from the sea floor and rolled about by currents to expose new growth surfaces. This is in contrast to having a fixed coral head growing continuously upwards from its base. The Latrania Formation fossil species is similar to *S. hyades* from Pleistocene rocks of Florida and the living *S. bournoni* from the West Indies.

Poritidae (finger corals)

Six species of *Porites* are still living in the Gulf of California today. Fossil specimens from the Latrania Formation are assigned to *P. carrizensis* and typically occur as small rounded bioclasts (40-60 mm, 1.6-2.4 in) in sandy limestone strata. The surface of the coralla appear smooth because the polygonal corallites of this species are almost microscopic (1-1.5 mm in diameter, 0.06 in) and are very closely crowded together. The septa are relatively thick for such a small corallite. The fossil species from the Coyote Mountains is similar to the extant *P. astreoides* from the Caribbean Sea.

Mollusca (bivalves, clams, and snails)

Molluscs are by far the most diverse group of marine invertebrate fossils from the Imperial Group and were first described by Hanna (1926). Currently there are over 65 species of gastropods and over 60 species of bivalves reported as fossils from these rocks (see Appendix, Table 2). The composite molluscan assemblage from the Latrania Formation is more diverse than that from the Deguynos Formation. The former contains nearly equal numbers of gastropods and bivalves, while the latter is dominated by species of bivalves. Fossil molluscs in the Latrania Formation often occur in well-cemented sandstones as dense concentrations of shells and molds. Sometimes fossils occur in sandy limestones, while other occurrences consist of thick massive sandstones with widely dispersed shells and/or molds. Fossil molluscs in the Deguynos Formation generally occur in well-cemented shell coquinas, which due to their high calcium carbonate volume (shells) often form resistant shelly strata capping hogbacks and ridgelines in the badlands of the Anza-Borrego Desert State Park and adjacent Bureau of Land Management lands.

Fossil preservation in the Latrania Formation is variable and includes fossil shells with original calcite or recrystallized calcite and in some cases even original aragonite (carbonate mineral). In rare cases some specimens even retain original coloration (e.g., cones, scallops, and oysters). The most common style of preservation consists of internal and external sandstone molds with all original

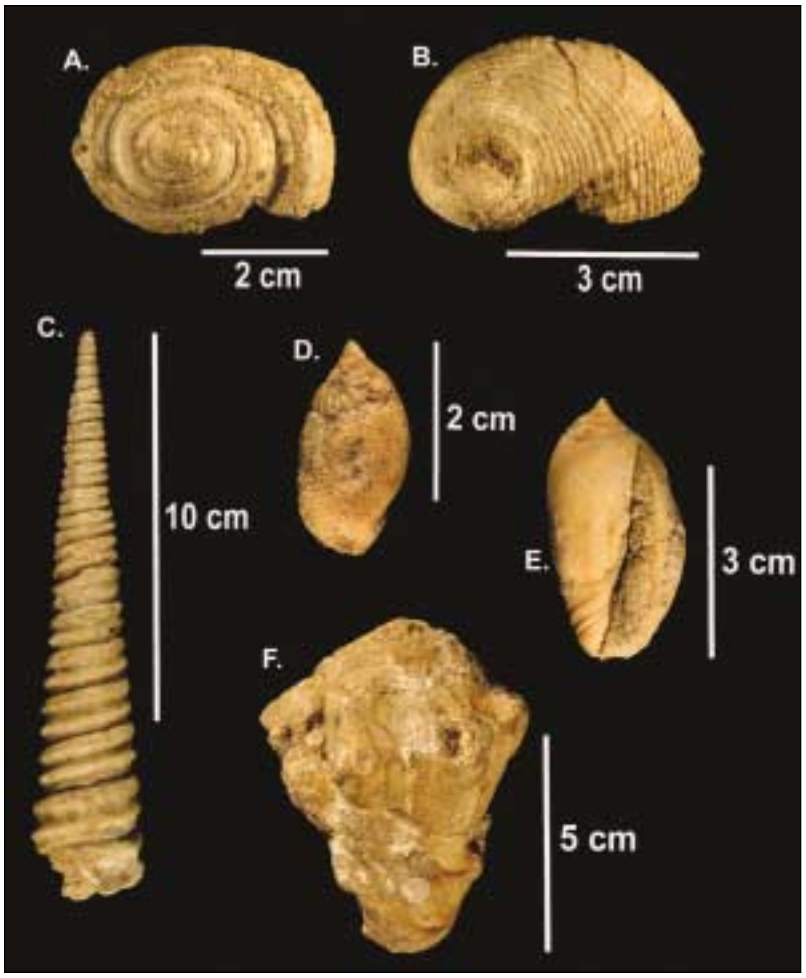


Figure 3.5
Gastropods.
Preserved with original crystalline shell material.
A. *Architectonica nobilis* (SDSNH 23148),
B. *Nerita scabricosta* (SDSNH 53865),
C. *Turritella imperialis* (SDSNH 97265),
D. *Cancellaria obesa* (SDSNH 12142),
E. *Oliva spicata* (SDSNH 12332), and
F. *Vasum pufferi* (SDSNH 23112).
(Photographs by Barbara Marrs)

shell material leached away (e.g., the venerid and lucinid clams and strombid and cypraeid snails).

Gastropoda (snails)

Most gastropods reported from the Imperial Group have been collected from sandstone strata in the Latrania Formation. The majority of these fossil snails are species that lived in and on a sandy substrate at shallow marine depths. A very few, including *Nerita scabricosta,* lived in rocky areas. Species of the Family Calyptraeidae lived attached to solid objects, such as the surfaces of living and/or dead clam and snail shells lying on the sandy sea floor.

Although a number of the Imperial Group fossil snails represent species still found in the Gulf region today, many are actually very similar or nearly identical to living species from the Caribbean Sea. A few examples include *Melongena patula, Pleuroploca princeps,* and *Vasum pufferi.*

While some gastropod species are typically preserved as sandstone steinkerns, including species of *Strombus* and *Macrocypraea,* many of the gastropod species are frequently preserved with some or all of the original crystalline shell material intact. Species that are most commonly preserved as steinkerns are thin shelled taxa, such as *Malea ringens* and species of *Bulla*. Specimens that have been preserved with the entire original shell intact can be very beautiful. A few examples of these are: *Turritella imperialis, Oliva spicata,* and several of the *Conus* species with original shell ornamentation and even color patterns preserved.

The discussions below focus on those gastropod families best represented by fossils in sedimentary rocks of the Imperial Group. Several families have been omitted from this listing because species attributed to them are either very rare or the original identifications are incorrect. Omitted families include Haliotidae, Lottiidae, Turbinidae, Potamididae, Cerithiidae, Modulidae, Littorinidae, Hipponicidae, Personidae, Muricidae, Columbellidae, Mitridae, Turridae, Fissurellidae, Trochidae, Calyptraeidae, Ficidae, Terebridae, and Bullidae (see Appendix, Table 2).

Neritidae (nerites)

Fossil nerites collected from the Latrania Formation include relatively large (for the Family) specimens 38-45 mm (1.5-1.8 in) in diameter, preserved as original shell material with numerous fine spiral lines. These large specimens have been identified as *Nerita scabricosta* (Figure 3.5B), an extant species living today along the Pacific coast of Baja California Sur throughout the Gulf of California and south to Ecuador. Other nerites reported as fossils from the Latrania Formation include *N. funiculata,* an extant species living from the west coast of Baja California throughout the Gulf of California and south to Peru, and *Theodoxus luteofasciatus,* an extant species living in the Gulf of California and south to Peru.

Turritellidae (turret shells)

Of the eleven species of turret shells living in the Gulf of California today, only *Turritella gonostoma* has been reported as a fossil in the Imperial Group. This record, however, cannot be confirmed. Additionally, the only other fossil turritellid reported from these rocks is the extinct species, *T. imperialis* (Figure 3.5C), first described from the Coyote Mountains. Shells of *T. imperialis* have been primarily collected from the sandstone and limestone strata of the Latrania Formation. However, certain strata within the mudstone beds of the Deguynos Formation contain dense concentrations of this distinctive fossil snail. *T. imperialis* is characterized by its two heavy spiral ridges, one at the shoulder, and one at the base of each whorl (one complete turn of the spiraled shell). Adult specimens are long and slender and can measure up to 145 mm (5.7 in) in length with a diameter of only 25 mm (1 in). *T. imperialis* is similar to *T. altilira* from the Miocene Gatun Formation of Panama.

A partially uncoiled member of the family Turritellidae, *Vermicularia pellucida eburnea,* is locally common in sandy limestone beds of the Latrania Formation. Fossil specimens cannot be separated from modern shells of the extant species, which lives today from southern California throughout the Gulf of California and south to Panama.

Strombidae (conch shells)

Fossils representing at least three different species of this group of large gastropods occur in the Latrania Formation. Although occasionally specimens are found that preserve original crystalline shell material, most fossil strombids from this region occur as internal and external sandstone molds. Two fossil forms are referable to extant taxa still living in the Gulf of California. Fossils of *Strombus gracilor* measure 70 to 85 mm (2.8-3.4 in) in length with a short flaring lip and small pointed nodes on the shoulder of the final whorl. This species still lives from the Gulf of California south to Peru. *Strombus pugilis* is a closely

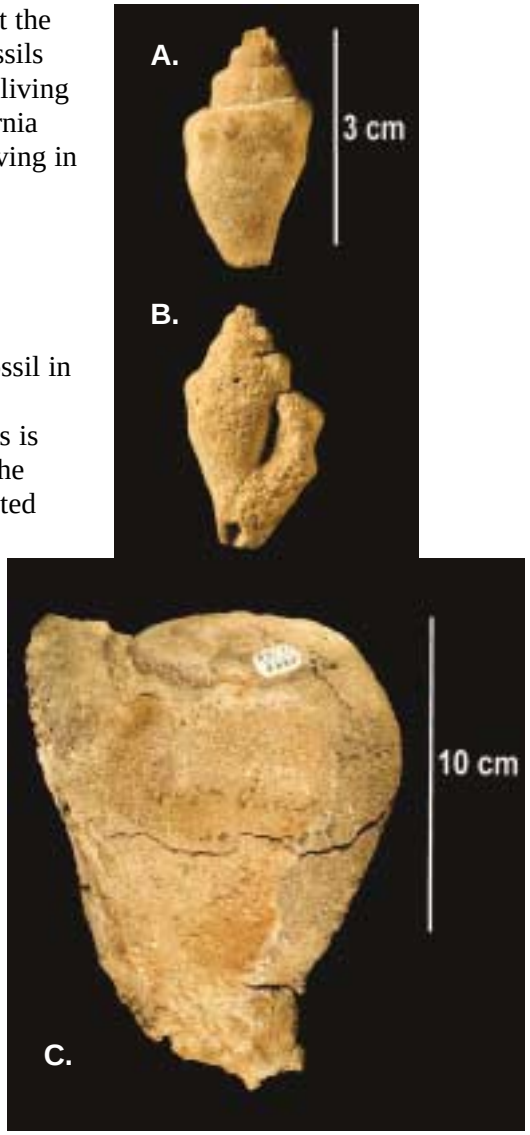


Figure 3.6
Conch Species.
A. *Strombus obliteratus.* Juvenile steinkern (SDSNH 12155),
B. *S. obliteratus.* Front view of specimen shown in A., and
C. *Strombus galeatus.* Steinkern (SDSNH 12148).
(Photographs by Barbara Marrs)

related Caribbean species. The largest strombid from the Latrania Formation is *S. galeatus* (Figure 3.6C), a species that still lives today in the Gulf of California. Some fossil specimens measure up to 150 mm (6 in) in length with a large flaring outer lip that is often only partially preserved. It should be noted that the steinkern of juvenile fossil specimens is conical in shape, lacking the flaring lip of the adult, and may be mistaken as a fossil of a large *Conus*. *Strombus goliath* is a closely related Atlantic species. A third species, *S. obliteratus* (Figures 3.6A, B), is extinct and was originally named from fossils collected from the Latrania Formation. This fossil species is closely related to the extant *S. granulatus* and is characterized by its relatively small size (50-60 mm, 2-2.4 in) and robust rounded nodes on the shoulder of the final whorl.

Cypraeidae (cowries)

Fossil cowries are uncommon from the Latrania Formation and are unknown from the Deguynos Formation. In the Latrania Formation, specimens typically occur as sandstone steinkerns with minor amounts of crystallized shell material preserved. For this reason, identification to species level is difficult. However, there are at least two different fossil taxa recognized. One is tentatively identified as *Macrocypraea* sp. cf. *M. cervinetta*, a species living today from Sonora, Mexico, to Peru and Islas Galapagos. Known fossil specimens of this species may reach 50 mm (2 in) long, but living specimens may reach 115 mm (4.5 in) in length. The second type of fossil cowrie from the Latrania Formation is represented by large, globose sandstone steinkerns that reach 70 mm (2.8 in) in length and 50 mm (2 in) in diameter. These cowries are assigned to the genus *Muracypraea* (Figure 3.7), but specific identification is hampered by the lack of original shell material. This genus is extinct in the Gulf of California today. However, *Muracypraea* is known throughout the Caribbean Basin, Panama, Ecuador, Peru, Costa Rica, and Baja California Sur, Mexico, from the early Miocene to recent. *Muracypraea* specimens from the Latrania Formation may represent a new species (Arnold, 1998).

Figure 3.7
Muracypraea sp.
Steinkerns:
A. SDSNH 88085 and
B. SDSNH 97227.
(Photographs by Barbara Marrs)

Naticidae (moon shells)

Fossil naticids are locally common in the Latrania Formation and are usually preserved with crystalline shell material. The two dominant genera are *Polinices* and *Natica*. Specimens of *Natica* are more globular in shape than those of *Polinices*. However, reliable identification is only possible if the umbilical callus (thickened shelly area) is present and this feature may be missing if the crystalline material has crumbled or if only the sandstone steinkern has been

preserved. Although *N. chemntizii* is the most common living *Natica* found in the Gulf of California today, it is rare as a fossil in the Imperial Group. The two most common species of fossil *Polinices* can be difficult to distinguish (even when the callus is present). *Polinices uber* is an extant species living along the west coast of Baja California throughout the Gulf of California and south to Peru. This species may be related to *P. stanislasmeunieri* from the Miocene of the Caribbean (Woodring, 1957). The generally larger *P. bifasciatus* is extant and lives from the Gulf of California to Panama. Fossil naticids from the Latrania Formation are small, generally not exceeding 30 mm (1.2 in), but specimens of *P. bifasciatus* may reach 40 mm (1.8 in) in length.

Cassididae (helmet shells)

Specimens of the extinct species *Cassis subtuberosa* are occasionally found in the Latrania Formation as sandstone internal molds. These fossils are conical in shape and easily may be confused with internal molds of *Conus fergusoni*, the largest fossil cone from the Imperial Group. *Cassis* may be distinguished from *Conus* by the presence of a few widely spaced vertical rows of shallow depressions on the fossil, which correspond to the "teeth" that run along the inside edge of the outer lip of the aperture (opening in shell from which body protrudes). The fossil species is small, about 60 mm (2.4 in) long by 70 mm (2.8 in) in diameter. Most of the closest living relatives are found in the Indo-Pacific, Atlantic Ocean, and the Caribbean Sea, none survive today in the eastern Pacific Ocean. These species have a thick outer lip, and most reach impressively large sizes. The largest, *Cassis cornuta* of the Indo-Pacific, can reach 387 mm (15 in) in length.

Tonnidae (tun shells)

Malea ringens (Figure 3.8) is a locally common fossil gastropod in the Latrania Formation and is typically found as sandstone internal molds (steinkerns) up to 70 mm (2.8 in) in length and 50-65 mm (2-2.6 in) in diameter. This is considerably smaller than the maximum shell size (up to 240 mm, 9.5 in) of living *M. ringens*, which today occurs from the Gulf of California south to Peru. Modern shells are relatively thin, which probably contributes to its loss by dissolution in fossil forms. Steinkerns typically preserve distinctly separated fine spiral lines and some specimens even preserve impressions of the thickened and toothed outer aperture lip.

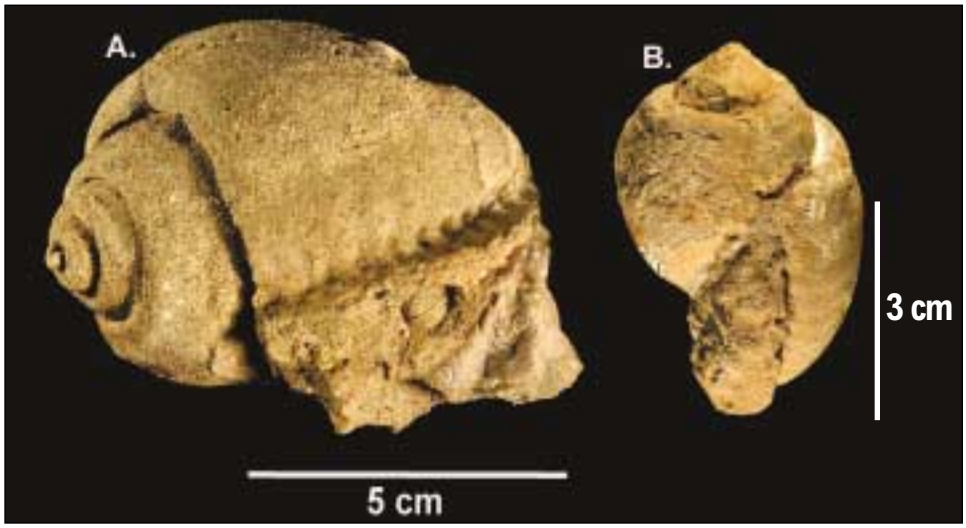


Figure 3.8
Malea ringens.
Steinkerns:
A. SDSNH 103648 and
B. SDSNH 12234.
(Photographs by Barbara Marrs)

Figure 3.9
Solenosteira sp.
Possibly a new species
(ABDSP 1326).
(Photograph by Barbara Marrs)

Turbinellidae (vase shells)

Fossil shells referable to this group of tropical neogastopods are rare from the sandstone strata of the Imperial Sea. They are represented by only a single species, *Vasum pufferi* (Figure 3.5F), characterized by its heavily built shell with broad nodous shoulder, thick spiral ridges, strong columellar folds, and flattened spire. This extinct species was originally named from the Latrania Formation as exposed in the Coyote Mountains. Specimens of this fossil species were formerly misidentified as *V. caestum* by Hanna (1926), an extant species living today in the Gulf of California and south to Ecuador. The fossil species, however, more closely resembles the living *V. muricatum* from the Caribbean Sea.

Buccinidae (whelks)

There are at least two species of buccinid snails found as fossils in the Deguynos Formation. Specimens typically are preserved with crystalline shell material intact. *Solenosteira anomala* is an extant species living along the Pacific coast of Baja California, throughout the Gulf of California south to Ecuador. This species has a coarse sculpture of axial ribs crossed by strong spiral chords, and grows to about 40 mm (1.6 in) in length. By contrast, the second species has a relatively smooth shell, with no distinct axial ribs, and evenly spaced spiral cords (small ridges). This species, which reaches 50 mm (2 in) in length, may represent a new and undescribed form (Figure 3.9).

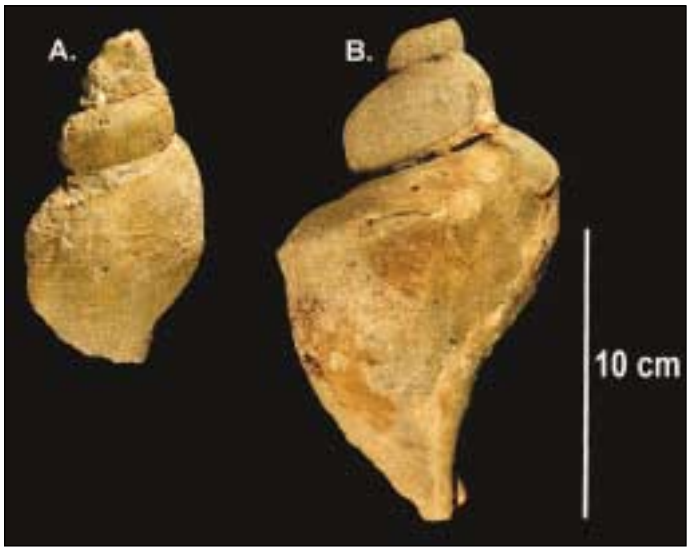


Figure 3.10
Pleuroploca princeps.
Steinkerns:
A. Smooth form
(SDSNH 12174) and
B. Shouldered form
(SDSNH 12183).
(Photographs by Barbara Marrs)

Melongenidae (crown conchs)

The only species from this family found as a fossil in the Imperial Group is *Melongena patula*. This very large species – fossils over 100 mm (4 in) in length are common – may be found living from the Gulf of California south to Panama. Because this species is so large and shaped much like a large conch with a wide, open aperture, fossils of *M. patula* are often mistaken for fossils of *Strombus galeatus*. By comparison, *M. patula* has a lower spire than *S. galeatus*, and has a row of knobs at the shoulder. In contrast *S. galeatus* has a continuous, very low-lying bulge at the shoulder.

Fasciolariidae (horse conchs and tulip shells)

Representative taxa of this family are characterized by a very long siphonal canal (narrow channel near aperture), particularly in *Pleuroploca* and *Fusinus*, the most common genera that occur in the Latrania Formation. *Pleuroploca princeps* (Figure 3.10A, B) is the largest fossil gastropod from the

Imperial Group; the large sandstone steinkerns can be up to 162 mm (6.4 in) long and 60-90 mm (2.4-3.5 in) in diameter. This species lives in the Gulf of California today and is closely related to the Caribbean species *P. gigantea.* Although several extant species of *Fusinus* are common in the Gulf of California today, only one is common as a fossil in the Latrania Formation, *F. dupetitthouarsii*. Internal sandstone molds of this species are usually missing most of the siphonal canal. Incomplete specimens can be 80 mm (3.2 in) in length or larger.

Olividae (olive shells)

A number of extant species of *Oliva* and *Olivella* are found as fossils in the Latrania Formation, usually with the crystalline shell present. *Oliva spicata* is the most common fossil olivid and is today found living in the Gulf of California south to Panama. Fossils of this species are often beautifully preserved and reach up to 42 mm (1.7 in) in length. Two other species, *O. porphyria,* living today from the Gulf of California to Panama, and *O. incrassata,* found today from the Gulf of California to Peru, are less common as fossils in the Imperial Group.

It might seem that identification of species of *Oliva* would be difficult, because as fossils they appear to be very similar. However, if shell material has been preserved, some characteristics may be very helpful in identifying the species. In *O. spicata* (Figure 3.5E) the spire is elevated and the sides of the shell are nearly parallel. The spire of *O. incrassata* is also elevated, but the outer aperture lip angles out from the top edge, and is greatly thickened. *Oliva porhyria* has a very low spire with only the very earliest part of the whorls elevated. The latter two species are larger than *O. spicata*. Fossils of *Olivella* have also been reported from the Imperial Group, but are uncommon. Compared to *Oliva* species, shells of *Olivella* are usually much smaller and have a more elevated spire.

Cancellariidae (nutmeg shells)

Characteristic features of shells of this family include strong folds on the collumella and ornate decoration on the outer surface, often with knobs on the shoulders and strong reticulate, net-like sculpture. *Cancellaria obesa* (Figure 3.5D) is a relatively large species common today from Magdelena Bay, Baja California Sur throughout the Gulf of California and south to Ecuador. This species is also locally common as a fossil in the Latrania Formation and is usually preserved with the crystalline shell intact. Individual fossils are up to 30 mm (1.2 in) in length, while living specimens may grow to be nearly 60 mm (2.4 in) in length. Many species of *Cancellaria* live in the Gulf of California, and in addition to *C. obesa,* several species may be found as fossils from the Imperial Group. Identification, however, may be difficult due to the close similarity of surface sculpture between some species.

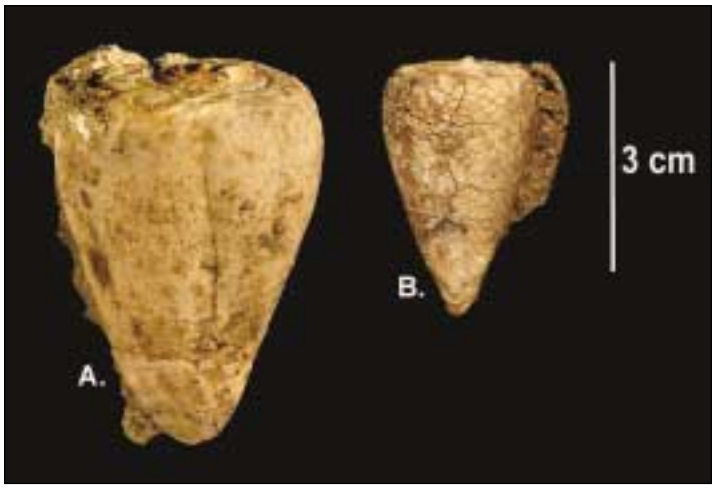


Figure 3.11
Extinct Cone Shell Species.
Preserved with crystalline shell and color patterns:
A. *Conus bramkampi* (SDSNH 23257), and
B. *Conus durhami* (SDSNH 103738).
(Photographs by Barbara Marrs)

Conidae (cone shells)

There are several species of fossil cones reported from the Latrania Formation, including extant and extinct forms. It is not uncommon to find specimens that are preserved with original crystalline shell material. However, this shell layer is fairly thin in relation to the underlying sandstone steinkern, and frequently, much of this fragile crystalline material breaks away. Specimens preserved only as steinkerns or with poorly preserved shell are extremely difficult to identify to species level because all cones have a superficially similar form. Therefore, the rare fossil specimens with all, or virtually all, shell material preserved are extremely important because they preserve such features as spire shape and surface sculpture, and even color patterns in some specimens.

The most common fossil species from the Latrania Formation are *Conus fergusoni*, and *C. regularis*, both still living today from the Gulf of California to Panama. These two species are very similar in form with elevated spires, so it is possible to misidentify one as the other. The less common *C. ximenes*, *C. arcuatus*, and *C. patricius* are also reported as fossils from the Imperial Group, however, these identifications need to be confirmed by detailed study. At least two extinct fossil cones have been named from the Latrania Formation. One is *C. bramkampi*, with a beautiful shell up to 53 mm (2.1 in) long and 35 mm (1.4 in) in diameter. This species is often preserved with a color pattern of small dark spots on a white shell. Unless the color pattern is present, this species could easily be confused with *C. fergusoni* or *C. regularis*. Another extinct fossil cone named from the Latrania Formation is *C. durhami*. This rare, low-spired fossil cone can be up to 50 mm (2 in) in length and specimens have been found preserved with a color pattern of white spots on a dark colored background.

Architectonicidae (sundial shells)

A rare, but beautifully ornamented fossil gastropod from the Latrania Formation, *Architectonica nobilis discus* (Figure 3.5A) represents an extinct subspecies of the living species, *A. nobilis*, which lives today from the Gulf of California south to Panama. This species also survives in the Gulf of Mexico. Fossil shells of this snail are generally preserved as original shell material and can measure up to 35 mm (1.4 in) in diameter. They are characterized by their very low, disk-like, flattened spire.

Bivalvia (oysters, scallops, and clams)

Most of the 60 or more species of bivalves known from the Imperial Group, are from the Latrania Formation. Like the gastropods, most of the

bivalves are species that lived in or on a sandy substrate. Only a few species lived attached to solid objects. Attached species include *Spondylus bostrychites*, *Arcinella californica*, and a few species of oysters (Family Ostreidae and Family Gryphaeidae). While these species might seem to indicate the presence of a rocky habitat, it is more likely that attaching forms settled on empty mollusk shells lying on the ancient sea floor.

Dendostrea vespertina and *Anomia subcostata* are the dominant species from the Deguynos Formation, occurring in strata of substantial thickness and incredible numbers of individuals. Other species, also characteristic of tropical estuaries are *Pinna* and *Atrina*, and the pholad *Cyrtopleura costata*. While *C. costata* is extinct in the Gulf of California today, it still exists along the Atlantic coast in estuaries from Massachusetts to Brazil.

Another fossil bivalve with an Atlantic coast relative is *Arcinella californica*, which is nearly identical to *A. arcinella*, a species common in the Caribbean Sea today. *Arcinella californica* also may be found living in the Gulf of California.

The discussions below focus on those bivalve families best represented by fossils in sedimentary rocks of the Imperial Group. Several families have been omitted from this listing because fossils attributed to them are either very rare or the original identifications are incorrect. These omitted families include Nuculidae, Nuculanidae, Glycymeridae, Limidae, Corbiculidae, Semelidae, Donacidae, Corbulidae, Carditidae, Cardiidae, and Myidae (see Appendix, Table 2).

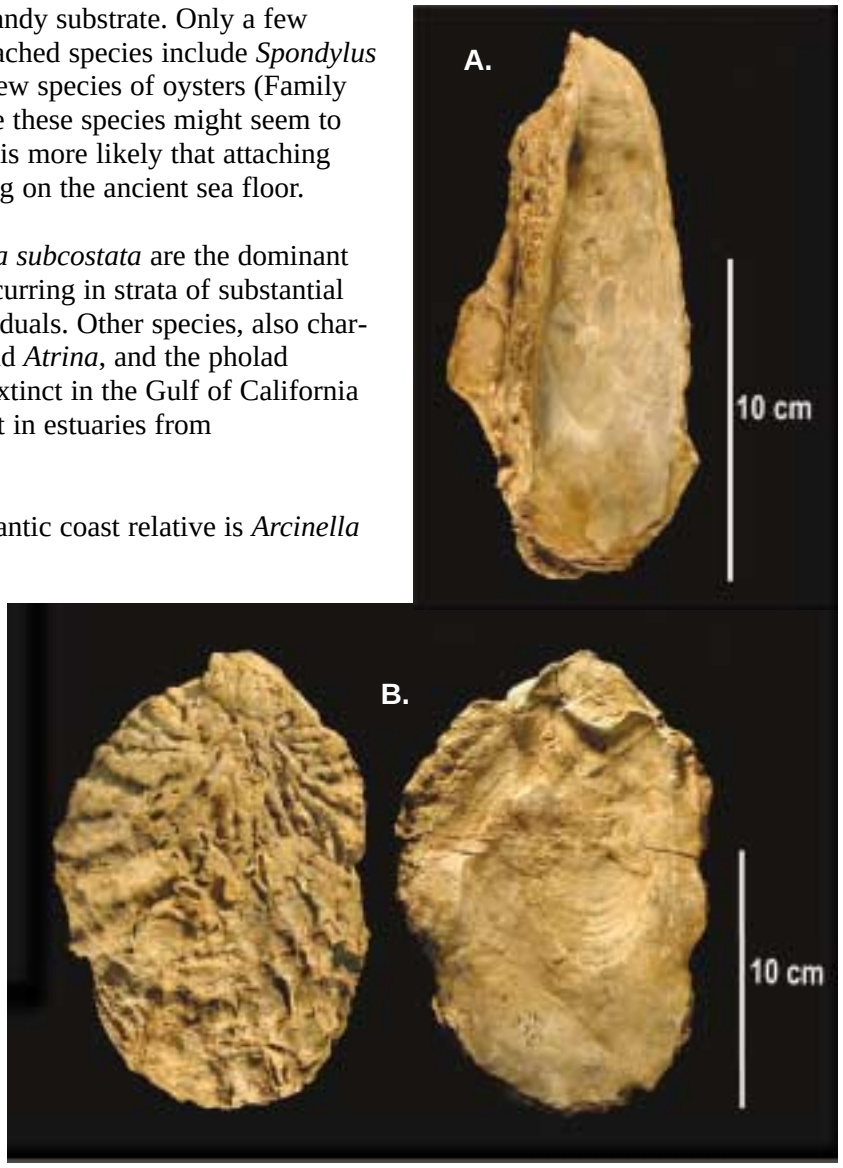


Figure 3.12
Fossil Oyster Species.
Both oyster species are preserved with original crystalline shell.
A. *Ostrea iradescens*, left valve (SDSNH 23101), and
B. *Pycnodonte heermani*, left valve and right valve of a pair (SDSNH 23331).
(Photographs by Barbara Marrs)

Arcidae (ark shells)

Ark shells identified as fossils from the Imperial Group include several species that still live today in the warm waters of the Gulf of California and south to Peru. *Arca pacifica* and *Barbatia reeveana* are intertidal species, while *Anadara formosa* (Figure 3.16C) is a subtidal species. *Anadara carrizoensis* Reinhart is an extinct species similar to *A. formosa*, but more closely resembling *A. secticostata* from the western Atlantic Ocean and Caribbean Sea. Sandstone steinkerns of these species are characterized by sharply angular hinge lines (top edge of valve where hinge teeth are located) and numerous tiny hinge teeth. *Arca pacifica* is an extant species from the Gulf of California similar to the extant *A. zebra* from Caribbean Sea. Fossil specimens from the Latrania Formation are large, measuring 52 mm (2 in) high by 72 mm (2.8 in) long.

Mytilidae (mussels)

Of the many species of mussels living in the Gulf of California, only one species, *Lithophaga* sp.cf. *L. plumula* has been reported as a fossil from the Imperial Group. This taxon is usually preserved as small (20-30 mm long, 0.8-1.2 in) cylindrical sandstone steinkerns embedded within fossil coral heads. The fossils occur in corals because in life *Lithophaga* bores into thick mollusc shells, corals, and/or rock. A species similar to *L.* sp. cf. *L. plumula* is *L. antillarum* from the Caribbean Sea.

Pinnidae (pen shells)

The largest bivalves known from the Imperial Group belong to the family Pinnidae. Shells of *Pinna latrania* measure up to 264 mm (10.4 in) in length and are typically found as large sandstone steinkerns of articulated valves (both valves still attached at the hinge). Often only the narrow apical portions (tip of hinge) (apical angle of 35º) of the original prismatic crystalline shell is preserved. These fossils are smaller than the extant *P. rugosa* which lives intertidally on protected mudflats from the Gulf of California south to Panama. A second species of extinct pinnid from the Imperial Group is *Atrina stephensi,* a smaller form with a broader apical angle (55º) first described from the mudstones of the Deguynos Formation. Fossil pinnids from the Latrania Formation typically occur as transported shells lying parallel to bedding, while specimens from the Deguynos Formation often occur in life position. A third species, *P.* (*P.*) *mendenhalli,* named from the Imperial Formation may be conspecific with *P. latrania.*

Ostreidae (true oysters)

One species of oyster is an exceedingly common fossil in the Imperial Group. *Dendostrea vespertina,* an extinct species originally named from exposures of this rock unit in Carrizo Creek, is a small oyster generally not exceeding 40 mm (1.6 in) in length. In the Deguynos Formation, *D. vespertina* is so abundant in some places it forms beds of solid shells 10-100 cm (3.9 in-3.3 ft) thick. Shells of this species may be recognized by the presence of a few widely spaced, distinct radial ribs. *Ostrea iridescens* (Figure 3.12A) is uncommon as a fossil but has been found in the Latrania Formation. Today it lives from La Paz, Baja California Sur, in the Gulf of California, to Peru. Living and fossil specimens on the average are 75-100 mm (3- 3.9 in) long. Fossils of this species are characterized by their long, narrow shells, many with a dark, metallic sheen inside the valves.

Gryphaeidae (pycnodont oysters)

Shells of gryphaeid oysters closely resemble the true oysters (Ostreidae) but tend to have upper and lower valves of equal size, whereas the true oysters generally have a flatter upper valve, and a more cupped lower valve. Also,

gryphaeids have a flat area on the hinges with a U-shaped furrow in the center on both valves. In ostreids, the hinge on the lower valve has a concave furrow, and the hinge on the upper valve has a convex form. The one representative of this family from the Imperial Group, *Pycnodonte heermani* (Figure 3.12B) is by far the most common large bivalve in both the Deguynos and Latrania formations. This large oyster – specimens can be 150 mm (6 in) long – is locally abundant at some outcrops of the Deguynos Formation (e.g. Yuha Buttes). The shell texture, similar on both upper and lower valves, is a beautiful branching pattern of heavy, scaly ribs. The valves are very thick and heavy, some as thick as 40 mm (1.6 in).

Pectinidae (scallops)

Species of scallops make up the most diverse group of bivalves from the Imperial Group. Although most represent extinct species, the fossil scallops can be assigned to genera still found in the Gulf of California today. Some shell beds in the lower part of the Latrania Formation are nearly monospecific (composed of a single species) containing abundant shells of *Euvola keepi* (Figure 3.13F). This extinct species was first described from the Latrania Formation and is similar to the living *E. ziczag* from the West Indies. Shells of *E. keepi* measure up to 80 mm (3.2 in) in height and are characterized by their inflated upper valve and flat lower valve. The radial ornamentation consists of broad flattened ribs. The large scallop *Lyropecten tiburonensis* is an extinct form originally described from Miocene rocks on Isla Tiburon in the Gulf of California. Earlier workers assigned this Imperial Group pectinid to either *L. modulatus* or *L. subnodosus.* Distinguishing features include its size (up to 100 mm in length and 90 mm in height) and 11-12 broad, flattened, radiating ribs with fine ridges in the interspaces. *Flabellipecten carrizonensis* is another common fossil scallop from the Latrania Formation and is recognized by its inflated right valve with 18-19 radial ribs and flat left valve with 16-17 ribs. In contrast, both valves of *Argopecten mendenhalli* (Figure 3.13E) are only slightly convex and possess 19-20 radiating ribs. The *Anomia-Ostrea* shell beds of the Deguynos Formation often contain shells of a small extinct scallop, *Argopecten deserti* (Figure 3.13A-D). Individual shells of this species measure

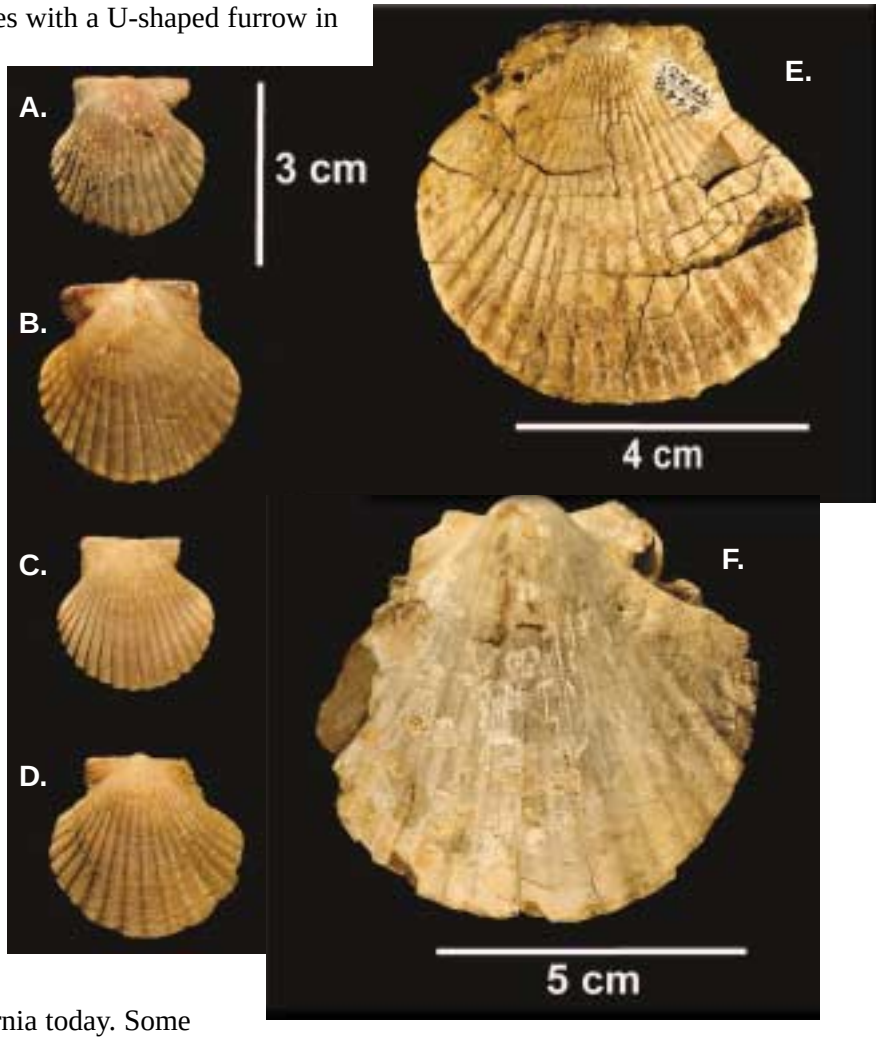


Figure 3.13
Various Scallop Species.
A.-D. Valves of *Argopecten deserti* (SDSNH 12003),
E. *Argopecten mendenhalli* pair of valves (SDSNH 97281), and
F. *Euvola keepi* pair of valves (SDSNH 12030).
(Photographs by Barbara Marrs)

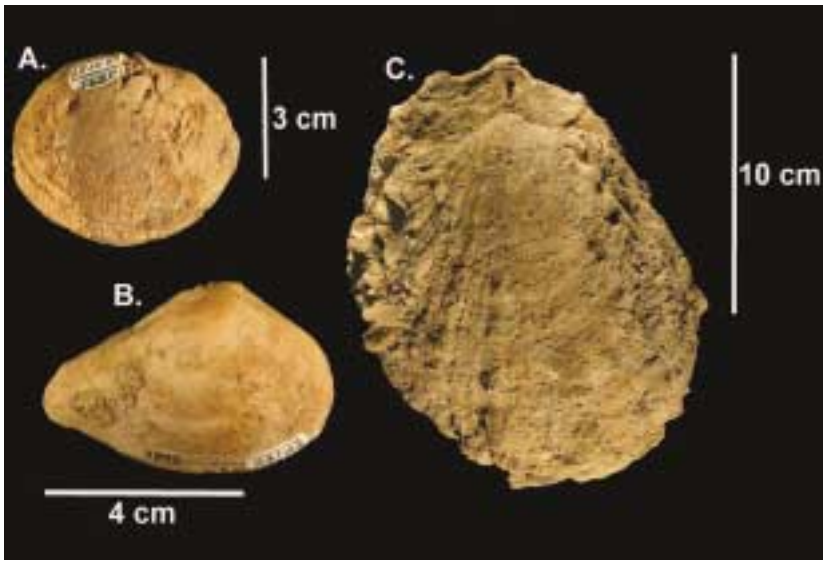


Figure 3.14
Paired Bivalves Preserved with Original Crystalline Shell.
A. *Codakia distinguenda* (SDSNH 12120),
B. *Eucrassatella subgibbosa* (SDSNH 23122), and
C. *Spondylus bostrychites* (SDSNH 23240).
(Photographs by Barbara Marrs)

only 30-40 mm (1.2-1.6 in) in height and are characterized by their equally inflated valves with 22-23 radiating ribs.

Plicatulidae (kitten's paw)

While a number of species of plicatulids exist today in the Gulf of California, only one species, *Plicatula inezana* occurs as a fossil in the Imperial Group. This species lives today from the southern Gulf of California to southern Mexico. The exterior sculpture of the valves, with numerous, scaly ribs, is remarkably similar to that of *Myrakeena angelica*, a medium-sized oyster (average length of 75 mm, 3 in) not known from the Imperial Group but extant in the Gulf of California, and is often misidentified as such. However, *P. inezana* has a very different "ball-and-socket" style hinge like that of the spondylid scallops. The size of the living species and fossils is up to 50 mm (2 in) in length.

Spondylidae (thorny oysters)

Probably one of the more unusual fossil bivalves from the Latrania Formation, *Spondylus bostrychites* (Figure 3.14C) represents an extinct species named from the Caribbean Sea. Well-preserved shells can measure up to 150 mm (6 in) in height and are often ornamented with large flattened spines. Occasionally, specimens are found with fossil acorn barnacles attached to the outer shell surface. The fossil species for the Latrania Formation is similar in size to *S. calcifer* Carpenter an extant species living from the Gulf of California south to Ecuador.

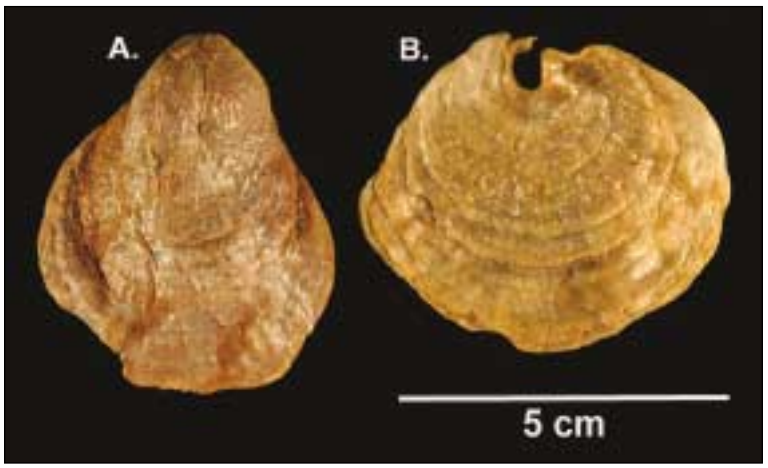


Figure 3.15
Anomia subcostata.
(SDSNH 97260)
A. Left valve, and
B. Right valve.
(Photographs by Barbara Marrs)

Anomiidae (jingle shells)

One member of this family, *Anomia subcostata* (Figure 3.15), is common in the Latrania and Deguynos formations. Shells of this extinct species can be up to 40 mm (1.6 in) in length. The upper valve is the one most commonly found. However, the lower (right) valve, with a hole near the hinge through which the attaching byssus apparatus (horny material secreted by a gland and used to attach bivalves to objects) passed, is much thicker than most modern and fossil relatives, so it is not unusual to also find fossils of whole right valves. The outer surface of the valves of these species is characterized by a series of fine radiating threads.

Although the color of most fossils is usually brownish, specimens may be found with an attractive iridescent red or orange-brown color.

Lucinidae (lucines)

A number of species of lucinids assigned to different genera occur as fossils in strata of the Imperial Group. All are still living today. The diversity of forms exhibited by shells of these species ranges from *Miltha xantusi*, a large and very flat lucinid that lives in the southern part of the Gulf of California, to the highly inflated *Pegophysema edentuloides* (Figure 3.16B) that lives from Cedros Island throughout the Gulf of California to Tenacatitia Bay, Jalisco, Mexico. *Miltha xantusi* may be found as sandstone steinkerns 70 mm (2.8 in) high by 80 mm (3.2 in) wide, occasionally as original shell with fine concentric lines. *Pegophysema edentuloides* is locally common in the Latrania Formation and typically occurs as paired valve sandstone steinkerns, 51 mm (2 in) high by 47 mm (1.88 in) wide. *Pegophysema schrammi* is a closely related Caribbean species. *Codakia distinguenda* (Figure 3.14A) is another warm water lucinid from the Latrania Formation. Fossils of this species typically occur as beautiful flattened circular shells with a reticulate sculpture of fine radial lines crossed by concentric ridges. This species lives today from Magdalena Bay, Baja California Sur south to Panama. Fossil specimens with preserved shell may be up to 60 mm (2.4 in) in diameter. *Divulinga eburnea* is a small lucinid (25 mm in diameter, 1 in) found in the sandstone strata of the Latrania Formation. Fossil specimens are usually preserved with original shell material and are ornamented with a series of fine, chevron-shaped ridges on the outer valve surface. *Divulinga quadrisulcata* is a closely related Caribbean species.

Crassatellidae (crassatellas)

Three species of crassatellids are found as fossils in the Imperial Group, *Eucrassatella digueti, E. subgibbosa* (Figure 3.14B), and *Crassinella mexicana.* Fossils are preserved either as steinkerns or as specimens with the crystalline shell material intact. The most common species, *E. digueti* and *E. subgibbosa* are about the same size, up to 60 mm (2.4 in) in length. *Eucrassatella subgibbosa* is an extinct species named from the Latrania Formation exposed in the Coyote Mountains (similar to the extant *E. gibbosa*). This species has a distinct siphonal beak (posterior edge of shell extended to accommodate the incurrent and excurrent siphons). *Eucrassatella digueti* is an extant species now living from the Gulf of California to Colombia, usually dredged from depths of 13-64 mm (0.5-2.5 in). Shells of this species are relatively flat, whereas *E. subgibbosa* has a fairly well inflated shell.

Chamidae (jewel boxes)

Of the several species of *Chama* and *Pseudochama* living in the Gulf of California today, any could have been preserved as fossils in the Imperial Group. However, unless the spines characteristic of these genera were somehow preserved, identification to species would be virtually impossible. One species

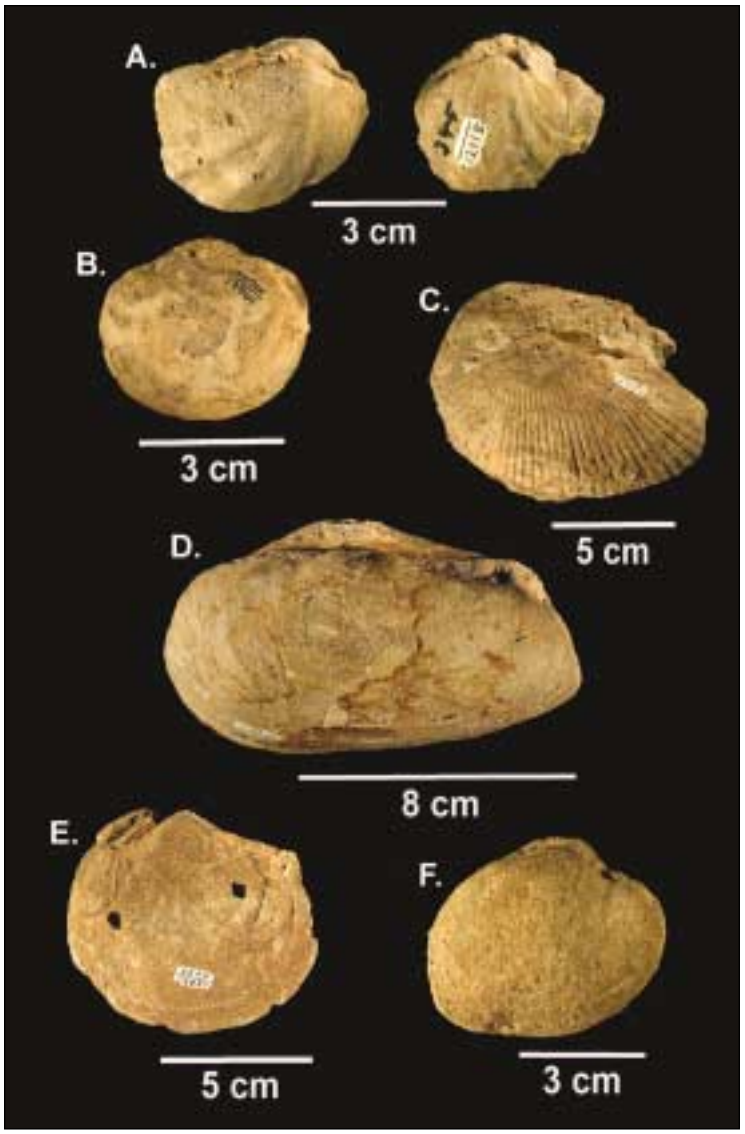


Figure 3.16
Bivalve Species Preserved as Steinkern Pairs.
A. *Arcinella californica* (SDSNH 12115),
B. *Pegophysema edentuloides* (SDSNH 17701),
C. *Anadara formosa* (SDSNH 12026),
D. *Panopea abrupta* (SDSNH 12101),
E. *Dosinia ponderosa* (SDSNH 53797), and
F. *Megapitaria* sp. (SDSNH 23150).
(Photographs by Barbara Marrs)

however, *Arcinella californica* (Figure 3.16A) may be recognized by the unusual paired steinkern, triangular in shape, with a few strong radiating ribs. This oddly shaped fossil does not resemble at all the beautiful, spiny shell from which it was formed. Living specimens, found from Cedros Island, Baja California to Panama, and fossils from the Latrania Formation, are uncommon. This species very closely resembles *A. arcinella,* a species common in the Caribbean today.

Veneridae (Venus clams)

The Venus clams represent the most diverse living bivalve family, with over 400 living species worldwide, many of these in the Gulf of California. Several venerid species have been reported as fossils in the Imperial Group. An unidentified species of *Megapitaria* is often found as sandstone steinkerns of articulated valves measuring up to 50 mm (2 in) in length. Two species (*M. squalida* and *M. aurantica*) occur today from the Gulf of California to northern South America. Living specimens of both species grow to a length of a little more than 100 mm (3.9 in) and are very similar in appearance with smooth, compressed, and oval shells. This similarity in general form makes steinkerns of *Megapitaria* difficult to identify. The same can be said for sandstone steinkerns of another venerid identified as either *Dosinia ponderosa* (Figure 3.16E) or *D. dunkeri.* Both species have nearly circular shells and live today in the Gulf of California and south to Peru. Steinkern fossils of *Dosinia* from the Latrania Formation are generally under 100 mm (3.9 in) in length.

The most massive venerid fossil found in the Latrania Formation is referred to the extant species, *Periglypta multicostata.* Usually, these fossils are found with the original crystalline shell material intact. Living specimens grow up to 118 mm (4.7 in) in height and have a thick, well-inflated shell. This species lives from the Gulf of California to Peru. Another species of venerid reported from the Latrania Formation is *Ventricolaria isocardia,* which lives today from the Gulf of California to Colombia. Fossils of this species generally preserve original shell material and are characterized by their strong concentric growth lines on distinctly inflated valves. Fossils can be rather large and often attain the same size as the living species, which can grow to a length of 87 mm (3.4 in), a height of 81 mm (3.2 in), and a diameter of 64 mm (2.5 in). The

extant Caribbean species *V. rigida* is very similar in appearance to fossils recovered from the Latrania Formation.

Tellinidae (tellins)

This family of thin-shelled bivalves includes the genera *Tellina, Macoma,* and *Florimetis,* with many more species in the first two genera. Fossil tellinids are almost always preserved as steinkerns, generally as an articulated pair of valves. A very high diversity of tellinids exists in the Gulf of California today, as in other tropical areas of the world. However, few species are known from the Imperial Group. This is largely due to the difficulty in distinguishing between the steinkerns of different species of tellinids. It can even be difficult to determine if a specimen belongs to the genus *Macoma* or *Tellina.*

One tellin from the Latrania Formation is *Tellina lyra*, a small species represented by fossils up to 40 mm (1.6 in) in length. Today it is found from Baja California, Mexico to Tumbes, northern Peru. Internal sandstone molds of this tellin may be recognized by the neat, oval shape and the evenly spaced, sharply defined growth lines pressed onto the specimen from the external mold. Other species reported from the Imperial Group include *T. ulloana*, an extant species living from Magdalena Bay, Baja California Sur, south to Panama (*T. martinicensis* is a closely related Atlantic species), *T. ochracea*, an extant species living throughout the Gulf of California (*T. laevigata* is a closely related Atlantic species), and *Florimetis dombei*, an extant species living from Panama to Peru.

Solecurtidae (tagelus clams)

A number of very similar species from this family occur in the Gulf of California today, and precise identification of steinkern fossils may not always be possible. Specimens identified as *Tagelus californianus*, an extant species living along the coast of southern California, throughout the Gulf of California, and south to Panama, are known. These long and narrow steinkerns measure from 30-50 mm (1.2-2 in).

Hiatellidae (geoducks)

The one representative of this family that may be found as sandstone internal molds in the Latrania Formation is *Panopea abrupta* (Figure 3.16D). These steinkerns usually represent articulated valves, with the characteristic gaping of the posterior and anterior ends visible. The fossils are up to about 130 mm (5 in) in length, which is smaller than the living species, which grows to a length of 160 mm (6.3 in). Today it lives from Alaska to the Gulf of California.

Pholadidae (rock piddocks)

The one example of this family known as a fossil from the Imperial Group is *Cyrtopleura costata.* It is found today living along the western Atlantic

from Massachusetts south to Brazil, but is extinct in the Gulf of California. Local extinctions (extirpation) like this also characterize many Imperial Group corals. Fossils of this thin-shelled species are more common in the Deguynos Formation where they occur as sandstone internal molds. Specimens may be up to 60 mm (2.4 in) in length. An extant relative living in the Gulf of California today is *C. crucigera.* This species is rare throughout its range from Guaymas, Sonora, Mexico to Ecuador. The living species of *Cyrtopleura* may be found burrowing in silty mud.

Thraciidae (thracias)

This family typically includes species of very thin-shelled clams that generally live offshore. *Cyathodonta undulata* is the only thraciid reported from the Latrania Formation and usually is found as sandstone steinkerns. *Cyathodonta undulata* lives today from Sonora, Mexico, to Peru in water depths of 3-110 m (10-215 ft). The squarish, paired steinkerns can be up to 50 mm (2 in) long and are characterized by undulating, low-lying concentric ribs.

Echinodermata (sand dollars, sea biscuits, urchins, and sea stars)

Although not as diverse as the fossil molluscs, the echinoderm assemblage from the Latrania Formation is none-the-less a conspicuous element of most fossil collections from this rock unit (Kew, 1914) (see Appendix, Table 2). Specimens represent members of all three main echinoderm groups including sea stars, sea urchins, and brittle stars. Fossils are typically preserved with their original crystalline tests intact and many specimens retain even the most delicate structures of the ambulacral petals (specialized zones of pores that support respiratory tube feet) on their aboral or upper surfaces. Sand dollars and heart urchins possess a characteristic five-pointed petal system on their aboral surfaces, while their oral surfaces have a more-or-less centrally placed mouth (peristome) and a marginal, posteriorly placed anus (periproct). In sea urchins the peristome is on the oral surface of the roughly spherical test, while the periproct is centrally placed on the aboral surface. The test is constructed from ten columns of plates on which are located the tubercles (tiny circular structures on test) to which the spines attach. Heart urchins (spatangoids) are also constructed of ten columns of plates, but have a bilaterally symmetrical, generally oval test with sunken ambulacral petals.

In his review of the Imperial Group echinoderms, Powell (1995) noted that the echinoderm assemblage primarily consists of subtropical to tropical taxa, many with affinities to species living today in the Caribbean Sea.

The discussions below focus on those echinoid families best represented by fossils in sedimentary rocks of the Imperial Group. Brittle stars have been omitted from this listing because they are very rare, and have not been studied.

Asteroidea (sea stars)

Astropectinidae (sand stars)

The general absence of hardparts makes it unlikely that sea stars will be preserved in the fossil record. However, fragmentary specimens of a robust sea star have been collected from the Latrania Formation. These specimens consist of portions of “arms” preserved with the relatively thick crystalline plates intact and have been referred to the genus *Astropecten* by Powell (1995).

Echinoidea (sea urchins and sand dollars)

Cidaridae (club-spined urchins)

Fragmentary remains (spines and partial test plates) of a regular (i.e., symmetrical) urchin tentatively referred to *Eucidaris thouarsii* have been reported from the Imperial Group (Latrania Formation) as exposed in the Coyote Mountains. Fossil specimens preserve the characteristic large tubercles of this urchin. This species lives today in the eastern Pacific Ocean from southern California south to Panama and Islas Galapagos.

Arbaciidae (regular urchins)

Small tests of a regular sea urchin similar to the living purple urchin, *Arbacia* sp., have been collected from the Latrania Formation as exposed in the Coyote Mountains. These fossils have not yet been described and may represent a new fossil species (Powell, 1995). Today, species of *Arbacia* live from southern California to Peru.

Toxopneustidae (white urchins)

Tripneustes californicus (Figure 3.18C) is an extinct species of regular sea urchin originally named from the Latrania Formation. Typical specimens measure 85 mm (3.4 in) in diameter and have fewer tubercles and a more distinctly conical shape than the extant *T. depressus* from the Gulf of California and tropical eastern Pacific Ocean. The fossil species has tiny tubercles and resembles *T. esculentus* from the Caribbean Sea. These three species may represent a closely related group.

Powell (1995) reported fragmentary specimens of a second member of this urchin family from Imperial Group deposits in the Coyote Mountains. These specimens are tentatively referred to *Toxopneustes* sp. cf. *T. roseus,* a species living today from Guaymas, Mexico, south to Isla La Plata, Ecuador.

Clypeasteridae (sea biscuits)

Clypeaster bowersi (Figure 3.17A) is a large extinct species of sea biscuit originally described from exposures of the Latrania Formation in the Coyote

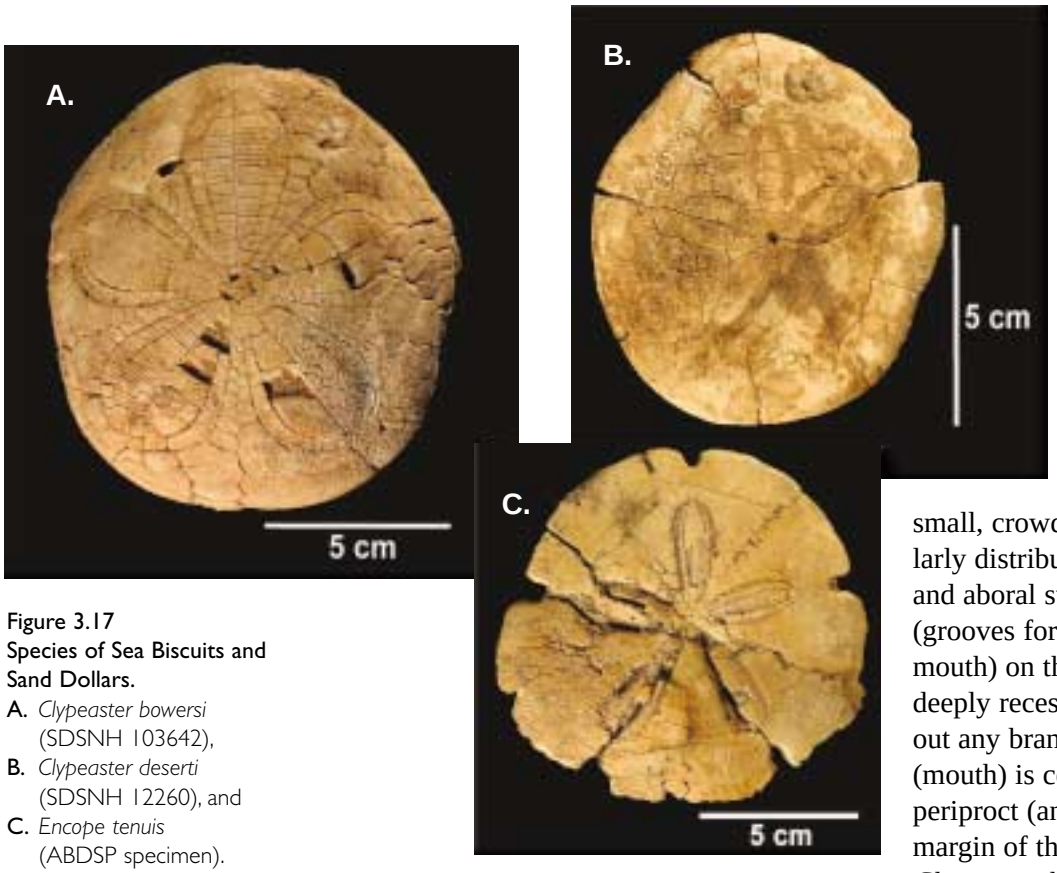


Figure 3.17
Species of Sea Biscuits and Sand Dollars.
A. *Clypeaster bowersi* (SDSNH 103642),
B. *Clypeaster deserti* (SDSNH 12260), and
C. *Encope tenuis* (ABDSP specimen).
(Photographs by Barbara Marrs)

Mountains. Large specimens measure 135-145 mm (5.3-5.7 in) in length, 120 mm (4.7 in) in width, and up to 50 mm (2 in) in height. The general outline is suboval to slightly pentagonal. On the aboral (upper) surface, the ambulacral petals are broad and ovate and not elevated. Tubercles are small, crowded together, and irregularly distributed over both the oral and aboral surfaces. Food grooves (grooves for transport of food to the mouth) on the oral surface are deeply recessed and straight, without any branching. The peristome (mouth) is centrally located and the periproct (anus) is on the posterior margin of the oral surface. *Clypeaster bowersi* resembles *C. caudatus* from Miocene rocks in the Dominican Republic and is also similar to *C. pallidus*, a recent species from Barbados Island.

Clypeaster carrizoensis is a rare small fossil species originally named from the Latrania Formation as exposed in the Coyote Mountains. Typical specimens have a flattened oval outline and measure only 24 mm (1 in) in length, 21 mm (.8 in) in width, and 7 mm (0.3 in) in height. The ambulacral petals are open at their lateral ends. Tubercles are small and of uniform size. *Clypeaster carrizoensis* is similar to *C. cotteaui* from the Miocene of Jamaica. The fossil species also resembles *C. subdepressus* a living clypeasterid from the Caribbean Sea.

Clypeaster deserti (Figure 3.17B) is another extinct species of sea biscuit originally named from sandstones of the Latrania Formation. The general outline is distinctly pentagonal with an elevated central region at the ambulacral apex. Larger specimens measure 93 mm (3.7 in) in length, 81 mm (3.2 in) in width, and 15 mm (0.6 in) in height at the center. The height of the margin is only 8 mm (0.3 in). Food grooves on the oral surface are recessed and straight, without any branching. The peristome is more strongly recessed. *Clypeaster deserti* is similar in size to the extant *C. rotundus* from the modern Gulf of California.

Mellitidae (key-hole sand dollars)

Encope tenuis (Figure 3.17C) is a large extinct sand dollar originally named from the Latrania Formation as exposed in the Coyote Mountains. Large individuals measure up to 110 mm (4.3 in) in diameter, but only 8-11 mm (0.3-0.4 in) in height. Many specimens are slightly wider than long. Distinctive features include 5 marginal notches each aligned with one of the delicate narrow abulacral petals. The notches tend to close in older individuals. A distinct oval lunule (opening) occurs between the posterior two petals. The food grooves on the oral surface have an elaborate branching pattern radiating from the centrally placed peristome (mouth). The oval periproct (anus) is located between the peristome and the lunule. Tests of *E. tenuis* are locally common to abundant in certain strata within the Latrania Formation and their well-preserved test fragments often litter the ground. Some workers have identified other species of *Encope* from the Latrania Formation (*E. sverdupi* and *E. arcensis*), however, the amount of morphological variation observed in large samples of *Encope* tests collected from a single locality suggests only a single highly morphologically variable species. *E. tenuis* is the oldest valid name applied to this group.

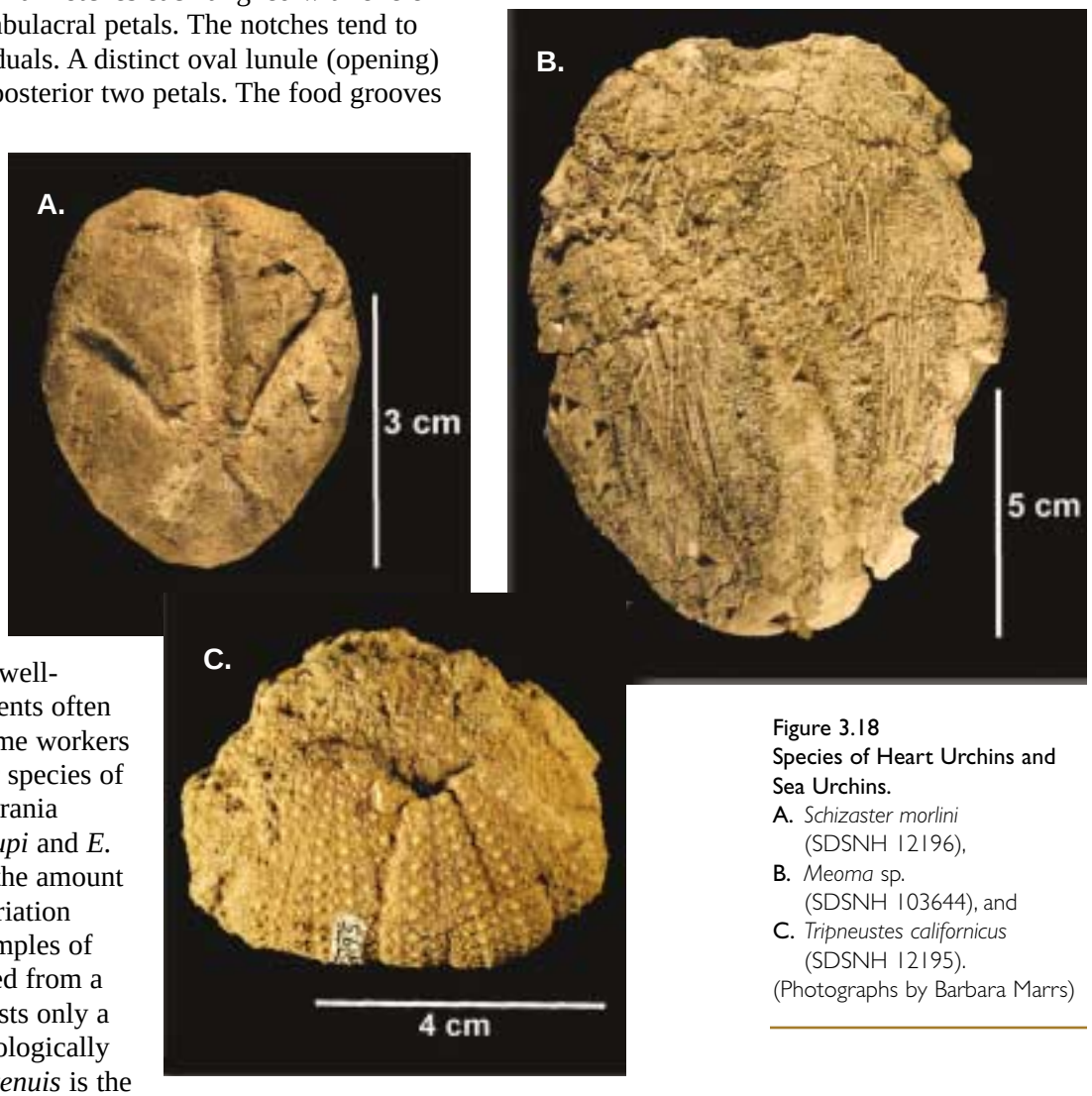


Figure 3.18
Species of Heart Urchins and Sea Urchins.
A. *Schizaster morlini* (SDSNH 12196),
B. *Meoma* sp. (SDSNH 103644), and
C. *Tripneustes californicus* (SDSNH 12195).
(Photographs by Barbara Marrs)

Echinoneidae (irregular heart urchin)

Echinoneus burgeri is an extinct species of irregular echinoid originally named from rocks of the Latrania Formation exposed in the Coyote Mountains. The test of this rare urchin is walnut-sized, measuring 40-50 mm (1.6-2 in) in length, 30-40 mm (1.2-1.6 in) in width, and 20-30 mm (0.8-1.2 in) in height.

The test outline is oval with delicate and elongated ambulacral petals on the aboral surface. The oral surface is characterized by a horizontal grouping of tubercles and a very large oval periproct placed relatively close to the peristome. Species of *Echinoneus* are common today in the Atlantic Ocean and Caribbean Sea, as well as in the Indo-Pacific. Its absence from the eastern tropical Pacific Ocean suggests that this genus has been extirpated from the region.

Schizasteridae (puffball heart urchins)

Schizaster morlini (Figure 3.18A) is an extinct species of heart urchin originally named from specimens collected from the Latrania Formation exposed in the Coyote Mountains. Specimens measure 42-55 mm (1.7-2.2 in) in length, 35-49 mm (1.4-2 in) in width, and 24-29 mm (1-1.1 in) in height. The ambulacral petals are sharply depressed into the aboral surface and consist of a posterior pair of short petals, an anterolateral pair of longer petals, and a single, centrally placed, elongate anterior petal. The large oval periproct occurs high on the posterior margin of the test.

Brissidae (heart urchins)

Powell (1995) reports three species of brissids from the Latrania Formation. These include poorly preserved specimens referable to *Brissus* sp., *Metalia spatagus*, and *Meoma* sp. (Figure 3.18B). Species of all three genera still live in the Gulf of California and range south to at least Panama. One fossil specimen of *Meoma* sp. measures 120 mm (4.7 in) in length and 95 mm (3.7 in) in width. This specimen preserves delicate aboral spines measuring over 25 mm (1 in) in length.

Loveniidae (porcupine heart urchins)

Specimens of a gracefully heart-shaped urchin found in the Imperial Group of the Coyote Mountains have been tentatively identified as *Lovenia* sp. cf. *L. hemphilli*. This extinct species is similar to living *L. cordiformis* from the temperate and subtropical eastern Pacific Ocean. The fossil taxon is also similar to *L. dumblei* from the Miocene of northeastern Mexico.

Conclusions

Maine invertebrate fossils from the Latrania and Deguynos formations are locally abundant in the Imperial Valley (e.g., Loop Wash, Shell Reef, East Mesa, Fossil Canyon, Painted Gorge, and Yuha Buttes) and, consequently, are the only fossils that most people directly observe and enjoy in this region. As discussed in this chapter, the fossils provide critical evidence for understanding the evolutionary, biogeographic, ecological, and environmental history of the Imperial Sea. From an evolutionary perspective the Imperial fossils show a general pattern of extinct species mixed with extant species. Nearly 100% of the

corals represent extinct species, while approximately 20% of the gastropods, 25% of the bivalves, and almost 50% of the echinoderms are extinct. A careful study of this pattern eventually may lead to a clearer understanding of the timing of particular speciation and extinction events for these groups.

The discovery of both western Caribbean and tropical eastern Pacific species in the Imperial fossil beds suggests a former biotic interchange between the two biogeographic regions and serves as evidence that the modern separation of these two regions only occurred within the past three to five million years. Some 15-20% of the species (or closely related species) survive today in the Caribbean, while 60-70% still live in the tropical eastern Pacific. It is noteworthy that an inverse relationship of interchange, termed complementarity, often exists between terrestrial and marine environments and their biotas. A classic case of complementarity occurred during formation of the Isthmus of Panama in the mid-Pliocene. Elevation of the isthmus created a corridor for terrestrial interchange between North and South America (see McDonald, this volume, *The Great American Biotic Interchange*), but it also created a barrier to marine interchange between the tropical Pacific Ocean and the Caribbean Sea.

Fossil molluscs from the Latrania Formation comprise species that played a variety of ecological roles including epifaunal (living on or above sea floor) predatory snails (e.g., *Conus* spp., *Malea ringens,* and *Natica* spp.), epifaunal grazing snails (e.g. *Nerita scabricosta, Strombus* spp., *Macrocypraea* sp., and *Plueroploca princeps*), infaunal (living within sediments of sea floor) suspension feeding bivalves (e.g. *Miltha xantusi, Divulinga eburnea, Eucrassatella* spp., and *Megapitaria* spp.), and attached epifaunal suspension-feeding bivalves (*Dendostrea vespertina, Pycnodonte heermani, Spondylus* spp., *Anomia subcostata*, and *Arcinella californica*). The species diversity in the Deguynos Formation is much lower, as is the complexity of paleoecological communities.

Although approximately 3% of the Imperial species live today in temperate waters along the California coast and another 15% live in subtropical waters off Baja California Sur, the majority of species (60%) survive today in the tropical Panamic region of the eastern Pacific between 25º north latitude and 5º south latitude (including the Gulf of California). The warm, tropical Imperial fossil assemblages clearly define a dichotomy between clear water, shallow marine paleoenvironments preserved in the Miocene-age Latrania Formation and turbid water, marine-dominated deltaic paleoenvironments preserved in the Plicene-age Deguynos Formation. This transition correlates with the initial growth of the Colorado River delta during the early Pliocene. The buildup of this huge sediment dam eventually lead to the southward regression of the Imperial shoreline and the development of the Salton Trough, at over 5000 square kilometers (2000 square miles) the largest below-sea-level dry basin in the Western hemisphere. The fossil biotas of the various terrestrial and freshwater habitats that existed in this basin from the later Pliocene through the Pleistocene are discussed in subsequent chapters of this book.