

REVISION OF LATE CENOZOIC *HYOTISSA* (BIVALVIA: PYCNODONTEINAE) FROM WESTERN NORTH AMERICA

ALEJANDRO CRISTÍN

Posgrado en Ciencias de la Tierra, Instituto de Geología, Universidad Nacional Autónoma de México, México D.F.
alcris@unam.mx

MARÍA DEL CARMEN PERRILLIAT

Departamento de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, México D.F.
mariacp@geologia.unam.mx

ABSTRACT – Some Neogene *Pycnodonte* species, related to the ancient Gulf of California and coastal California, are morphologically similar to *Hyotissa hyotis* (Linnaeus), the living honeycomb oyster. Morphological variation in these species or in *H. hyotis* has never been studied. In order to document variation and use the results to detect a possible taxonomic oversplitting, the present authors described the morphology and morphometry of fossil shells of *H. hyotis* from the early Pleistocene Loreto Basin, Baja California Sur, Mexico. It was compared with type and non-type specimens from the Early Miocene Vaqueros sandstone (coastal California), Late Miocene rocks of Isla Tiburón (Gulf of California), Pliocene Imperial Formation (southern California) and Pleistocene rocks in Loreto area (Gulf of California). The specimens from coastal California and Isla Tiburón were re-assigned to a new genus, and to *Hyotissa* cf. *H. hyotis*; and synonymized *P. (Pycnodonte) heermanni* (Conrad) from southern California with *H. hyotis*. With this new information, the fossil record of *Hyotissa* in western America ranges from Early Miocene to Recent; *H. hyotis* lived through the whole ancient Gulf of California during the Pliocene, contrary to the current distribution in the modern gulf. Finally, *Hyotissa* species exhibit a little variable morphology, which is contrary to traditional views, complicating Pycnodontinae taxonomy and classification.

Key words: *Hyotissa*, *Pycnodonte*, Gulf of California, morphometry, Neogene.

RESUMO – Algumas espécies de *Pycnodonte* do Neógeno, relacionadas ao antigo Golfo da Califórnia e Costa da Califórnia, são morfológicamente semelhantes à *Hyotissa hyotis* (Linnaeus), a atual ostra da rocha. A variação morfológica nas espécies de *Pycnodonte* ou em *H. hyotis* nunca foi estudada. Para documentar a variação e usar os resultados para detectar uma possível *oversplitting* taxonômica, foram descritas a morfologia e morfometria de conchas fósseis de *H. hyotis* do Pleistoceno inferior da bacia Loreto, Baja California Sul, no México. Foram comparados com os espécimes tipo e não-tipo do arenito Vaqueros do Mioceno Inferior (costa da Califórnia), Mioceno Superior da Isla Tiburón (Golfo da Califórnia), Plioceno da Formação Imperial (sul da Califórnia) e Pleistoceno das Ilhas Carmen e Coronados (Golfo da Califórnia). Os espécimes da Costa da Califórnia e Ilha Tiburón foram reassignados a um novo gênero e *Hyotissa* cf. *H. hyotis*, sendo sinonimizado *Pycnodonte (Pycnodonte) heermanni* (Conrad) do sul da Califórnia com *H. hyotis*. Com esta nova informação, o registro fóssil de *Hyotissa* na América ocidental vai do Mioceno Inferior ao Recente; *H. hyotis* viveu por toda o antigo Golfo da Califórnia durante o Plioceno, ao contrário da atual distribuição no Golfo moderno. Finalmente, as espécies de *Hyotissa* exibem uma morfologia pouco variável, contrário à visão tradicional, complicando a taxonomia e classificação de Pycnodontinae.

Palavras-chave: *Hyotissa*, *Pycnodonte*, Golfo da Califórnia, morfometria, Neógeno.

INTRODUCTION

The Gulf of California is a young, deep marine basin formed by the tectonic interaction of the Pacific and North American plates. The Early Pleistocene Loreto Basin in Baja California Sur, Mexico (Figure 1) has been a significant area for understanding the geological evolution of the gulf (Umhoefer *et al.* 1994; Zanchi, 1994; Dorsey & Umhoefer, 2000).

Loreto Basin is rich in marine fossils, and although there are some important paleontological studies (*e.g.* Stump, 1979; Smith, 1991; Piazza & Robba, 1994; 1998), there is still an

important gap in the paleontological knowledge. During an ongoing systematic and stratigraphic research, specimens were collected from several beds with abundant Pycnodontinae oysters. On the basis of present accepted taxonomy (Moore, 1987), several specimens fit well as members of *Hyotissa hyotis* (Linnaeus, 1758), and ambiguously as members of some *Pycnodonte* species.

Hyotissa is a genus of both fossil and living oysters, usually characterized by a sub-circular, strongly folded, and heavy shell. *Parahyotissa* differs from *Hyotissa* by the smaller size and the wholly cemented, flat left valve (Harry,

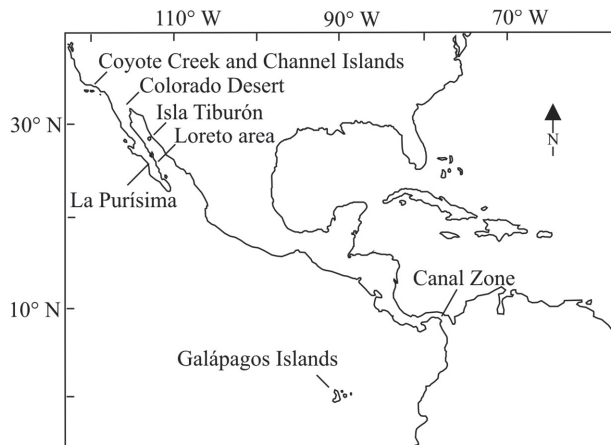


Figure 1. Fossil record of *Hyotissa* in Western America. Loreto area includes the Carmen and Coronados islands. For more information see the text.

1985). In spite of this some authors synonymized both genera (Kinkerdale *et al.* 2004; Coan & Valentich-Scott, 2012).

Currently, *Hyotissa* (including *Parahyotissa*) is widely distributed, from tropical to subtropical western Atlantic, Indo-Pacific and Eastern Pacific oceans (Harry, 1985; Coan & Valentich-Scott, 2012). In eastern America, the fossil record of *Hyotissa* ranges from Oligocene to Recent. In western America, it ranges from Miocene to Pleistocene (Keen, 1971; Moore, 1987; Gastil *et al.* 1999). On the other hand, *Pycnodonte* is an extinct genus, characterized by an inequivalve, circular to oval heavy shell. It was a diverse genus; the Cenozoic fossil record ranges from Eocene to Pleistocene in both eastern and western North America (Stenzel, 1971; Moore, 1987; Squires & Demetron, 1990).

Although typical shells of *Pycnodonte* are clearly dissimilar from *Hyotissa* ones, some fossil species described from southern California, such as *Pycnodonte* (*Pycnodonte*) *heermanni* (Conrad, 1855), *P. (P.) loeli* (Hertlein, 1928), *P. (P.) wiedeyi* (Hertlein, 1928), among others, are similar to genus *Hyotissa*. Their inclusion in the *Pycnodonte* genus was proposed by Moore (1987), but she emphasized the uncertainties that still remained. Nowadays, the classification of these species remains controversial.

Furthermore, many authors pointed out that these species are highly variable (Hanna, 1926; Hertlein, 1928; Loel & Corey, 1932; Squires & Fritsche, 1978; Moore, 1987), but the knowledge of this variation has not been carefully studied or documented. Similarly, variation has not been studied in the *Hyotissa* genus, except by Dodge (1952) and Stenzel (1971), who emphasized its wide variation on the shell shape and sculpture.

The wide morphological variation in oysters is mainly caused by their life habit and growing conditions. During life, oysters are cemented to hard substrates, modifying their original morphology (idiomorphism) by mirroring the substrate relief in both, left and right valves (xenomorphism) (Stenzel, 1971). Additionally, individuals can grow attached to each other, forming shell banks. Under these conditions,

individuals modify their shell shape when restricted space is available for growing (Stenzel, 1971).

Because the specimens from Loreto Basin show similarity with *Hyotissa* and *Pycnodonte* species, studying their variability is of interest in order to reveal whether the respective specimens actually belong to different taxa or represent only variants of one or a few species. The goals of the present paper are to document morphologic and morphometric variability of fossil *Hyotissa* from Loreto Basin, and apply the results for taxonomic comparison between specimens from different sites and ages, in order to detect taxonomic oversplitting.

GEOLOGICAL OVERVIEW

The early Pleistocene Loreto Basin was a syntectonic shallow marine depression located in the western margin of the Baja California peninsula, at 26°08'N. The basin formation and evolution was related to the tectonic regime (trans-tension) that has controlled the current expansion of the Gulf of California (Umhoefer *et al.*, 1994; Zanchi, 1994). The basin has been a very significant site to understand regional deformation. Based on the stratigraphic and structural features, for example, the starting point of the trans-tension was estimated at ~3.4 Ma (Umhoefer *et al.*, 1994, Zanchi, 1994). Tectonic deformation determined distribution of depositional settings in the basin. In the beginning, the basin was filled by non-marine deposits. Then, faulting, subsidence, and uplifting transformed the area; dividing it in two marine sub-basins, named Central and Southeast sub-basins (**CSB**, **SESB**) (Dorsey *et al.*, 1997; Dorsey & Umhoefer, 2000). The CSB was the larger and deeper (~40 m), semi-enclosed sub-basin, where the subsidence controlled deposition. In contrast, the SESB was an open sub-basin, with a depth of ~10 m, exposed to more energetic current regime. In the SESB, the eustatic changes controlled deposition (Piazza & Robba, 1998; Dorsey *et al.*, 1997; Dorsey & Umhoefer, 2000). In the northern part of the CSB, the Mancenares Volcanic Complex was formed as a consequence of an extension, block-faulting and tilting. The complex developed in three phases: an emplacement of rhyolitic domes, followed by an andesitic-dacitic volcanism producing the Mancenares stratovolcano, and a final emplacement of dacitic and rhyolitic domes and flows. Pyroclasts and lava flows associated with the second stage are interbedded or interfingering with surrounding sedimentary rocks (Bigioggero *et al.* 1995). The sedimentary rock units are presented in Table 1. Some dated tuff beds constrain the age of deposits. The tuffs in the lower member of the Piedras Rodadas Formation were dated in 2.61 and 2.46 Ma (Umhoefer *et al.* 1994). The tuffs in the lower and upper parts of the Troquero Formation were dated in 2.36 Ma and 1.97 Ma (Umhoefer *et al.* 1994). Additionally, andesite lava flow interfingering with San Juan Limestone were dated in 1.86 Ma (P. Y. Gillot in Bigioggero *et al.* 1995). On the basis of correlations between deposits and sea level curves, the ages of some shell beds from Piedras Rodadas Formation were estimated (Dorsey & Umhoefer, 2000) (Figure 2).

Table 1. Rock units of the Loreto Basin.

Unit	Lithology	Depositional conditions
Middle breccia and lava flow (Miocene basement)	Massive, poorly sorted, matrix-supported breccia. Clasts are subangular, ranging in size from mm to 2 m. Clasts include andesite, dacite, andesite porphyry and minor rhyolite and sandstone. Matrix is a fine- to coarse-grained mixture of ash and sand. Thin andesite lava flows are locally interbedded (Umhoefer <i>et al.</i> , 2001; see also McLean, 1988; Zanchi, 1994).	Large debris flow in volcanic setting (McLean, 1988; Umhoefer <i>et al.</i> , 2001).
Upper lava flow and breccia (Miocene basement)	Lava flows composed by an aphanitic to porphyric andesite, with phenocrysts of plagioclase (~6 mm) and amphibol (0.1 mm-3 mm). This is the dominant lithology. Breccia has similar lithology as the precedent unit (Umhoefer <i>et al.</i> , 2001; see also McLean, 1988; Zanchi, 1994).	Large debris flow in proximal vent volcanic setting (McLean, 1988; Umhoefer <i>et al.</i> , 2001).
La Vinorama Conglomerate	Unit with two members. The Red member is a hematite-cemented, poorly sorted, and clast-supported conglomerate; and minor pebbly sandstone. Conglomerate clasts are subangular to subrounded, ranging from pebble to small boulder size. The grey member is a sand-supported, poorly sorted to unsorted conglomerate; and pebbly sandstone. Conglomerate clasts are angular to subrounded, ranging from cobble to boulder size (Dorsey & Umhoefer, 2000; see also McLean, 1988)	Mud-poor debris-flows and braid-stream systems associated with alluvial fan settings (Dorsey & Umhoefer, 2000).
Piedras Rodadas Formation	Several lithologies composed this unit, as pebble-cobble conglomerate, pebbly sandstone, bioturbated sandstone, sandstone, siltstone, massive bioturbated siltstone, and shell beds with a siliciclastic to calcarenitic matrix. Two members (lower and upper) and different lithofacies (GD1-GD5) have been recognized (Dorsey <i>et al.</i> , 1995; Dorsey & Umhoefer, 2000; see also McLean, 1988). A pair of volcanic ash layers are interbedded in the lower member.	Stacked Gilbert-type fan delta (Dorsey <i>et al.</i> , 1995)
Uña de Gato Formation	Unit with distinct fine grained lithologies, as gypserous fine- to medium-grained sandstone, siltstone, mudstone, and claystone. Gypsum occurs in coarse and fibrous veins, which are parallel and discordant to bedding (Dorsey & Umhoefer, 2000; see also McLean, 1988; Piazza & Robba, 1998)	Sand- and mud-bearing turbidites, deposited in the most distal part of footwall-derived fan deltas represented by the Piedras Rodadas Formation. Gypsum has a diagenetic origin. Claystone records suspension settling from deltaic fresh water plumes. Paleodepth estimated between 20 m-40 m (Dorsey & Umhoefer, 2000).
Arroyo de Arce Limestone	Unit constituted by an unusual mixed carbonate-siliciclastic deposits. Principal lithologies are shelly, sandy calcarenite; pebbly calcarenite, calcarenitic hash, and calcirudite. The carbonate content in these facies is $\geq 50\%$. Secondary lithologies are shelly, pebbly calcarenitic sandstone; and shelly conglomerate with hashy sandy calcarenitic matrix (Dorsey & Kidwell, 1999; Dorsey & Umhoefer, 2000; see also McLean, 1988).	Different depositional processes have been interpreted, as high- to low-density turbidite currents, coarse-grained debris flow, high-energy tidal currents, and long-shore currents. Deposition occurred in the shoreface to shallow-shelf settings. Carbonate derived from uplifted hanging-wall (Sierra Microondas) (Dorsey & Kidwell, 1999; Dorsey & Umhoefer, 2000).
El Troquero Formation	Unit constituted by gypsiferous, massive mudstone and claystone, with interbeds of marl, siltstone, and very fine grained sandstone. Mudstone is the dominant lithology. The unit is interbedded with thick sets of pyroclastics beds. Gypsum occurs in a similar way as in Uña de Gato Formation (Bigioggero <i>et al.</i> , 1995; Dorsey & Umhoefer, 2000; see also Zanchi in Piazza & Robba, 1994, 1998; and McLean, 1988).	Suspension settling in outer-shelf to upper-slope marine setting. Gypsum has a diagenetic origin (Dorsey & Umhoefer, 2000).
San Juan Limestone, also named Lower Pleistocene Limestone	Informal unit, simply described as a coarse bedded and clinostatified coquina or bioclastic limestone. It interfingers with pyroclastic beds and thick lava flows (McLean, 1988; Zanchi, 1994; see also Zanchi in Piazza & Robba, 1994, 1998; Bigioggero <i>et al.</i> 1995).	
Punta El Bajo Limestone	Unit constituted by sandy coralgall and molluscan calcarenite. Interbeds of shelly calcarenitic pebbly sandstone, calcarenite-matrix cobble conglomerate. Coralgall lithology is the most abundant variety (Dorsey <i>et al.</i> , 1997; Dorsey & Umhoefer, 2000).	Deposition occurred in shallow-marine, moderate energy shelf setting. Mixed siliciclastic facies represents episodic input by storm events; pebbly sandstone facies record large storm events. Conglomerate facies near base records rocky shoreline deposits. Carbonate was produced <i>in situ</i> (Dorsey & Umhoefer, 2000).

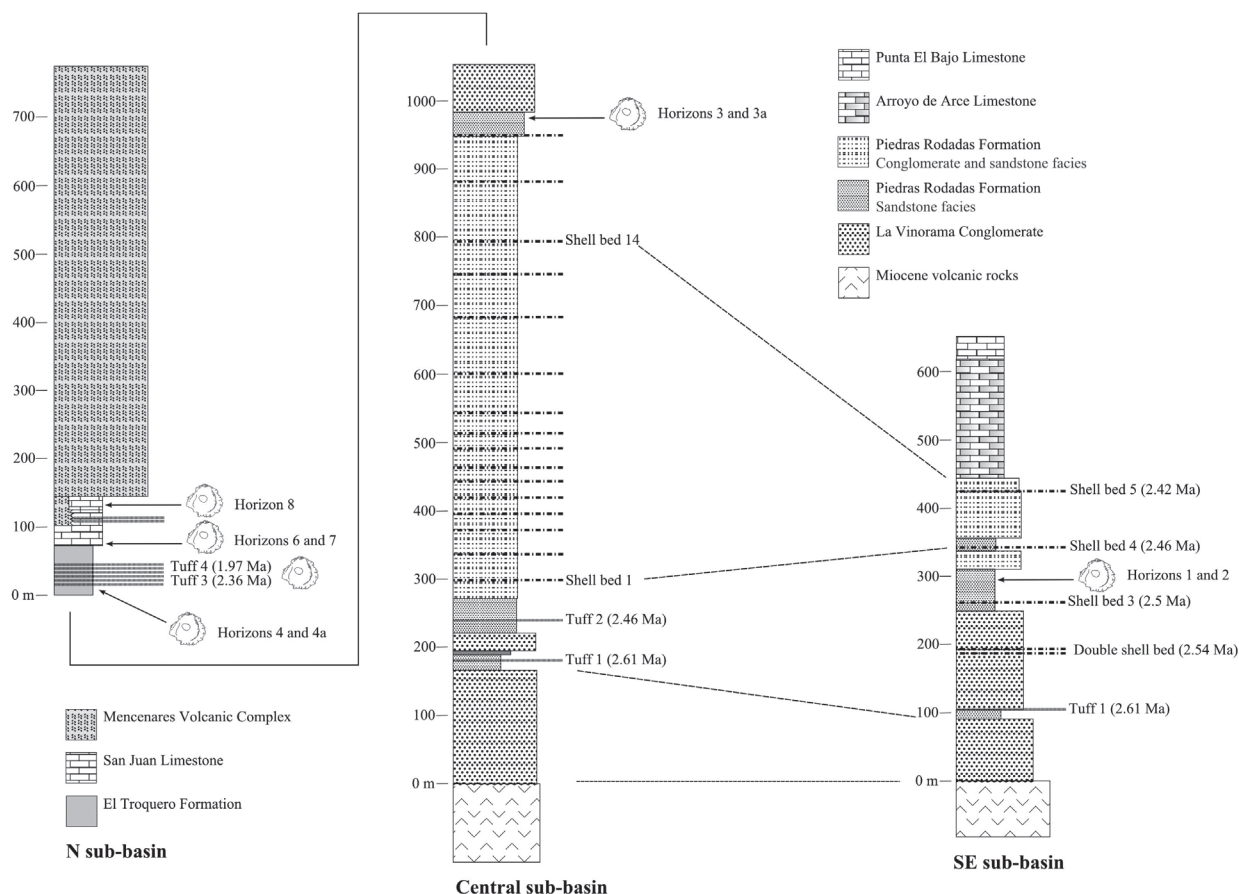


Figure 2. Composed stratigraphic section of the Loreto Basin. Horizons 1-8 represent the stratigraphic occurrence of *H. hyotis* (modified from Dorsey & Umhoefer, 2000).

The northern sub-basin (NSB)

The northern part of the CSB was considered as a third sub-basin, named northern sub-basin (NSB). According to Dorsey & Umhoefer (2000), the rocks of this area were deposited in the distal outer shelf, with a depth that ranged 100 to 150 m. However, evidences were gathered that suggest shallower conditions: the almost exclusive occurrence and high abundance of benthonic foraminifers, found in rocks of the Troquero Formation and San Juan Limestone (pers. com. A. Miranda-Martínez); the occurrence of fossil leaves in marl beds of the Troquero Formation (probably Fabaceae, pers. com. S. Cevallos-Ferriz); the occurrence of *Glycymeris gigantea* (Reeve, 1843) and *Hyotissa hyotis* in sandstone beds of the Troquero Formation; and the presence of spherulitic (phosphatic) sandstone interbedded with conglomerate, indicating conditions of high evaporation (pers. com. J.L. Sánchez-Zavala). Based on Phleger (1960), Bandy (1967), van der Zwaan (1990), and Keen (1971); the present authors inferred a depth range between 10 to 40 m.

In addition, the Troquero Formation and the San Juan Limestone do not outcrop in any place of the CSB or SESB, and the geomorphological patterns are completely different in the NSB (Zanchi, 1994; Umhoefer & Stone, 1996; Dorsey & Umhoefer, 2000). All evidences indicate that NSB stood

as a shallow depression, while the CSB and SESB were disappearing by a tectonic uplift (Dorsey & Umhoefer, 2000). Since basin's evolution was related to regional trans-tension, NSB might have originated by a large-scale rotational fault.

MATERIAL AND METHODS

Specimens from Loreto Basin

A set of 48 free valves and nine shells were examined. They were collected from eight horizons in three rock units (Table 2). Eight of the nine shells can be disarticulated. Additionally, it was examined various specimens from lots housed at the Museo María del Carmen Perrilliat, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City (Table 2). The fossils collected are deposited in the Museo María del Carmen Perrilliat (catalog numbers in Table 2).

Specimens for comparisons

The set of specimens is showed in Table 3. This is composed by fossils collected by the authors at Isla Coronados, deposited in the Museo María del Carmen Perrilliat (catalog numbers in Table 3); and by specimens housed at the Invertebrate Zoology and Geology Collection, California Academy of Sciences, San Francisco; and at the Museum of Paleontology, University of California, Berkeley.

Table 2. Specimens from Loreto Basin. **A.** Fossils collected by authors and colleagues.

Specimens	Site	Formation	Horizon and lithology	UTM coordinates (12R)
1 left valve	IGM 8874	Arroyo Arce	Piedras Rodadas	Horizon 1, medium grained sandstone 463888 m E 2884735 m N
1 right valve	IGM8875	Arroyo Arce	Piedras Rodadas	Horizon 2, medium grained sandstone 464655 m E 2884662 m N
5 left valves	IGM 8876- IGM 8880	Rancho San Antonio	Piedras Rodadas upper part	Horizon 3a, medium grained sandstone 454421 m E 2891457 m N
1 right valve link to 1 shell	IGM 8881			
2 left valves	IGM 8882- IGM 8883			
3 right valves	IGM 8884- IGM8886	Rancho San Antonio	Piedras Rodadas upper part	Horizon 3b, same lithology 454880 m E 2891336 m N
2 shell	IGM 8887- IGM 8888			
5 left valves	IGM 8889- IGM 8893			
1 right valve	IGM 8894	Rentoy	El Troquero lower part	Horizon 4a, shell bed in matrix of shell hash and fine grained sandstone 456032 m E 2897120 m N
1 shell	IGM 8895			
4 left valve	IGM 8896- IGM 8899	Rentoy	El Troquero lower part	Horizon 4b, fine grained sandstone 455890 m E 2897781 m N
7 right valves	IGM 8900- IGM 8906			
1 left valve	IGM 8907	El Sacatón	San Juan Limestone base	Horizon 5, fine grained calcarenite 456484 m E 2900207 m N
1 right valve	IGM 8908			
3 shells	IGM 8909- IGM 8911	El Atacado-Cañada Prieta	San Juan Limestone lower part	Horizon 6, fine grained calcarenite 457527 m E 2901068 m N
4 left valves	IGM 8912- IGM 8915			
6 right valves	IGM 8916- IGM 8921	El Atacado-Cañada Prieta	San Juan Limestone upper lower part	Horizon 7, medium grained calcarenite 457276 m E 2901124 m N
1 shell	IGM 8922			
5 left valves	IGM 8923- IGM 8927			
1 right valve	IGM 8928	Boca Los Bateques	San Juan Limestone upper part	Horizon 8, calcirudite 461714 m E 2900358 m N
1 shell	IGM 8929			

B. Specimens housed at IGM.

Specimens	IGM localities
17 left valves	IGM 8930-IGM 8946
9 right valves	IGM 8947-IGM 8955
1 valve	IGM 8956
1 shell	IGM 8957
5 left valves	IGM 8958-IGM 8962
7 right valves	IGM 8963-IGM 8968, IGM 8973
1 shell	IGM 8974
1 left valve	IGM 9111
1 right valve	IGM 9112
1 left valve	IGM 9113
	IGM loc. 127
	IGM loc. 252
	IGM loc. 253
	IGM loc. 469

Table 3. Specimens compared.

Specimens		Rock unit and age	Locality
3 undescribed left valves, IGM 9114-9116			Isla Coronados, Gulf of California, UTM coords.:
1 undescribed right valve, IGM 9117	<i>Hyotissa hyotis</i>	Coral-reef deposits, Late Pleistocene after Johnson <i>et al.</i> (2007)	12R 0472320 m E, 2888154 m N
3 undescribed shells, IGM 9118-9120			
2 left valves, vouchers UCMP 15502, UCMP 15504	<i>H. hyotis</i> according with Moore (1987, p. 22)	Unnamed strata, Pleistocene after Moore (1987, age mentioned in pl. 16, figs., 1 and 2); Late Pliocene after Durham (1950)	Marquer Bay, Isla Carmen, Gulf of California
1 right valve, voucher UCMP 15503			
2 undescribed left valves, lot UCMP loc. D5424	Unidentified		Yuha Basin, southern California
1 undescribed left valve, lot CAS loc. 61621, labeled 61621.01	<i>Ostrea</i> sp., anonymous identification		Site between Signal Mount and Coyote Hills, Colorado Desert; southern California
1 left valve, voucher CAS 1825	<i>P. (P.) heermanni</i> (Conrad, 1855) according with Moore (1987, p. 21)		Yuha Buttes, Colorado Desert; southern California
1 shell, voucher CAS 1826			
2 undescribed left valves, lot CAS loc. 61622			
2 undescribed right valve, lot CAS loc. 61622	Unidentified	Imperial Formation, Pliocene following Carreño & Smith (2007)	
1 undescribed shell, lot CAS loc. 61622			
3 undescribed left valves, lot UCMP loc. 735	<i>O. cf. vespertina</i> Conrad 1854, anonymous identification		Near the center of the Yuha Buttes, and top of the anticline there; southern California
2 undescribed left valves, lot CAS loc. 61623			
1 undescribed shell, lot CAS loc. 61623	Unidentified		Small washes on west side of Alverson Canyon, Colorado Desert; southern California
1 undescribed left valve, lot UCMP loc. 738	<i>O. vespertina</i> Conrad, identified by G. Dallas Hanna		
3 undescribed left valves, lot CAS loc. 33277			
1 undescribed right valve, lot CAS loc. 33277	Unidentified	Imperial Formation, Late Miocene and Pliocene after Carreño & Smith (2007)	Painted Gorge, north hills of Coyote Mountains, Colorado Desert; southern California
1 undescribed valve, lot CAS loc. 33277			
1 undescribed shell, lot CAS loc. 33277			
1 undescribed right valve, lot UCMP loc. A1265			
1 undescribed left valve, labeled A262; lot UCMP loc. A1272	Unidentified	Imperial Formation, Late Miocene and Pliocene after Carreño & Smith (2007)	Carrizo Mountain, Colorado Desert; southern California
1 undescribed shell, lot UCMP loc. 2064	<i>O. vespertina</i> Conrad, identified by G. Dallas Hanna	Imperial Formation, Late Miocene and Pliocene following Carreño & Smith (2007)	Head of Garnet Canyon, north side of Coyote Mountains, southern California
1 undescribed right valve, lot CAS loc. 36432			T14S, R9E, SB.B+M, southern California
1 undescribed left valve, lot CAS loc. 34951, found in the lot CAS Loc. 33277	Unidentified		Colorado Desert, Imperial Co.; southern California
1 undescribed left valve, lot UCMP loc. B5493		Imperial Formation, Pliocene (?)	
1 undescribed right valve, lot UCMP loc. B5493			
1 undescribed shell, lot CAS loc. 34971	<i>O. heermanni</i> , anonymous identification		Sec. 33, T.13S, R.8E., SBBM; southern California.
1 left valve, voucher IGM 7520	<i>Pycnodonte (Crenostrea) veracruzana</i> Perrilliat, 1994; according with Gastil <i>et al.</i> (1999)	Unit M8c, Late Miocene (< 5.6 ma) after Oskin (2002)	Isla Tiburón, Gulf of California
1 left valve, voucher UCMP 31755	<i>P. (P.) loeli</i> (Hertlein, 1928), according with Moore (1987, p. 21)	Early Miocene after Tan <i>et al.</i> (2003).	Coyote Creek, Ventura Co.; coastal California
2 left valves, paratypes CAS 4134, CAS 4138		Vaqueros Sandstone	
3 right valves, holotype and paratypes CAS 4129, CAS 4133, CAS 4135	<i>P. (P.) wiedeyi</i> according with Moore (1987, p. 20)	Early Miocene after Dibblee & Ehrenspeck (1999)	Santa Rosa Island, coastal California

Morphological traits

A set of traits, illustrated in the Figure 3, was studied in detail. They are briefly described below. The terms and descriptions follow Carter *et al.* (2012), Stenzel (1971), Harry (1985) and Moore (1987). Besides some terms used here were defined.

Lamellae. External projections of non-vesicular shell layers, by which they can be tracked into shell interior. They characterize the outer surface.

Vesicular structure. It is a very porous, calcareous shell layer or part of a shell layer; on which the numerous cavities have small, rounded to irregularly polygonal shapes. The cavities are visible to the naked eye or with low magnification (10x).

Hyote. Narrow tubular or nearly tubular projections that rise over the shell folds. They have a U-shaped cross-section, open on the underside and on their tips.

Folds. Radial, rather broad undulations in the surface of the shell, which affect the entire thickness of it, especially in its margin.

Ligament area. A wide portion where the functional part of the ligament is inserted, characterized by ligament's growth tracks. It can be divided into the resilifer and bourrelets. The resilifer is a triangular to square depression that contains the fibrous ligament or resilium; and bourrelets are the relatively flat external areas on both sides of the resilifer, on which is inserted the lamellar ligament.

Lath-type chomata. Elongate, straight, well-defined ridges, spaced about as far apart as their widths. They are thin (~1 mm) and long, or wide (1-3 mm) and rather stout; antimarginally oriented. In Pycnodontinae, lath-chomata occur ventral to vermiculate chomata on both left and right valves.

Vermiculate chomata. Elongate, closely spaced, fine ridges; oriented normal to the shell margins. They are slightly twisted and taper, having variable lengths, or can

be divided and fused. The vermiculate chomata are mostly restricted to the shell margins near the ligament, and contrary to typical chomata in Ostreidae, they do not interdigitate in opposite valves.

Chomatal troughs. Elongate, narrow to slightly wide cavities, located in the left valve that lodges vermiculate chomata. They were defined by Moore (1987), but she did not mention the corresponding projections in the right valve. The projection is referred here as chomatal protrusion, since it carries vermiculate chomata on its surface.

Commisural shelf. A nearly flat to undulate, internal surface, along the periphery of the shell. It is positioned distal to a circumferential curb that limits the animal's body area. On the shelf's surface there are numerous chalky deposits.

Branchial depression. Cavity that replicates the form of the gills. It is developed in both left and right valves, varying on depth and length. The dorsal end of the branchial depression holds the Quenstedt muscle scar. The posteroventral end is known as branchitellium, a site nearest to the animal's palliobranchial fusion.

Quenstedt muscle scar. Circular small scar, sometimes developed as a deep foramen, produced by the Quenstedt muscle. The scar is located ventrally to the ligamental area, proximal to its margin, indicating a point near the mouth, where there was the adoral part of the gills.

Adductor muscle scar. Scar produced by the attachment of the adductor muscle. The myostracum is an aragonite, thin pad, covering the scar; but not always is preserved due to its composition.

Scar plane. The plane on which adductor muscle scar extends.

Midsagittal plane. The plane dividing the shell into left and right halves.

Chalky deposits. They are calcitic, lensatic sublayers; characterized by a minutely porous microstructure consisting

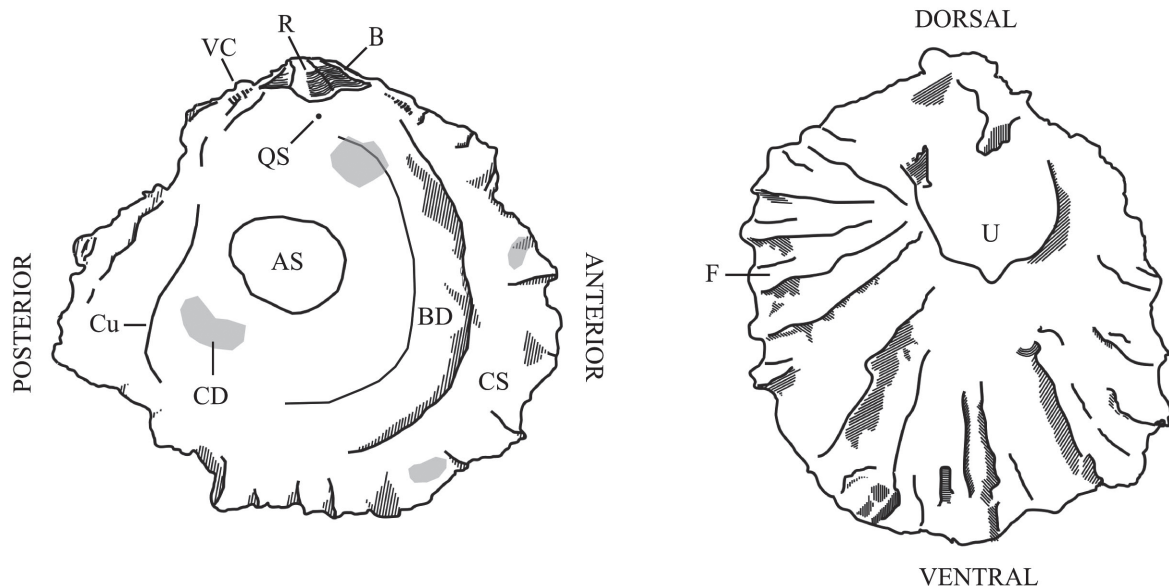


Figure 3. Morphological traits treated in this study. **Abbreviations:** AS, adductor muscle scar; B, bourrelet; BD, branchial depression; CD, chalky deposits; CS, commisural shelf; Cu, curb; F, folds; QS, Quenstedt muscle scar; R, resilifer; VC, vermiculate chomata; U, umbo.

of parallel and irregularly aggregated blades, fibrous prisms, and/or irregular spherulitic prisms (chalky microstructure). The pores are smaller than those in vesicular structure.

Measurements

To study variation of the main shell features, eight measurements were taken (Figure 4). They are the maximum length (**L**) and maximum height (**H**) of the shell; the maximum length (**LL**) and maximum height (**LH**) of the ligament area; the maximum length (**SL**) and maximum height (**SH**) of the adductor muscle scar; the minimum distance among ligament area and adductor scar (**L-SD**); and the width of the shell (**W**). Also, the number of folds was considered. In order to uniform the measurements, the medial and the ligament axes were used as references (dotted lines in Figure 4). The L and LL are parallel to the anteroposterior axis of the ligament area. Measures H and L-S D were perpendicular to L. Similarly, LH was perpendicular to LL as long as resilifer had been straight. In curved resilifers, LH was obtained by measure it in sections (Figure 4B). The width is the distance among two parallel planes. One of them is tangential to the valve external surface, and the other is the midsagittal plane (Figure 4C). All valves were measured, including incomplete specimens. All measurements are given in mm. The raw data are tabulated in the Appendix 1.

Descriptions, re-descriptions and statistical comparisons

The morphology and morphometry of the specimens from Loreto Basin, Isla Coronados and southern California

(Imperial Formation) were described. Since descriptions of both type and voucher specimens are insufficient to our aims, the present authors re-described them. It was completed by a morphometric description. Given that authors have based taxonomic identifications in qualitative comparisons, often useless to distinguish taxa (see Moore, 1987; Powell, 2008), the present authors also performed statistical comparisons among morphometric data sets. They were made in order to evaluate if in the data would be replicated the morphological differences or similarities.

Statistical comparison. Data were statistically tested, parameter by parameter, using for that comparative groups. Each group is a data sub-set associated to a sub-set of specimens. The groups were assembled with at least two elements in order to performed statistical tests; basing on next criteria: (i) a common stratigraphic occurrence, (ii) membership to the same museum's lot, or (iii) by a common and meaningful trait.

The conformation of each group is in Table 4. Based on the third criterion, the group 1 reunites the data of specimens with the fewer amounts of folds. The group 8 reunite fossils from different sites and ages because they could not be situated in other groups.

The statistical analysis is based on a series of test figured by Lich (1990) to elucidate possible morphometric differences. The test and its order in the series are: Homogeneity of Variance (**HV**), one-way ANOVA or Kruskal-Wallis (**KW**), Tukey's Honestly Significant Difference (**HSD**), and Student-Newman-Keuls (**SNK**). Tests were done with the statistical software SPSS v16.0 for Windows®. See Anderson (1993) for a detailed explanation of the procedure.

Institutional acronyms. ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, United States of America; CAS, California Academy of Sciences, San Francisco, California, United States of America; IGM, Museo María del Carmen Perrilliat, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico; UCMP, Museum of Paleontology, University of California at Berkeley, California, United States of America; USNM, National Museum of Natural History, Washington, D.C., United States of America.

SYSTEMATICS

Phylum MOLLUSCA Linnaeus, 1758
 Class BIVALVIA Linnaeus, 1758
 Order PTERIOIDA Newell, 1965
 Superfamily OSTREOIDEA Rafinesque, 1815
 Family GRYPHAEIDAE Vyalov, 1936
 Subfamily PYCNODONTEINAE Stenzel, 1959

Hyotissa Stenzel, 1971

Type species. *Mytilus hyotis* Linnaeus, 1758. Recent. Tropics of Indo-West and Eastern Pacific Ocean.

Hyotissa hyotis (Linnaeus, 1758)
 (Figures 5A-C; 6B-C, G-H)

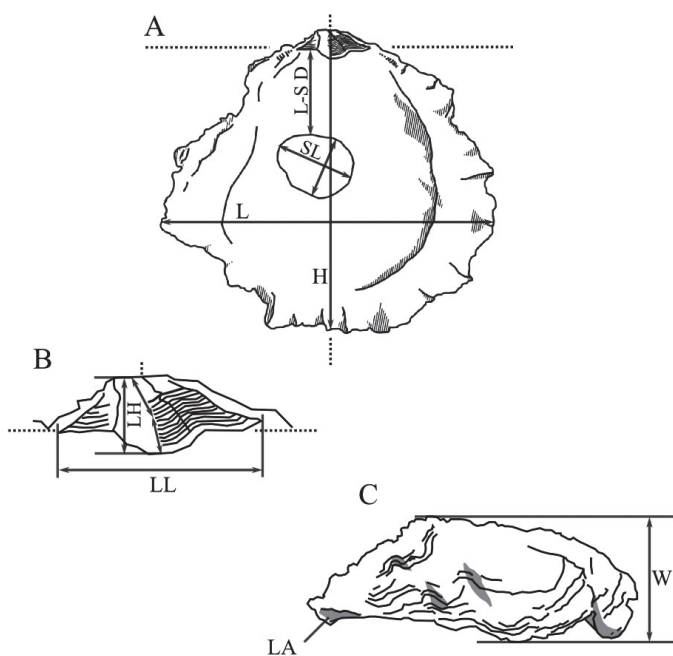


Figure 4. Shell measurements. **A**, inner view; **B**, ligament area; **C**, margin view. For abbreviations see Material and Methods, Measurements caption. See in C that W does not strictly measures the valve thickness, but also the convexity.

Table 4. Comparative groups. **Abbreviation: N,** number of valves.

Sample		N	Lot / Stratigraphic provenance
		2	CAS Loc. 693
1	Colorado Desert	2	UCMP Loc. 2064
		2	UCMP Loc. B5493
		1	UCMP Loc. A1265
2	Colorado Desert	7	CAS Loc. 33277
3	Colorado Desert	2	CAS Loc. 34971
4	Colorado Desert	6	CAS Loc. 61622
5	Colorado Desert	4	CAS Loc. 61623
6	Colorado Desert	3	UCMP Loc. 735
7	Colorado Desert	2	UCMP Loc. D5424
		1	CAS Loc. 693
	Colorado Desert	1	CAS Loc. 34951
		1	CAS Loc. 36432
8		1	UCMP Loc. 738
	Loreto Basin	1	IGM Loc. 469
	Coyote Creek	1	UCMP Loc. 10035
	Isla Tiburón	1	IGM Loc. 2289
9	Isla Carmen	2	UCMP Loc. A3521
		1	UCMP Loc. A3522
10	Loreto Basin	29	IGM Loc. 127
11	Loreto Basin	14	IGM Loc. 252
12	Loreto Basin	2	IGM Loc. 253
13	Loreto Basin	1	Horizon 1
		1	Horizon 2
14	Loreto Basin	8	Horizon 3
15	Loreto Basin	9	Horizon 4
16	Loreto Basin	19	Horizon 5
17	Loreto Basin	1	Horizon 6
		19	Horizon 7
18	Loreto Basin	9	Horizon 8
19	Coronados Island	10	Coral reef

1758 *Mytilus hyotis* Linnaeus, p. 704, n. 207.

1869 *Ostrea veatchii* Gabb, p. 60-61, pl. 17, figs. 21, 21a. nec

Ostrea veatchii Gabb, 1869, p. 34-35, pl. 11, fig. 59.

1873 *Ostrea hyotis* Reeve, pl. 4., fig 7; Dodge, 1952, p. 206.

1895 *Ostrea jacobea* Rochebrune, p. 241.

1914 *Ostrea fisheri* Dall, p. 1; Keen, 1958, p. 66, fig. 121; Hertlein, 1957, p. 65, 66; Keen, 1971, p. 82, 84, fig. 171.

1926 *Ostrea heermanni* Conrad. Hanna, p. 467, pl. 22, fig. 7,8; pl. 23, figs. 1, 2; Emerson & Hertlein, 1964, p. 354.

1950 *Ostrea fisheri* Dall. Durham, p. 59, pl. 6, figs. 1, 4.

1961 *Ostrea (Alectryonia) fisheri* Dall. Olsson, p. 173, 174, pl. 23, fig. 6.

1971 *Hyotissa hyotis* (Linnaeus). Stenzel, p. N1108, N1109, fig. J85; Harry, 1985, p. 130, figs. 10, 11; Moore, 1987, p. C22, pl. 16, figs. 1, 2; Carriker & Gaffney, 1996, p. 8.

1987 *Pycnodonte?* (*Pycnodonte?*) *heermanni* (Conrad). Moore, p. C21, pl. 13, figs. 1, 4, 6, 7; pl. 14, fig. 4; pl. 16, fig. 4; pl. 17, figs. 6, 7.

1994 *Pycnodonte (Pycnodonte) heermanni* (Conrad, 1855) Piazza & Robba, pl. 5, fig. 3.

Hyotissa hyotis (Linnaeus, 1758). Sevilla-H., García-D. & Uria-G., 1998, p. 27, figs. 1, 2.

Specimens. IGM 8874-IGM 8968, IGM 8973-IGM 8974, IGM 9111-IGM 9120; UCMP 15502-15504; CAS 1825, CAS 1826; seven valves, lot CAS Loc. 33277; one valve, lot CAS Loc. 34951; two valves, lot CAS Loc. 34971; one valve, lot CAS Loc. 36432; one valve, lot CAS Loc. 61621; six valves, lot CAS Loc. 61622; four valves, lot CAS Loc. 61623; three valves, lot UCMP Loc. 735; one valve, lot UCMP Loc. 738; two valves, lot UCMP Loc. 2064; one valve, lot UCMP Loc. A1265; one valve, lot UCMP Loc. A1272; two valve, lot UCMP Loc. B5493; two valves, lot UCMP Loc. D5424.

Occurrence. Pleistocene: Piedras Rodadas Formation, El Troquero Formation, San Juan Limestone, Loreto Basin, BCS. Carmen-Marquer Formation, Isla Carmen, BCS. Unnamed rocks (coral-reef deposits), Isla Coronados, BCS. Pliocene: Imperial Formation, Imperial County, California.

Description. Fossils from Loreto Basin: valves are small to large, subcircular to oblong shaped, convex and thick-shelled;

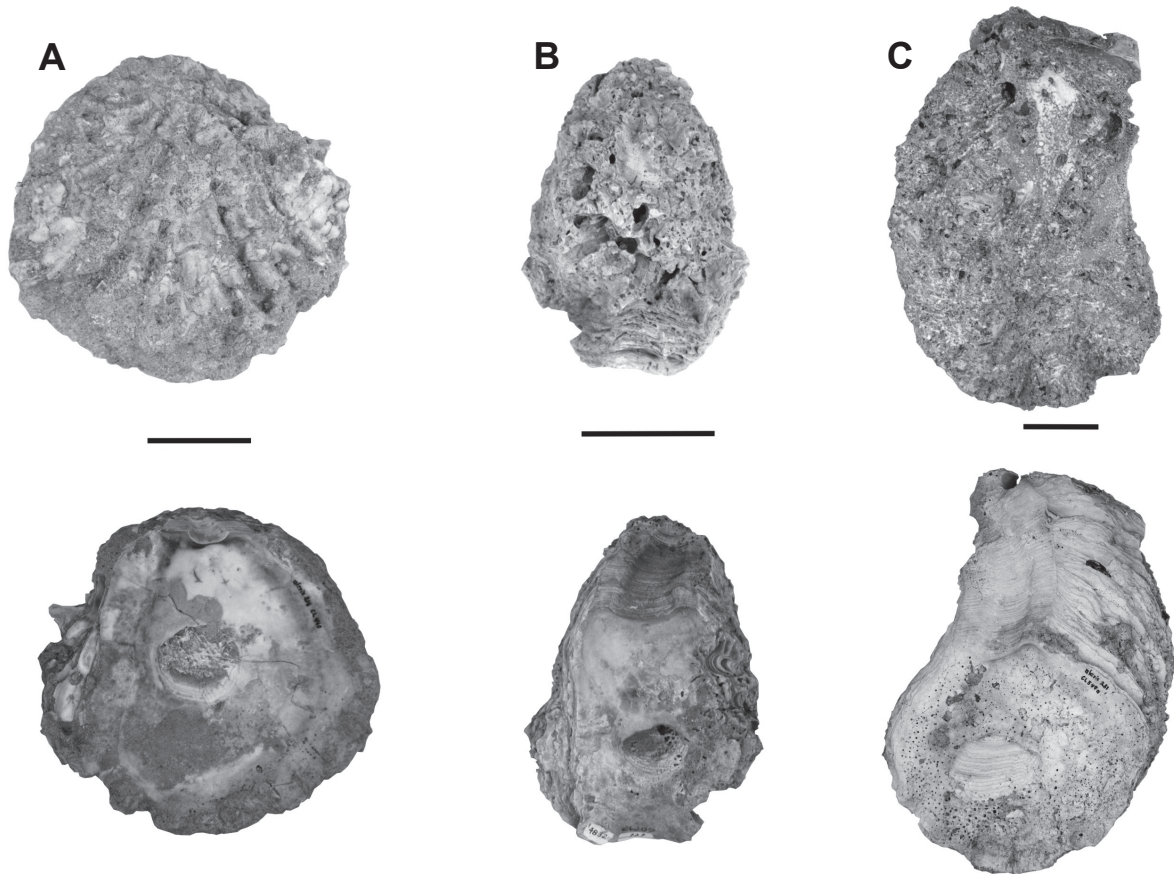


Figure 5. Fossils of *Hyotissa hyotis* (Linnaeus, 1758) from Loreto Basin. Exterior (top) and interior (base) views of: **A**, circular left valve (IGM 8879); **B**, oblong left valve (IGM 8932); **C**, oval and large left valve (IGM 8929). See the depressed adductor muscle scar in B, and the elongate ligament area in B and C. Scale bars = 50 mm.

some specimens are flat and thin-shelled (<25%). Subcircular valves are the usual forms, collected through horizons 1 to 8. The lamellae are thin and thick, non-appressed. Some specimens have only thin and appressed lamellae, as those from horizon 8. Vesicular layers are occasionally exposed in the outer surface; however, they are frequently modified by diagenetic mineralization losing their vesicular nature. Different stages of this modification can be observed in some broken fossils from the horizons 3a,b, and 8. The number of folds is highly variable (see below). They are high, wide, topped-rounded to topped-angled, generally branched in different degrees. Folds developed through the whole valve, being oblique to the valve margin. Short hyote occasionally developed, observed only in the 25% of the specimens. A considerable amount of left valves, ~50%, does not develop a large attachment area or lacks it. The ligament area varies from small- to very large-sized, subtriangular to rectangular. Various fossils from horizon 8, and lots IGM Loc. 253 and 469, are characterized by the extraordinary height of the ligament area; in some of them, it represents the 50% of total valve height. Resilifer's medial axis is straight (65%), sometimes curved (23%), preferentially toward the posterior margin. All valves lack lath-type chomata. Vermiculate chomata short to large, relict chomata frequently observed in the valve rim; however, the 24% of specimens lacks them. Chomatal trough

is developed in a considerable number of left valves, but the chomatal protrusion in the right valves is less frequent. The commissural shelf wide, sometimes narrow; flat to undulate, elevated or bounded by a curb. Branchial depression shallow to deep, not developed in a few specimens (13%). The branchitellium lies in the posteroventral quadrant, ventral to adductor muscle scar. The Quenstedt muscle scar developed in the 50% of valves. It can show different diameters. The adductor muscle scar is circular to oval, small- to large-sized; in several occasions the scar is dorsally subsided, and in only few valves (5%), the scar ventral margin rest on elevation. Scar lies subcentrally to posteroventrally. Usually the scar plane is oblique to midsagittal plane. Parallel planes are rare. In the 70% of the valves, the scar plane is oblique to commissure plane. Several specimens (45%) preserved the myostracum, but it was modified by diagenetic mineralization. Chalky deposits variable in size, lie around branchial depression, sometimes covered it. Also, they are around dorsal margin of the adductor muscle scar. Vesicular deposits mainly formed on the commissural shelf surface. Both chalky and vesicular deposits are frequently hard to recognize due to diagenetic modification. The oblong valves (Figure 5B) represent about the 10% of specimens studied, being collected from horizons 4a,b and 5. Also some additional specimens were found in lots IGM Loc. 127 and 252. They show a particular association

of features. Almost always, oblong valves are medium-sized and thick-shelled. In occasions, oblong valves are falcate. The commissural shelf is narrow and elevate. The branchitellium lies nearer to valve medial axis, and the adductor muscle scar is dorsally to wholly subside.

The measures are: L (n = 115) ranges from 42.7 to 183.2 mm, the 89.6% of values are into 65-160 mm range; the average is 116.3 mm (sd = 30.8), and the skewness value is -0.0067. H (n = 115) ranges from 53.4 to 246.5 mm, the 53% of values ranges from 110-165 mm; the average is 134.17 mm (sd = 39.5), and the skewness is 0.31. L/H ranges from 0.52 to 1.76, the 68 % of values ranges from 0.7 to 1.2; the average is 0.9 (sd = 0.2), and the skewness is 1.6. W ranges from 7.4 to 76 mm, the 73.6% of values ranges from 24 to 50 mm; the averages is 35.6 mm (sd = 12.51), and the skewness is 0.46. The number of folds (n = 109) ranges from 1 to 23 folds, the 54% of the valves has a number of folds that falls into 12-20 range; the average is 12 (sd = 4.9), and the skewness is -0.11. LL (n = 101) ranges from 12 to 85.2 mm, the 81% of values are into 30-58 mm range; the average is 43.9 mm (sd = 13.19), and the skewness is 0.64. LH (n = 101) ranges from 6.3 to 113.1 mm, the 56.4% of values range from 13 to 33 mm; the average is 31.1 mm (sd = 19.9), and the skewness is 2.06. LL/LH ranges from 0.46 to 4.14, the 73.2% of ratios ranges from 0.9 to 2.3; the average is 1.71 (sd = 0.69), and the skewness is 0.91. SL (n = 100) ranges from 11.3 to 82.6 mm, the 59% of values ranges from 19 to 35 mm; the average is 33 mm (sd = 12), and the skewness is 1.3. SH (n = 100) ranges from 6.7 to 56.1 mm, the 57% of values are into 18-26 mm range; the average is 27.3 mm (sd = 8.87), and the skewness is 0.88. SL/SH ratio (n=98) ranges from 0.44 to 2.67, the 56.1% of values ranges from 0.9 to 1.4; the average is 1.22 (sd = 0.31) and the skewness is 1.99. L-S D (n = 93) ranges from 16 mm to 62.2 mm, the 53.7% of values are into 36-49 mm range; the average is 41.8 mm (sd = 9), the skewness is -0.18. L-S D/H ranges from 0.13 to 0.59, the 73.1% of values ranges from 0.23 to 0.38; the average is 0.3 (sd = 0.07), and the skewness is 0.74.

Fossils from Isla Coronados: the specimens are medium-sized, subcircular valves; nearly flat and thin. Only one specimen is a canoe-like valve. The external surface in most of them is weathered. Lamellae are thin and compressed, and vesicular layers are not exposed. The fossils have not been modified by diagenetic mineralization. The number of folds is highly variable (see below). Folds are narrow to wide, low to high, topped-rounded, branched; occasionally poorly developed. They are oblique to valve margin. In only three specimens, the folds are developed through the whole valve. Hyote not developed. Almost all left valves lack attachment scar. Ligament area small (1/5 the valve height), subtriangular to triangular. Resilifer's medial axis straight to curve. All valves lack lath-type chomata, vermiculate chomata short to long, but not all specimens developed it. Chomatal troughs or chomatal protrusions are absent. Commissural shelf commonly wide, partially flat to undulate, bounded by a curb. Branchial depression deep or shallow; branchitellium marked, lying in the posteroventral quadrant, below adductor

muscle scar. Quenstedt muscle scar not developed. Adductor muscle scar small- to medium-sized, subcircular, subcentrally to posteroventrally situated. Scar plane parallel to midsagittal plane. Chalky deposits on the surface. The canoe-like valve with massive chalk deposits that form a flat surface in the valve interior. Vesicular deposits not observed.

The measures are: L (n=10) ranges from 70.4 to 133 mm; the average is 116.7 mm (sd = 17.7), and the skewness is -2.254. H (n = 10) ranges from 95.2 to 160.8 mm; the average is 130.1 mm (sd = 16.7), and the skewness is -0.368. L/H ranges 0.74 to 1.03; the average is 0.89 (sd = 0.083), and the skewness is -0.3. W (n = 10) ranges from 9 to 37.4 mm; the average is 20.43 mm (sd = 8.74), the skewness is 0.82. The number of folds (n = 8) ranges from 2 to 15; the average is 7.6 (sd = 4.1), and the skewness is 0.63. LL (n = 10) ranges from 31.7 to 53.3mm; the average is 44.8 mm (sd = 6.2), and the skewness is -0.8. LH ranges from 10.8 to 35.4 mm; the average is 24.2 mm (sd = 7.2), and the skewness is - 0.31. LL/LH ranges 1.2 to 4.8, the averages is 2.1 (sd = 1), and the skewness is 2.5. SL ranges 21 to 38.9 mm; the average is 31 mm (sd = 7.1), and the skewness is -0.23. SH ranges 18.3 to 33.3 mm; the average is 25.6 mm (sd = 4.23), and the skewness is 0.11. SL/SH ranges from 0.85 to 1.5; the average is 1.2 (sd = 0.22), and the skewness is -0.160. L-S D ranges from 24.3 to 57 mm; the average is 39.8 mm (sd = 10.5), and the skewness is 0.17. Finally, the L-S D/H ratio ranges from 0.20 to 0.42; the average is 0.3 (sd = 0.06), and the skewness is 0.4.

Fossils from Isla Carmen: the three specimens from Isla Carmen were described by Durham (1950). The specimen UCMP 15502 is a large, subcircular, left valve; somewhat convex and thin. The lamellae are thin and appressed. Vesicular layers not exposed. The number of folds is 18. They are high, topped-rounded, branched, and wider toward the margin. Folds are oblique to the valve margin, developed through the whole valve. Numerous short hyote developed. Attachment scar of medium-sized. The ligament area is subtriangular, small-sized (1/9 the valve height). Resilifer's medial axis curved toward posterior side. Lath-type chomata absent; vermiculate chomata poorly developed, only in the anterior margin. They are few and short. Chomatal troughs not developed. The commissural shelf wide, weakly undulated, with a striated surface, bounded by a weak curb. Branchial depression and branchitellium not developed. Quenstedt muscle scar absent. Adductor muscle scar large, oval, anteroposteriorly elongate. It lies in the anterodorsal quadrant, near the valve center. Scar plane parallel to midsagittal plane. Miostracum preserved. Chalky deposits are large, distributed along inner surface. The specimen preserves the original but faded purple color in the inner surface; also, it is preserved the moiré-luster commonly observed in the Recent shells.

The measures are: L, 137.6 mm; H, 132.4 mm; L/H, 1.03; W, 15.2 mm; LL, 39.6 mm; LH, 29.7 mm; LL/LH, 1.33; SL, 43.5 mm, SH, 27.6 mm; SL/SH, 1.57; L-S D, 36 mm; L-S D/H, 0.27.

Both specimens UCMP 15503 and 15504 constitutes the shell of a single individual. The outer surface in both valves is strongly weathered. The specimen UCMP 15504 is a large, subcircular, left valve; convex and thick. Lamellae are thin

and appressed. Vesicular layers not exposed. The number of folds is 14. They are high, rounded-topped, wide, unbranched, and oblique to valve margin. Folds developed only in the valve periphery. Hyote absent. Attachment area of medium sized (1/5 the valve height). The ligament area is rectangular, anteroposteriorly elongate; large (1/4 the valve height). Resilifer wide, medially divided by an irregular ridge toward the ventral margin. Resilifer's medial axis straight. Lath-type chomata absent. Vermiculate chomata and their corresponding chomatal trough only preserved in the posterior side. Chomata short, poorly developed; chomatal trough narrow and deep, very elongate. One half of the commissural shelf is preserved, the other one, lost. The preserved half is moderately wide, flat to slightly undulate in its ventral section; bounded by a curb. Branchial depression moderately deep; branchitellium developed, lying in the posteroventral quadrant, being ventral to adductor muscle scar and near the ventral margin. Quenstedt muscle scar not developed. Adductor muscle scar large, oval, anteroposteriorly elongate. It lies among posterodorsal and posteroventral quadrants, near the valve margin. Scar plane oblique to midsagittal plane. The dissolution of the miostracum produces a deep inner cavity, which opens in the dorsal margin of the muscular scar. The inner surface lacks vesicular and chalky deposits. The specimen UCMP 15503 is a large, subcircular right valve; convex and thick. The specimen lost a considerable part of its dorsoposterior margin, including a part of the bourrelet. The lamellae are thin, non-appressed. Vesicular layers exposed, but hard to recognize due to effects of weathering. The number of folds is eight. They are high, topped-rounded, somewhat branched, and wide. Folds are oblique to valve margin, developed along the whole valve. One or two hyote remains were recognized. The ligament area is large (1/3 the valve height) and rectangular, anteroposteriorly elongate, though, it is broken. Resilifer is divided by a low irregular ridge toward its ventral margin. The medial axis is somewhat curved, but it keeps a straight trend. Lath-type chomata not developed. The existence of vermiculate chomata and chomatal protrusion is uncertain. Relict chomata are preserved in the anterior valve rim. Only one half of the commissural shelf is preserved, the anterior one. It is wide, flat, and elevated, which is bounded by a slope. Branchial depression moderately deep; branchitellium marked, lying as in the left valve. Quenstedt muscle scar not developed. Adductor muscle scar large, oval, anteroposteriorly elongate. It mainly lies in the posteroventral quadrant, near the posterior valve margin. Scar plane oblique to midsagittal plane. Miostracum dissolved; a deep cavity opens in the scar dorsal margin. Chalky and vesicular deposits absent.

The average measures of both left and right valves are: L, 145.9 mm; H, 158.5; L/H, 0.92; W, 32.6 mm; LL, 67.9 mm; LH, 39.9 mm; LL/LH, 1.71; SL, 49.6 mm; SH, 39.2 mm; SL/SH, 1.27; L-S D, 40.8 mm; L-S D/H, 0.25.

Fossils from Imperial County, CA: almost all valves are externally weathered in a considerable manner. The valves are medium-sized, subcircular valves; only 1 from 34 has an oblong profile. Valves are flat to convex, thin- to thick-shelled. Lamellae thin, moderately appressed to non-appressed; vesicular layers not observed in the surface. Folds variable

in number (see below), low to high, topped-rounded, and branched; wider toward the margin and oblique to it. Folds developed through the whole valve; very few valves lack them (6%). Short hyote remains observed in the 15% of valves. Attachment area recognized in the 25% of left valves. Ligament area usually small, subtriangular to rectangular; resilifer's axis straight, rarely curved. Lath-type chomata not developed. Vermiculate chomata developed in the 50% of the valves; chomatal troughs observed in all left valves. Right valves lack chomatal protrusions. Commissural shelf wide to very wide, usually bounded by a curb; shelf can be undulate in thin-shelled valves or flat in thicker ones. Branchial depression shallow to moderately deep; branchitellium marked in the 50% of the valves, lying in the posteroventral quadrant, near valve margin. Quenstedt muscle scar observed in the 50% of valves. Adductor muscle scar subcircular to oval, small to large; it lies in the subcentral area or in the posteroventral quadrant, near posterior valve margin. None scar has an elevated ventral margin, and only the oblong valve has it partially subside. Scar plane oblique to midsagittal plane. Miostracum preserved in very few specimens, but modified by diagenesis. The inner surface is commonly covered by several patches of chalky deposits modified by diagenesis. Vesicular deposits not recognized.

The measures are: L (n = 34) ranges from 75.6 to 151.6 mm, the 70.4% of values are between 90 to 121 mm; the average is 111.3 mm (sd = 16.8), and the skewness is 0.28. The H (n = 34) varies from 89.9 to 169.7 mm, the 65% of values ranges from 106 to 122 mm; the average is 127.7 mm (sd = 20), and the skewness is 0.38. The L/H ratio ranges from 0.63 to 1.36, the 73% of calculated ratios are into 0.75-1 range; the average is 0.9 (sd = 0.14), and the skewness is 0.92. W (n = 34) ranges from 9 to 57 mm, the 67.6% of values ranges from 9 to 29 mm; the average is 25.6 mm (sd = 11.3), and the skewness is 0.98. The number of folds (n = 27) varies from 1 to 18, but in the 44.4% of valves it ranges from 9 to 14; the average is 9.3 (sd = 4.26), and the skewness is 0.14. LL (n = 31) ranges from 18.8 to 72.6 mm, the 61.3% of the values are into 26-42 mm range; the average is 41.8 mm (sd = 13), and the skewness is 0.85. The LH (n = 32) ranges from 5.6 to 81.3 mm, the 68.7% of values ranges from 13 to 28 mm; the average is 26.1 mm (sd = 14.9), and the skewness is 2.27. The ratio LL/LH (n = 31) ranges from 0.67 to 3.35, the 74.19% of the values ranges into 1.2-2.3 range; the average is 1.78 (sd = 0.58), and the skewness is 0.5. SL (n = 30) ranges from 19.5 to 61.3 mm, the 70% of values ranges from 28.5 to 37.5 mm; the average is 33.9 mm (sd = 7.69), and the skewness is 1.80. SH (n = 31) ranges from 15.9 to 39 mm, the 74% of the values fall into 21.5-33.5 mm range; the average is 27.3 mm (sd = 5.6), and the skewness is -0.3. The ratio SL/SH (n = 30) ranges from 0.8 to 1.9 mm; the 63% of ratios ranges from 0.85 to 1.05; the average is 1.25 (sd = 0.24), and the skewness is 1. L-S D (n = 31) ranges from 24.1 to 60.1 mm, the 60% of values ranges 36 to 48 mm; the average is 39.9 mm (sd = 7.74), and the skewness is 0.41. Finally, the ratio L-S D/H ranges from 0.23 to 0.43, the 67.7% of ratios fall into 0.23-0.33 range; the average is 0.31 (sd = 0.05), and the skewness is 0.35.

Specimens of Hanna (1926) (Imperial Formation): the specimen CAS 1825 is a large left valve, subcircular, flat and thick. Lamellae are thin and thick, intercalated, slightly appressed. Vesicular layers not exposed in the surface. The specimen has 17 narrow, somewhat branched folds; high, topped-rounded, oblique to the margin. Folds are developed through the whole valve. Hyote not developed. Attachment area very small, about 1/10 of the valve's height. Ligament area subtriangular, small, less than 1/3 of the valve height; the medial axis curved toward posterior side. Lath-type chomata absent; vermiculate chomata short; narrow and shallow chomatal troughs. Posterior trough is extremely elongate, lying along the bourrelet margin. Commissural shelf narrow, very slightly undulate, no bounded by a curb. Branchial depression moderately deep; branchitellium marked, lying in the posteroventral quadrant, near margin and ventral to adductor muscle scar. Quenstedt muscle scar absent. Adductor muscle scar large, oval, anteroposteriorly elongate. It has a subcentral position, though slightly displaced toward posteroventral sector. The scar is dorsally subsided into the shell; scar plane oblique to midsagittal plane. Chalky deposits large and irregular, modified by diagenesis; they are distributed along branchial depression margins, portions of the commissural shelf, and dorsally to adductor muscle scar.

The measures are: L, 137.7 mm; H, 134.6 mm; L/H, 1.02; W, 36 mm; LL, 46 mm; LH, 30.1 mm; LL/LH, 1.5; SL, 42.6 mm; SH, 28.9 mm; SL/SH, 1.47; S-L D, 47.2 mm; and S-L D/H, 0.35.

The specimen CAS 1826 is a large articulated shell with separable valves. Both are subcircular, flat, and moderately thick-shelled; the external surfaces strongly weathered. Lamellae thin and thick, intercalate, slightly appressed. Vesicular layers not exposed. Left valve with three narrow folds; short, topped-rounded and poorly preserved. Folds developed in the anterior half of the valve. The shell shows a very large undulation at the posteroventral quadrant. Hyote not observed. Attachment area small, about 1/6 the valve height. The ligament area small, 1/4 of the valve height; wide and short, subrectangular; anterior bourrelet broke, exposing an inner vesicular layer. Resilifer's medial axis straight. The valve lacks lath chomata. Chomatal troughs covered by sediment; the posterior trough is narrower and more elongate than the anterior one. Commissural shelf wide, no bounded by a curb. Branchial depression very shallow; branchitellium hardly marked, closed to margin at the posteroventral quadrant. Develop of the Quenstedt muscle scar uncertain due to a sediment cover. Adductor muscle scar large but weakly impressed; circular and subcentrally located. Scar plane parallel to midsagittal plane. Valve lacks chalky and vesicular deposits. Right valve with one, topped-rounded, short, poorly preserved fold; it lies into a wide trough associated to a valve undulation. Hyote not observed. Ligament area small, 1/4 of valve's height; wide, short, subtriangular. Resilifer's medial axis straight. Chomata and chomatal protrusions no developed. Commissural shelf wide and flat, lacking a curb. Branchial depression very shallow; branchitellium hardly marked, lying into posteroventral quadrant, extraordinarily separate from

adductor muscle scar. Existence of the Quenstedt muscle scar is uncertain due to a sediment cover. Adductor muscle scar hardly impressed, circular, large, subcentrally located, though it is closer to ligament area than to valve margin. Scar plane parallel to midsagittal plane. Chalky deposits recrystallized, very small, lying through inner surface.

The average measures of both left and right valves are: L, 154.8 mm; H, 178.8 mm; L/H, 0.86; W, 26 mm; LL, 68 mm; LH, 16.9 mm; LL/LH, 4; SL, 42.5 mm; SH, 33.2 mm; SL/SH, 1.3; S-L D, 41.9 mm; and S-L D/H 0.23.

Comments on morphology. There are several similitudes among all specimens. In the first place are the shape of the shell, ligament area, and adductor muscle scar; the similar size, convexity and sculpture in both left and right valves. In the second place, a general absence of hyote, lath-type chomata, and chomatal protrusions; the development of the vermiculate chomata and chomatal troughs; and the position of branchitellium, and adductor muscle scar.

The observations in some variants will be significant in taxonomy. The lamellae are arranged as intercalations of thick and thin shell layers, and usually they are non appressed. But this is not the unique condition. The valves from horizon 8 are built only by thin and very compressed lamellae; and several specimens from Loreto Basin and Isla Coronados show compressed layers. On the other hand, the vesicular layers can be clearly visible in any valve's cross-section. However, none vesicular layer have been recognized in many of the broken valves from horizon 3 or 8 using 10x lenses. The shells do not show modifications by diagenetic mineralization.

The folds shape seems to be related to the shell thickness, though this is not a perfect linear relationship. All the thinner valves, for example, only have rounded-topped folds; but in the thicker valves, they can be rounded- or angled-topped. Additionally, folds disposition is like in Ostreidae, which allows understanding the wide variation in developing and number.

Checa & Jiménez-Jiménez (2003) pointed out the oblique disposition of folds in relation with the shell margin, and related it to a specific morphogenetic process. The living organisms have the mantle with marginal plications. Since mantle secretes the shell, the marginal plications generate the folds, replicating their architecture. Thus, the number of marginal plications determines the number of folds in the shell. According to the authors, the number of marginal plications can vary depending on the mantle thickness and its excess got during organism's growth.

Additional observations suggest that stressing environmental conditions can decrease the number of shell folds among Ostreidae members. Arnold (1909) documented the reduction of folds in *Dendostrea vespertina* (Conrad, 1854), a fossil species from the Pliocene Etchegoin Formation (California). Based on geological observations, the author related the folds reduction to changes in the conditions, from marine to estuarine. Since the present authors observed the same fold disposition, they consider that folds morphogenesis can be too valid for the folded Pycnodontinae, and even, the potential role of the environmental conditions.

The ligament area not only shows one form, but two. The shells with the most elongate ligament area, particularly those from horizon 8 (Figure 5C), are aged specimens, which likely grew under stable conditions during organisms life-span. The troughs are a frequent trait, and thus, it has to be taken into account for future identifications or systematics studies. The commissural shelf exhibits a trend to be flat in thicker valves, albeit there are several exceptions. The obliquity of the scar plane seems to be related to shell convexity, as is suggested by flatter valves in which scar and midsagittal planes are parallel. Finally, the form, width, and elongation of branchial depression are vastly homogenous.

Comments on morphometry. The set of measures associated with the Loreto specimens indicate the prevalence of the sub-circular shell, slightly higher than long; sub-triangular ligament area, longer than high; and the oval adductor muscle scar, anteroposteriorly elongate. Measures also indicate a small variation in the distance between the adductor muscle scar and ligament area.

A similar predominance in the shapes is indicated by the measures associated to remainder specimens; but with few exceptions. The three specimens of Isla Carmen show a most circular valve; and in the specimens of Isla Coronados and Imperial County prevails an oval, but slightly higher than long muscular scar. No differences are observed for the L-S D. On the other hand, the measures in all fossils indicate a wide variation in the shell thickness-convexity, and in the number of folds.

Regarding to statistical comparison, the comparative groups 1-7 are formed by Pliocene specimens, and the groups 9-19 are Pleistocene specimens (Table 4). Group 1 includes specimens from three lots and the voucher CAS 1826. These fossils have less than four folds. Groups 2 to 7 are formed by fossils from just one lot and group 9 includes specimens from Isla Carmen. The Loreto's specimens are distributed in the groups 10-18; and in the group 19 are the specimens from Isla Coronados. In the mixed group 8, are included the voucher CAS 1825, and other four Pliocene valves.

The averages for each comparative group are in Table 5, and dispersion of data is plotted in the Figures 7 and 8. Among Pleistocene specimens, the group 11 regularly shows the smallest average values, especially for the parameters L, H, SL and SH. This group is composed by specimens from lot IGM Loc. 252. In contrast, the groups 9, 12, and 18 regularly show the higher values for almost all the parameters. These groups are formed by fossils from Isla Carmen, lot IGM Loc. 253, and Horizon 8, respectively. The less convexity and thickness (W parameter) is observed in fossils from Isla Coronados (group 19); and the less amount of folds were observed in fossils from horizon 8 and Isla Coronados.

Among Pliocene specimens, the group 7 show minima values in parameters L, H, SL, SH, and L-S D. This group is composed by specimens from lot UCMP Loc. D5424. The groups 1, 5 and 6 show higher averages in L, LL, SL, and SH. The group 6 highlights in the parameter W and in the number of folds. Group 5 is formed by specimens from lot

CAS Loc. 61623; the group 6 is composed by specimens from lot UCMP Loc. 735.

In Figures 7 and 8 are compared the data distributions. For parameters L, W, LL, and SL, the box-plots exhibit a division of groups in at least two classes. However, the values located between the percentiles 25th and 75th overlap. The clearer distinction is observed in parameter L.

More homogeneous distributions are observed in the parameters H, LH, SH, L-S D, and in the number of folds. Some groups regularly highlight over others, such as the groups 12 and 18, showing ranges of higher values. Regarding to the number of folds, the groups 1, 18 and 19 distinguished from others by their ranges of lower values.

In Table 6 are shown the results from statistical tests, indicating the metric similitude among almost all groups. The groups 9, 12 and 18 are significantly different in at least five parameters (A.S. < 0.05; P < 0.05). This result means that specimens from Isla Carmen, lot. IGM Loc. 253, and Horizon 8 are largest shells, with the largest adductor's muscle scar, and largest ligament area. The fossils from Horizon 8 are the most convex and thick-shelled specimens. The group 1 is distinguished from others by a lower number of folds (A.S. < 0.05).

Taxonomic remarks. The genus *Hyotissa* is characterized by a medium- to very large-sized and thick shell, subcircular or usually oval, with internal vesicular layers. It is sculptured by rounded folds and hyote. The commissure is usually in zig-zag; the adductor muscle scar with the ventral margin elevated at least in the largest specimens (Harry, 1985; Coan & Valentich-Scott, 2012).

Pycnodonte differs from *Hyotissa* by its inequivalve circular shell. Left valve is markedly convex and thick, while

Table 5. Averages (mm) in comparative groups. **Abbreviation:** F, number of folds. For other abbreviations see Material and Methods, Measurements caption.

Group	L	H	W	LL	LH	SL	SH	L-S D	F
1	117.14	138.96	23.83	46.36	19.09	36.76	30.90	43.30	2
2	109.84	125.70	22.27	44.93	37.56	29.48	25.43	32.38	6
3	113.75	131.15	24.65	38.85	24.50	32.55	24.65	37.40	?
4	99.37	110.57	19.50	33.93	21.10	30.70	23.92	38.17	13
5	124.35	130.70	24.15	46.33	25.80	41.77	28.88	39.73	9
6	117.27	140.73	27.03	31.97	20.50	33.67	31.40	41.67	13
7	92.65	106.55	21.20	35.95	19.50	24.85	20.90	34.20	9
8	127.10	138.81	40.53	51.24	36.53	38.89	26.80	42.36	10
9	143.13	149.83	26.80	58.50	36.50	47.60	35.33	39.23	13
10	95.65	110.02	32.33	36.58	27.50	26.50	21.45	41.74	13
11	90.70	104.79	27.89	38.23	22.98	26.39	20.50	39.11	11
12	136.40	182.55	43.85	76.95	63.70	52.30	40.55	34.20	11
13	127.25	132.30	24.60	41.10	20.00	40.15	30.75	31.25	13
14	144.70	149.08	36.49	55.57	33.46	35.20	30.46	45.90	12
15	111.78	129.77	29.67	46.40	23.10	31.80	30.75	42.94	13
16	95.47	117.82	32.66	36.88	24.19	27.86	24.63	38.79	11
17	147.63	163.69	41.68	46.47	28.59	37.43	32.72	44.36	13
18	152.24	189.17	48.52	63.51	72.36	63.92	42.24	48.67	6
19	116.74	130.09	20.43	44.86	24.16	30.98	25.61	39.85	8

the right valve is flat to concave, smaller, lid-like. Only in some species, the left valve has well-developed folds; others have incipient folds or undulations, but in general folds are not well developed. Few species show two or three hyote. The right valve is frequently cut by radial, irregular and deep gashes. Ligament area is small, anteroposteriorly shorter, though flanked by vermicular chomata. The commissure shelf is flat, geniculate, and limited by a strong curb (Stenzel, 1971).

The largest folded and thickest oysters found in the Imperial Formation, have been traditionally assigned to *Pycnodonte heermanni* (Dall, 1914; Hanna, 1926; Moore, 1987). In recent times, taxonomic identification of these fossils is based in very few and taxonomically useless traits, such as shell thickness and size (e.g. Powell, 2008). The identification of Pycnodontinae fossils from the southern Gulf of California has been based on comparisons with Imperial fossils. Following Moore (1987), Piazza & Robba (1994) identified a single left folded valve from Loreto Basin as *P. (P.) heermanni*, but authors's description and illustration (p. 54, pl. 5, fig. 3) reveals it as *H. hyotis*. Further examples can be found in Emerson & Hertlein (1964) or Moore (1987). The Pliocene specimens here studied do not fit with the well-known morphology of *Pycnodonte*. The features of this genus have been observed consistently in numerous left and right valves of *P. erici* (Hertlein, 1929) that the present authors collected at Loreto Basin, near Horizon 7. A comparison made with these specimens (not reported here), and holotypes of *P. erici* CAS 2094 and *P. (C.) veracruzana* IGM 6325 and IGM 6326, corroborate that specimens examined cannot be assigned to *Pycnodonte*. Based on this comparison, it is disagree that several largest and thickest oysters from Imperial Formation can be related to *Pycnodonte*; including the syntypes of *P. heermanni* (Figures 6D, F). In the original description of *Ostrea heermanni* Conrad (1855) the basic combination of traits are hardly related to features typical of *Pycnodonte*.

Since differences are so clear between *Hyotissa* and *Pycnodonte*, it is possible that Moore (1987) considered the syntypes of *Ostrea heermanni* (ANSP 13367) as *Pycnodonte* members because they are poorly folded (Figures 6D,F). Although there are more poorly folded specimens recovered from Imperial Formation, e.g. fossils in the group 1; the observations suggest that this is an uncommon condition. Hertlein & Grant (1972) stated that the syntypes beds are dominated by large and folded shells. Besides, develop of folds is a feature widely variable by reasons exposed above. Thus, it seems that Conrad (1855) described *O. heermanni* based on rare, poorly folded shells. In contrast, the combination of traits associated with *Hyotissa* was recognized in all specimens examined. Such traits are the shell form and sturdiness, convexity, and the folds robustness and their shape. Both left and right valves show a similar size, shape, and sculpture. In relation with inner morphology, the size and form of ligament area, the presence of vermicular-type chomata, the commissural shelf architecture, and the form of adductor muscle scar. Furthermore, the specimens do not show significant metric differences among them, and with Pleistocene fossils.

The specimens also show essential characteristics of *Hyotissa hyotis*. According with Coan & Valentich-Scott (2012), *H. hyotis* exhibits a heavy, subcircular to subovate shell; the left valve is flat, slightly convex, or concave; right valve convex to concave. Folds broad, high, and strongest to the shell margin; sometimes forming hyote and projecting lamellae. Shell margin undulated. Resilifer is shallow, broad and short. Shell shows vermiculate chomata, absent in large specimens. Adductor muscle scar subovate, with a ventral margin raised.

Thus, the specimens from Loreto Basin, Isla Coronados, Imperial County, and CAS 1825 and CAS 1826, are assigned to *H. hyotis* because the traits of the species are recognized without ambiguity. Albeit the specimen CAS 1826 lacks folds, it does not show features that can be related it to *Pycnodonte*. The present authors considered it as an unusual variation of *H. hyotis*.

This assignment is congruent with previous observations made on species's morphology. The present authors registered an occasional development of hyote, as Olsson (1961) and Harry (1985) did. Dodge (1952) noted the low occurrences of specimens with large hyote, and stated that taxonomists tended to illustrate specimens with well-developed hyote. For the present authors, the absence of hyotes is a prevailing condition. In traditional descriptions of those authors, there is not any reference to chomatal troughs and protrusions. However, Moore (1987) discovered troughs in specimens from Imperial Formation.

Finally, many well-preserved left valves from Loreto Basin, Isla Coronados, and Imperial County lack attachment scar or have a small one (Figure 5A). A different condition was described by Stenzel (1971), who emphasized a large attachment to substrate.

Hyotissa cf. *H. hyotis* (Linnaeus, 1758)
(Figures 6A,E)

1932 *Ostrea vespertina loeli* (Hertlein). Loel & Corey, p. 193, 194; pl. 16, figs. 1a,b; pl. 17, figs. 1-3.

1987 *Pycnodonte?* (*Pycnodonte?*) *loeli* (Hertlein). Moore, p. C21. nec *Pycnodonte?* (*Pycnodonte?*) *loeli* (Hertlein), Moore, 1987, pl. 18, figs. 7, 8.

1999 *Pycnodonte* (*Crenostrea*) *veracruzana* Perrilliat. Gastil *et al.*, p. 18, fig. 15g.

Specimens. IGM 7520, UCMP 31755.

Occurrence. Late Miocene: unit M8c, marine sandstone; Isla Tiburón, Sonora. Early Miocene: Vaqueros Sandstone, Ventura County, California.

Description. Isla Tiburón specimen: the specimen IGM 7520 is a medium-sized left valve, sub-circular, convex, and thin. It is externally weathered. Lamellae are thin, somewhat appressed. Vesicular layers not exposed. Folds are wide and low, rounded-topped, unbranched, and oblique to valve margin. Some folds developed through the whole valve, others only in the dorsal half. The number of folds is five to seven. Hyote not observed. Attachment scar not developed. Ligament area triangular and small (~1/9 the valve's height); resilifer's medial axis straight. Lath chomata absent; vermicular chomata

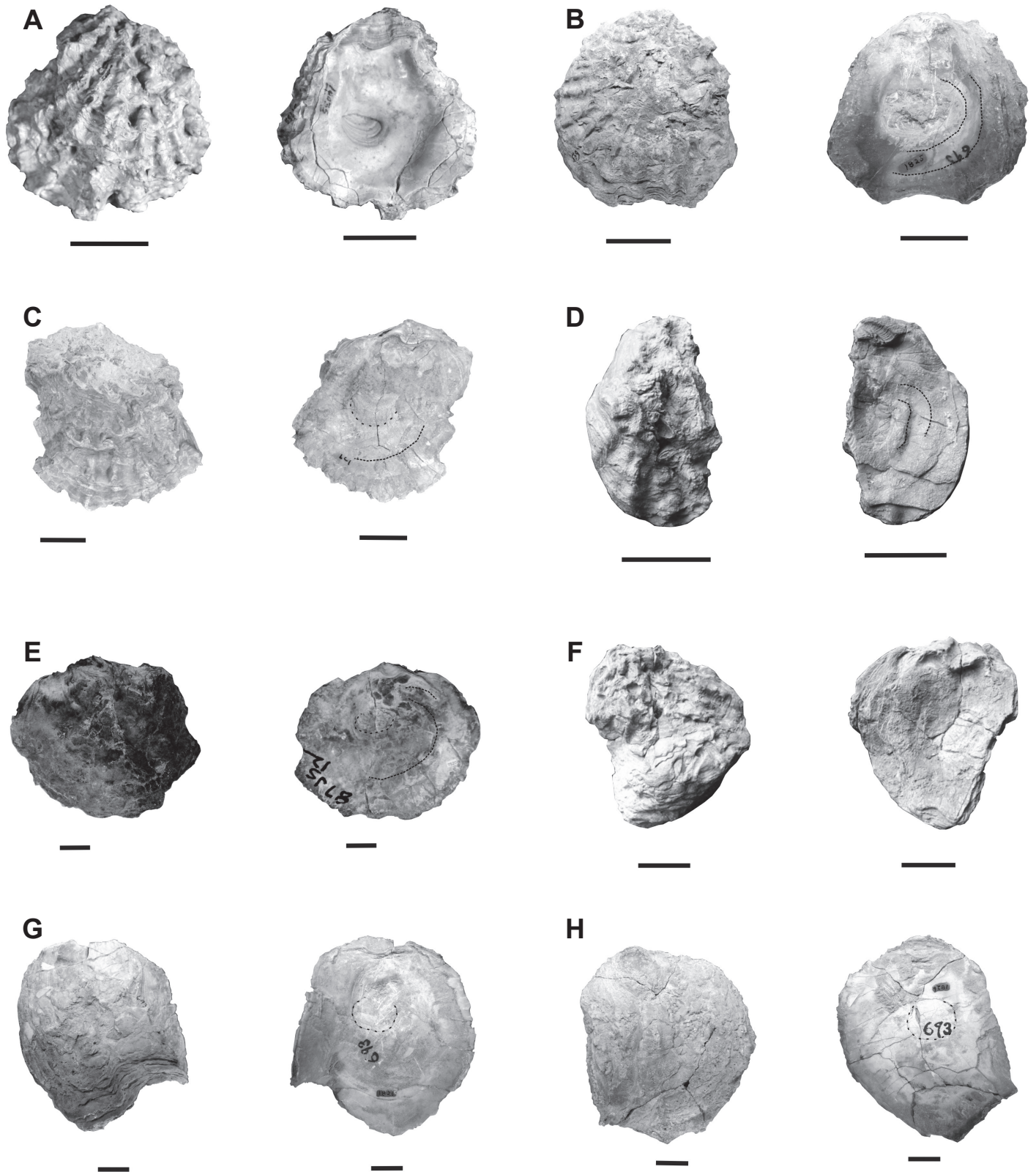


Figure 6. Pliocene and Miocene specimens. External and internal views. **A-C**, well folded valves; **D** and **E**, weakly folded valves; **F-H**, unfolded valves. **A**, left valve UCMP 31755 *H. cf. H. hyotis* (Linnaeus, 1758); **B**, left valve CAS 1825 *H. hyotis* (Linnaeus, 1758); **C**, left valve from lot CAS Loc. 61622 *H. hyotis* (Linnaeus, 1758); **D**, left valve, syntype ANSP 13367 *O. heermanni* of Conrad, 1855; **E**, left valve IGM 7520 *H. cf. H. hyotis* (Linnaeus, 1758); **F**, left valve (?), syntype ANSP 13367 *O. heermanni* of Conrad, 1855; **G-H**, left and right valves CAS 1826 *H. hyotis* (Linnaeus, 1758). Taxonomic identities discussed in the text. The photographs of Conrad's syntypes were kindly provided by Judith T. Smith. Scale bars: A, C, G-H = 30 mm; B, D, F = 50 mm; E = 25 mm.

short and weakly developed; only preserved in the anterior margin. Chomatal troughs elongate, wide, and shallow. Commissural shelf wide, slightly undulated, somewhat geniculate, and bounded by a curb. Branchial depression shallow, wide, hardly marked. Branchitellium not marked. Chalky deposits modified by diagenesis, concentrated in the zone between ligament area and the adductor muscle scar. Consequently, the Quenstedt muscle scar not developed or covered. Adductor muscle scar hardly marked, circular, and sub-central. Scar plane sub-parallel to midsagittal plane. Vesicular deposits not observed.

The measures are: L, 137.6 mm; H, 120.1 mm; L/H, 1.14; W, 19.7 mm; LL, 32.3 mm; LH, 13.8 mm; LL/LH, 2.34; SL, 29.3 mm; SH, 25.1 mm; SL/SH, 1.16; S-L D, 28.2 mm; S-L D/H, 0.23.

Coyote Creek specimen: UCMP 31755 is a small left valve, sub-circular, convex and thick. Lamellae are somewhat appressed and thin. Folds are high, rounded-topped, branched, wider in the margin and oblique to it. The number of folds varies from 12 to 15 and developed through the whole valve. Hyotes short and strong. Attachment scar absent. Ligament area triangular, medium-sized (~1/5 of the valve height). Resilifer's medial axis straight. Lath-type chomata not developed; vermicular chomata very incipient, hardly perceptible, found only in the posterior margin. A small circular cavity (chomatal trough?) is located between chomata and the posterior bourrelet. Commissural shelf rose, somewhat narrow, and undulate. Branchial depression shallow; branchitellium marked, lying in the posteroventral sector, ventral to adductor muscle scar. Quenstedt muscle scar not developed. Adductor muscle scar oval, anteroposteriorly elongate; gradually subsided toward the dorsal margin. Scar plane oblique to midsagittal plane. Chalky deposits absent; vesicular deposits recrystallized on commissural shelf. The inner surface is fracture or brake in some areas, exposing a internal vesicular layer.

The measures are: L, 78.5 mm; H, 78.9; L/H, 0.99; W, 36.1 mm; LL, 31.7 mm; LH, 14.4 mm; LL/LH, 2.2; SL, 18 mm; SH, 16 mm; SL/SH, 1.12; S-L D, 29.1 mm; S-L D/H 0.36 mm.

Comments on morphology. Similar to most of the Pliocene and Pleistocene specimens, IGM 7520 and UCMP 31755 exhibit a triangular ligament area; and the oval outline

of the adductor muscle scar. The valves slightly differ from the prevailing shape. IGM 7520 has a shell elongate anteroposteriorly, and UCMP 31755 is nearly circular, though not symmetrical (Figure 6A). However, similar variants were observed among Pliocene and Pleistocene specimens. The folds in IGM 7520 are in general wider and less numerous, but similar features are found in the specimens from southern California. UCMP 31755 differs from all specimens by its marked convexity and thickness, unusual in shells of comparable size.

Comments on morphometry. IGM 7520 has metrical similitude with the medium-sized Pliocene and Pleistocene specimens, but it is specially flat and thin-shelled, like specimens from Isla Coronados. On the other hand, UCMP 31755 is metrically similar to smaller Pliocene and Pleistocene specimens. This is smaller than IGM 7520, but both share similar values in the ratio SL/SH and L-S D. The measures of UCMP 31755 highlight its remarkable shell thickness, convexity, and L-S D value. Comparable conditions are observed in CAS 1825, but this is a much larger valve. UCMP 31755 has one of the smaller adductor muscle scar. Regarding to statistical comparison, the values of IGM 7520 and UCMP 31755 were included in the comparative group 8 (Table 4). Both specimens do not metrically differ from the others (Figures 7, 8); but in parameter L, the value of UCMP 31755 is an outlier of group 8. According to statistical results, group 8 does not differ statistically from other groups (Table 6).

Taxonomic remarks. IGM 7520 was originally confused with a right valve (Gastil *et al.*, 1999). The valve position can be verified observing the branchial depression. In inner view, the branchial depression of the right valve curves toward observer's left side; while in the left valve it curves toward right side. Thus, IGM 7520 is a left valve (Figure 6E).

Given this confusion, the specimen was misidentified as *Pycnodonte (C.) veracruzana* due to a strong resemblance with the right valve of the species' holotype, a representative shell of the *Pycnodonte* genus. In the holotype, the left valve is highly convex, while the right one is flat (see Perrilliat, 1994, pl. 1, figs. a, j; pl. 2, figs. a, j).

IGM 7520 exhibits the combination of traits associated with *Hyotissa*, such as a flat shell; absence of lath-type chomata; presence of vermiculate chomata; a wide and

Table 6. Statistical tests results. For morphometric parameters see Material and Methods, Measurements caption. Groups as in Table 4. **Abbreviations:** df, degree of freedom; **GSD**, groups significantly different.

	df	Chi-square	Asymptotic significance	F	P	GSD
L	18	99.159	0.000			9, 12, 14, 17, 18
H	18	75.682	0.000			12, 18
W	18			4.652	0.000	18
LL	18	63.019	0.000			9, 12, 14, 18
LH	18	32.789	0.018			9, 12, 18
SL	18	68.637	0.000			9, 12, 18
SH	18	71.432	0.000			1, 6, 9, 12, 17, 18
L-S D	18	23.728	0.164			
Folds	17	44.705	0.000			1

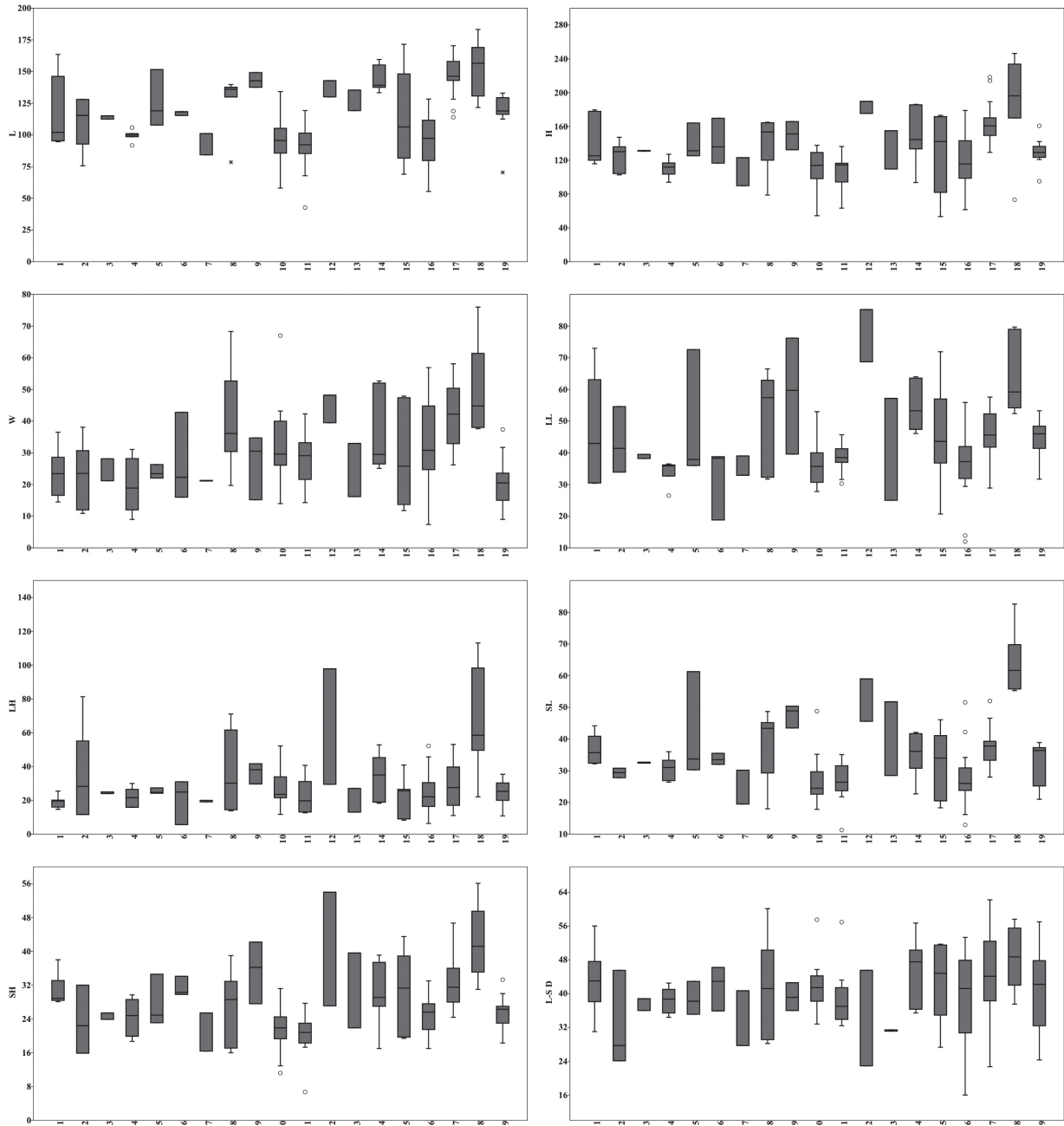


Figure 7. Data distributions among the comparative groups.

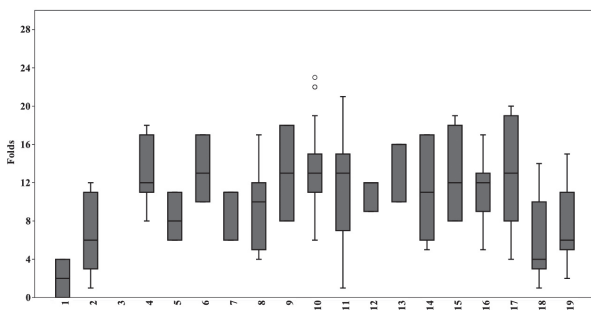


Figure 8. Number of folds among comparative groups.

undulate commissural shelf, bounded by a curb; and the shape of the adductor muscle scar. Thus, it is re-assigned to *Hyotissa*. The specimen is morphologically and metrically indistinguishable from Pleistocene and Pliocene flat valves, with exception of the number of folds. But given the wide variation in the number of folds and their possible causes exposed above, this is not a taxonomically reliable feature. IGM 7520 can be re-assigned to *H. hyotis*; however, the same combination of features has been recognized in a Miocene species, *H. haitensis* (Sowerby, 1850), well known in marine rocks associated to the Atlantic coast of America (Figure 1).

The present paper did not include a study of *Hyotissa haitensis*, but based on the original description of Sowerby (1850), and descriptions of Woodring (1982), the present authors cannot separate *H. haitensis* and *H. hyotis*. The illustrations of Woodring (1982, pl. 98, fig. 2; pl. 109, figs. 6, 10, 11) display a strong external resemblance with several of our specimens from Loreto Basin.

Gastil *et al.* (1999, p. 17) reported two specimens of *Hyotissa haitensis* from unit M8d of Isla Tiburón, the same rock unit where IGM 7520 was retrieved. Nevertheless, the identification is doubtful. The authors did not illustrate the specimen, and linked the stratigraphic occurrence of the extinct *H. haitensis* with the autoecology and current distribution of *H. hyotis*.

There is other Miocene species, *Hyotissa polylopha* Woodring 1982, known from the Canal Zone, tropical Pacific (Figure 1). This species exhibits 30 or maybe more folds (see Woodring, 1982, pl. 100, figs. 12, 13), which distinguishes it from *H. haitensis* and *H. hyotis*. Although the present authors observed that number of folds are widely variable, none specimen shows more than 25 folds in this study (Figure 8). More observations are needed on variation of *H. polylopha* and specimens from Isla Tiburón in order to place IGM 7520 as member of *H. polylopha*.

In sum, with available information it is hard to re-assign IGM 7520 to *Hyotissa hyotis*, *H. haitensis* or *H. polylopha* with certainty. It was opted to use open nomenclature (Matthews, 1973; Bengtson, 1988), following recommendations of Lucas (1986) and Bengtson (1988). Thus, IGM 7520 is provisionally re-assigned to species *H. hyotis* until further comparisons make possible a clearer placement.

Moore (1985) placed UCMP 31755 as member of *Pycnodonte (P.) loeli* (Hertlein). It is, however, markedly different from the holotype of *P. (P.) loeli*; which is a larger, quadrate, and thicker valve; with six wide, rounded-topped, closely spaced folds well developed near the edges (Hertlein, 1928; Loel & Corey, 1932). Compare Figure 6A with pl. 22, figs. 2, 3 of Hertlein (1928); or pl. 18, figs. 7, 8 of Moore (1987).

Furthermore, UCMP 31755 does not show the *Pycnodonte* traits; rather the specimen exhibits a set of traits associated to *Hyotissa*, such as internal vesicular layers, valve form and convexity, a well-developed sculpture, absence of lath-type chomata, presence of vermicular chomata, though they are poorly developed; a commissural shelf undulate, though it is elevated and narrow; and the shape of the adductor muscle scar. Therefore, this specimen is re-assigned to *Hyotissa*. UCMP 31755 is morphologically and metrically indistinguishable from Pliocene and Pleistocene specimens; but re-assignment of UCMP 31755 to *Hyotissa hyotis* or other mentioned species of *Hyotissa* faces the same problems on taxonomic uncertainty. Additionally, more observations on specimens from coastal California are needed in order to know variation and perform reliable comparisons. Loel & Corey (1932, pl. 17, figs. 1a,b, 2a,b) and Bremner (1933, pl. 2, fig. 1), for example, illustrated several specimens from different locations along southern coastal California and Channel

Islands. Those specimens externally strongly resemble to UCMP 31755. Again, the present authors opted to use open nomenclature and provisionally re-assigned UCMP31755 to species *H. hyotis*, until further comparisons make possible a clearer placement.

Orrstreidi gen. nov.

Type species. *Ostrea wiedeyi* Hertlein, 1928. Early Miocene. Vaqueros Sandstone, Santa Rosa Island, California.

Etymology. From Greek word *streidi* (στρείδι = oyster). This new genus is dedicated to Phil. C. Orr, former curator of anthropology and paleontology at the Santa Barbara Museum of Natural History; who found the Pleistocene bones of the Arlington Springs Woman in Santa Rosa Island.

Diagnosis. Shell sub-oval to oblong, convex, thick and strongly folded. Equivalve and equilateral. Vesicular layers not exposed. Ligament area rectangular, narrow, dorsoventrally elongate. Chomata, chomatal troughs and protrusions absent. Commissural shelf narrow and elevate, occasionally undulate. Adductor muscle scar oval, dorsoventrally elongate to arch-like in large specimens.

Orrstreidi wiedeyi (Hertlein, 1928)
(Figure 9)

1928 *Ostrea wiedeyi* Hertlein. Hertlein, p. 147, 148; pl. 23, figs. 1, 10.

1987 *Pycnodonte? (Pycnodonte?) wiedeyi* (Hertlein). Moore, p. C20, C21; pl. 15, figs. 1, 4, 5, 8.

Specimens. Lectotype CAS 4129; paralectotypes CAS 4133, CAS 4134, CAS 4135, CAS 4138

Occurrence. Early Miocene, Vaqueros Sandstone, Santa Rosa Island, California.

Description. The lectotype CAS 4129 is a medium-sized right valve, oblong, convex and thick. Lamellae are thin, moderately appressed. Vesicular layer not exposed. A strong growth line divides the valve into dorsal and ventral halves. Folds are high, angled-to rounded-topped, branched, distally wider and oblique to the valve margin. The folds developed through the whole valve; however, they gradually fade out from mid growth line toward the ventral margin. The number of folds is 18 to 19. Hyote not developed. Ligament area small (~1/7 the valve's height) and rectangular, narrow but dorsoventrally elongate. Resilifer's medial axis straight. Chomata and chomatal troughs not developed. Commissural shelf narrow, especially in the dorsal sector where it is elevated. The shelf is slightly undulated along the ventral margin, not bounded by a curb. Branchial depression and branchitellium hardly marked; branchitellium lies in the anteroventral quadrant. Quenstedt muscle scar not developed. Adductor muscle scar large, dorsoventrally elongate, with an arch outline. The scar lies in the midpoint between dorsal and ventral valve margin, close to posterior rim. Scar plane slightly oblique to midsagittal plane. Chalky and vesicular deposits not observed.

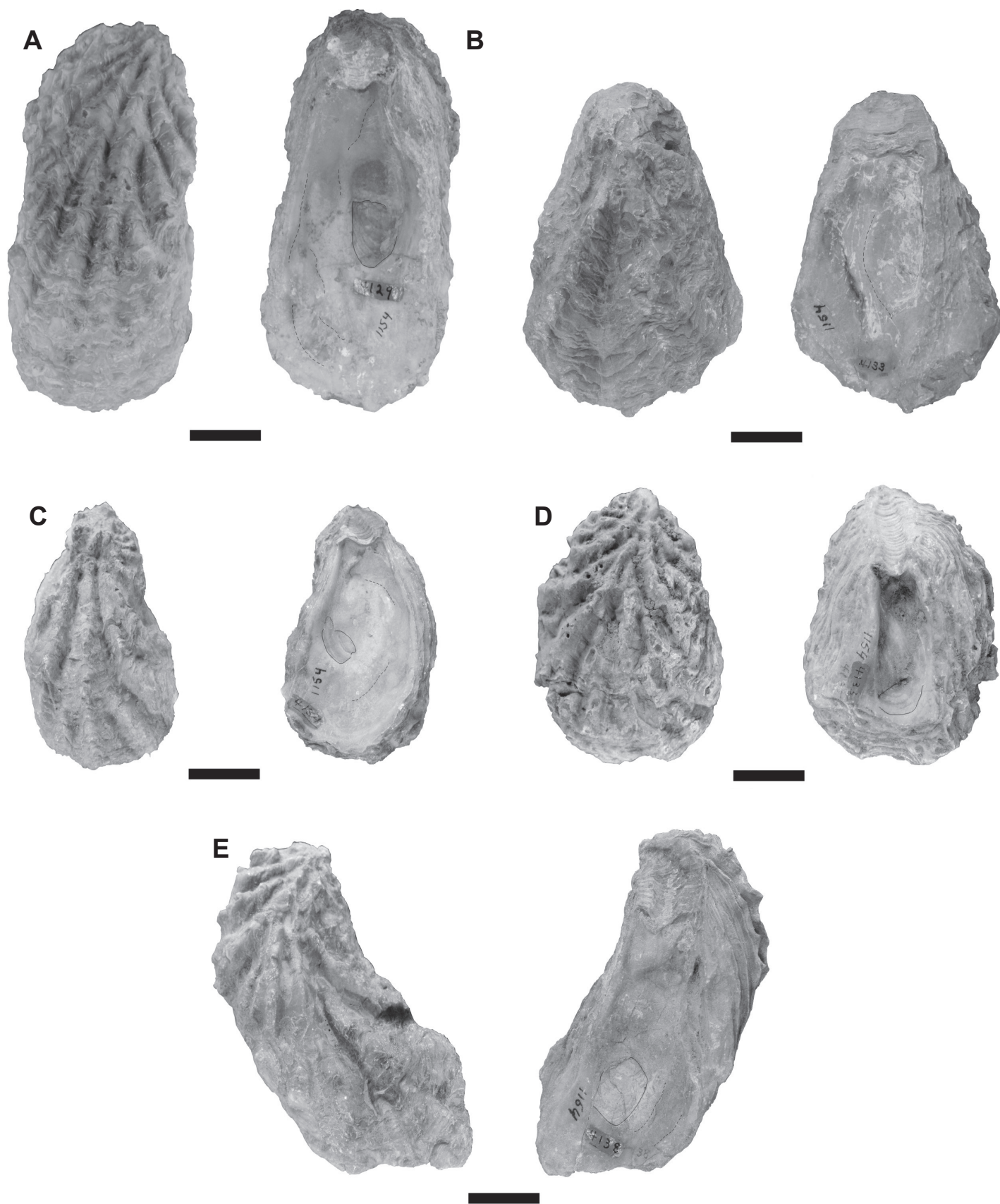


Figure 9. Fossils of *Orrstreidi wiedeyi* from Santa Rosa Island, California. External and internal views. **A**, right valve, lectotype CAS 4129; **B**, right valve, paralectotype CAS 4133; **C**, left valve, paralectotype CAS 4134; **D**, paralectotype CAS 4135; **E**, left valve, paralectotype CAS 4138. Scale bars = 30 mm.

The measures are: L, 72.5 mm; H, 141.8 mm; L/H, 0.51; W, 28.5 mm; LL, 30 mm; LH, 25 mm; LL/LH, 1.2; SL, 17.9 mm; SH, 23 mm; SL/SH, 0.77; S-L D, 47.7 mm; S-L D/H, 0.33.

The paralectotypes CAS 4133, CAS 4134, and CAS 4138 are oblong valves, moderately falcate except CAS 4133. This is a medium-sized right valve, convex and thick. Lamellae are somewhat appressed, arranged in intercalations of thin and thick layers. Vesicular layers not observed. Folds are wide, low, rounded-topped; unbranched, developed through the whole valve, and oblique to the valve margin. The number of folds is five. Hyote not developed. Ligament area rectangular, small, $\sim 1/4$ the valve's height. Resilifer markedly wide, medially divided toward the ventral part. Resilifer's medial axis straight. Chomata and chomatal protrusions not developed. Commissural shelf narrow, flat, elevated in the valve's dorsal half, no bounded by a curb. Branchial depression shallow; branchitellium hardly marked, lying in the anteroventral quadrant. Quenstedt muscle scar not developed. Adductor muscle scar oval, medium-sized, lying in the posteroventral sector near posterior valve margin. Scar plane oblique to midsagittal plane. Chalky deposits distributed in almost the whole inner surface, modified by diagenesis.

The specimen CAS 4134 is a medium-sized left valve, convex and thick. Lamellae arrange in intercalations of thin and thick layers; moderately appressed. Vesicular layers not observed. The valve exhibits 16 high folds, wide, rounded-topped folds; some folds branched, developed through the whole valve and oblique to the valve's margin. Hyotes not developed. Attachment area small, $\sim 1/10$ the valve's height. Ligament area sub-triangular, small, $\sim 1/5$ the valve's height. Resilifer's medial axis straight. Chomata and chomatal troughs not developed. Commissural shelf narrow, flat, elevated in almost the whole valve. Branchial depression shallow; branchitellium hardly marked, lying in the posteroventral quadrant, near the valve margin. The zone of the Quenstedt muscle scar is covered by sediment. Adductor muscle scar is circular, medium-sized. It lies in the midpoint between the dorsal and ventral margin, close to the posterior rim. Scar plane oblique to midsagittal plane. Chalky and vesicular deposits not observed.

The specimen CAS 4138 is a medium-sized left valve, convex and thick. Lamellae are thin and appressed. Vesicular layers not observed. The valve has 17 high folds, wide and rounded-topped. Some folds branched, but all oblique to valve's margin, developed through the whole valve. Toward the ventral margin, folds gradually lose height or branched into lower folds. Hyote not developed. Attachment scar not developed. Ligament area rectangular and large, $\sim 1/4$ the valve's height; dorsoventrally elongate. Resilifer's medial axis straight. Chomata and chomatal troughs not developed. Commissure shelf extremely narrow, flat and elevated. Branchial depression hardly marked; branchitellium inexistent. The zone of the Quenstedt muscle scar is covered by sediment. Adductor muscle scar large, oval, dorsoventrally elongate; dorsally subsided. The scar lies in a medial position, close to ventral margin. The scar plane oblique to midsagittal plane. Chalky and vesicular deposits not observed.

The average measures of the three oblong paratypes are: L, 73.1 mm; H, 111.9 mm; L/H, 0.65; W, 29.4 mm; LL, 26.96 mm; LH, 23.43 mm; LL/LH, 1.56; SL, 14.7 mm; SH, 17.2 mm; SL/SH, 0.92; S-L D, 44.36 mm; S-L D/H, 0.39.

The specimen CAS 4135 is a medium-sized, sub-circular right valve; convex and thick. Lamellae thin, somewhat appressed. Vesicular layers not observed. The valve has 19 high folds, wide, angled- to rounded-topped. Folds are branched and oblique to the valve's margin, developed through the whole valve. Hyote not developed. Ligament area rectangular, medium-sized, $\sim 1/3$ the valve's height. It is very narrow and dorsoventrally elongate. Resilifer highly projected toward body cavity; medial axis straight. Chomata and chomatal protrusions not developed. The specimen specially differs from the remainder paratypes by a very narrow and deep body cavity, ventrally bounded by a small, subcircular adductor muscle scar. Scar plane oblique to midsagittal plane. Commissural shelf elevated, narrow in the anterior margin but wider in the posterior one. Branchial depression hardly marked, narrow. Branchitellium not marked. The zone of the Quenstedt muscle scar is covered by sediment. Chalky and vesicular deposits not observed.

The measures are: L, 77 mm; H, 101.2 mm; L/H, 0.76; W, 35.1 mm; LL, 19.9 mm; LH, 40.5 mm; LL/LH, 0.49; SL, 16.4 mm; SH, 13.6 mm; SL/SH, 1.2; S-L D, 38.8 mm; S-L D/H, 0.38.

Comments. The specimens CAS 4129, CAS 4133-CAS 4135, and CAS 4138 are clearly dissimilar to Miocene, Pliocene and Pleistocene specimens. They can be distinguished by the shape of the shell and ligament area; the lack of chomata, chomatal troughs and protrusions; and the architecture of the commissural shelf.

Morphometric comparisons. The measures indicate a similitude among all type specimens, and slight differences related to valve size. Changes in size accentuated the oblong shell outline and the dorsoventral elongation of adductor muscle scar. In comparison with Miocene, Pliocene and Pleistocene specimens, CAS 4129, CAS 4133-CAS 4135, and CAS 4138 show a distinctive L/H, SL and SH values, which indicate the prevalence of oblong shells and small adductor muscle scars. The values of these specimens were not incorporated to statistical analysis.

Taxonomic remarks. Contrary to Moore (1987), it was not recognized in the specimens the combination of traits to place them in *Pycnodonte*. Instead, the specimens exhibits clear differences such as the shell shape, a similar convexity in both valves, with well-developed sculpture; the absence of gashes in the right valve, and the lack of a wide commissural shelf. Furthermore, CAS 4129, CAS 4133-CAS 4135, and CAS 4138 do not show features of *Hyotissa*. The main differences with this genus are the prevalent oblong shape of the shell, the absence of hyote, the predominant rectangular ligament area; the absence of chomata, chomatal troughs and protrusions; and the architecture of the shelf. This combination of features is persistent in almost all specimens. Still, some features were observed in oblong valves from Loreto Basin and Imperial County. Besides, oblong valves are numerically rare. On the other hand, CAS 4129 has an arch-like adductor muscle scar

(Figure 9A), not described by Hertlein (1928) and Moore (1987). However, none of the specimens linked to *Hyotissa* shows a similar scar.

According to Moore (1987), the same specimen has broken hyote. Nevertheless, in her illustration (pl. 15, fig. 5) the hyote remains cannot be recognized; Hertlein (1928) just mentioned the “nodose” aspect of the folds, and the present authors did not observe any hyote remain. Moore (1987) also noted that double-valved specimen CAS 4130 has hyote, and pointed out its external resemblance to specimen USNM 647296 *Hyotissa haitensis* of Woodring (1982, pl. 98, fig. 2). In the illustrations of CAS 4130 (Hertlein, 1928; pl. 23, fig. 10; Moore, 1987; pl. 15, figs. 1, 4) hyote are clearly visible in both valves, along with a large attachment scar. However, the internal morphology is inaccessible.

Hertlein (1928) distinguished *Ostrea wiedeyi* fossils from Pliocene specimens CAS 1825 and CAS 1826, and pointed out a trend in the elongation of the shell. This tendency is congruent with our metrical observations. Still, the sub-ovate specimens have an external and internal resemblance with *Hyotissa*. Unfortunately, it was not examined ovate specimens such as CAS 4130-CAS 4132, CAS 4136, and CAS 4137; small valves with *Hyotissa*-like morphology, collected from the same locality and horizon (Hertlein, 1928). However, Hertlein & Grant (1972) emphasized the absence of chomata in *O. wiedeyi*.

Since specimens CAS 4129, CAS 4133-CAS 4135, and CAS 4138 cannot be assigned in *Pycnodonte* or *Hyotissa*, and given that any known genus, recent or fossil, is not appropriate to place the specimens; it was defined the new genus *Orrstreidi*.

It is kept in the family Gryphaeidae since the genus differs from Ostreidae members by the shape of the adductor muscle scar, and the presence of the commissural shelf (Stenzel, 1971; Harry, 1985; Coan & Valentich-Scott, 2012). The features of the ligament area in Exogyrinae exclude *Orrstreidi* gen. nov. from the subfamily. The genus shows the traits of the Mesozoic Gryphaeinae, such as the lack of chomata and a vesicular structure (Stenzel, 1971). However, the present authors considered *Orrstreidi* gen. nov. as a Pycnodontinae, though it lacks a vesicular structure, chomata, and commissural shelf bounded by a curb; traits associated to the subfamily (Stenzel, 1971). The fact that the present authors, as well as Moore (1987) have not observed the vesicular structure in the exterior surface does not necessarily imply its inexistence. Eventually, vesicular structure might be found into shell interior, and chomata might be found in young specimens.

Comments on morphometric approach. The morphometric data reported in taxonomic literature have been scarce and disperse (see Conrad, 1855; Gabb, 1869; Hanna, 1926; Olsson, 1961; Emerson & Hertlein, 1964; Keen, 1971; Zuschin & Piller, 1997; Zuschin & Baal, 2007); though, some authors have documented useful values ranges. Woodring (1938) reported shell length ranges of small specimens of *Ostrea heermanni* from Imperial Formation (37.8-44.8 mm and 27.3-40.7 mm). Regarding to *Hyotissa hyotis*, based on Recent specimens collected in the Gulf of California, Sevilla *et al.* (1998) reported a shell length range from 120 to 200 mm,

and a diameter range from 10 to 200 mm; and Duprat-Bertazzi & García-Domínguez (2005) reported a shell length variation from 135 to 235 mm (n= 418, mean= 175 mm).

However, there is not more information. In order to fill this gap, and to have more elements for comparisons, it was gathered new metric data; useful to verify taxa identifications based on qualitative criteria like the relative shell size or thickness (*e.g.* Hanna, 1926; Powell, 2008). It was opted to use the common parameters L, H, W, LL, LH, SL, SH, to get basic information on size variation and shape modifications (ratios L/H, LL/LH, SL/SH). Due to the manner in how W was taken (Figure 4), values indifferently reflect the shell thickness and convexity.

The followed procedure is a classical morphometric approach, which essence does not differ from the modern geometrical methods (Viscosi & Cardini, 2011). In both methods, researcher is free to establish the measurements points or landmarks in the geometrical jargon; and a kind of measurement is done. In the classical method is used a caliper or rule, and measurements are directly taken over the specimens. In geometrical morphometrics, measurements are assisted by a computer, done over a series of images. Measurements can be expressed in different kind of units, *e.g.* millimeters or pixels. In both approaches, data explorations and comparisons are supported by a plethora of statistical tools, nowadays all assisted by computers. Again, researcher is free to select the tests.

Morphological observations suggest a similarity among specimens examined, but some size differences among the groups were indicated by the metric data (Figure 7). In order to show if differences are or not significant, the present authors performed the statistical comparison. The analysis was based on a slight modification of the Lich's (1990) procedure. It was figured to recognize morphological differences among several fossils samples, from several stratigraphic levels. Lich's procedure ponders the statistical effects of limited morphological data.

A set of statistical models related to ANOVA is performed in series (Lich, 1990; see Anderson, 1993 for a detailed explanation). Following the order, the models are: Homogeneity of Variance (**HV**), one-way ANOVA, Tukey's Honestly Significant Difference (**HSD**), and Student-Newman-Keuls (**SNK**). The HV was used to recognize if data sets are suitable to one-way ANOVA test. Since usually the data was not suitable for a one-way ANOVA, this was replaced by the non-parametric Kruskal-Wallis (**KW**) test. Once that either one-way ANOVA, this or KW indicated differences in at least one comparative group, they were identified using HSD, SNK, and the mean rank values derived from KW.

The results in the Table 6 indicate significant size differences in few groups (9, 12, and 18); even, the mixed group 8 does not differ from others. Only the ligament area of some aged specimens show an important change in the shape (Figure 5C). These observations are opposite to the wide variability in the Pycnodontinae species stated by Hanna (1926), Hertlein (1928), Loel & Corey (1932), Squires & Fritsche (1978) and Moore (1987). It is a fact

that environmental conditions modified shell morphology, but according to our observations the modifications are occasional, e.g. some fossils from Isla Coronados and Imperial County. In these cases, the inner morphology is the less altered.

In comparison with the value ranges reported in the literature, our specimens overlaps with the somewhat larger Recent specimens (Sevilla *et al.*, 1998; Duprat-Bertazzi & García-Domínguez, 2005); but not with smaller fossils from the Imperial Formation (Woodring, 1938). The trend to find specimens > 50 mm in height (Figure 7) suggests a preservation of adult specimens. Kidwell & Bosence (1991) documented the selective destruction of juvenile shell of Recent bivalves. The selective destruction in *Hyotissa hyotis* is supported by its low growth rate of 0.8 to 3.3 mm year⁻¹ (Titschack *et al.*, 2010), which means that an individual must have lived 15 years at least, to reach and height of 50 mm.

Finally, the number of folds is the most variable feature, but specimens with less than 7 folds are rare. This explained the metrical and statistical distinction of group 1 (Figure 8, Table 6); but since it was intentionally formed by the less folded specimens, it is likely that a different configuration of the groups obliterates this quality.

CONCLUDING REMARKS

The taxonomic revision shows on one hand, that *Pycnodonte heermanni* does not occur in Loreto Basin as was reported by Moore (1987) and Piazza & Robba (1994). Instead, the larger, sturdier and folded oysters in the basin belong to *H. hyotis*. On the other hand, taxonomic revision shows that *H. hyotis* occurs in the Pliocene Imperial Formation from southern California, the same rock unit and area where *P. heermanni* was originally described (Conrad, 1855; Moore 1987).

The comparison between two sets of specimens from both areas indicates that there are not marked morphological and morphometrical differences to consider them as members of two different taxa. Furthermore, the present authors argue that the poor folded syntypes of *P. heermanni* could be unusual specimens in the Formation, as was pointed out by Hertlein & Grant (1972) and supported by own observations (Figure 8). The understanding of the folds morphogenesis in oysters (Checa & Jiménez-Jiménez, 2003), and the influence of the environmental conditions in this process (Arnold, 1909) can explain the folds variation in specimens like syntypes.

The present authors revised all occurrence reports of *Pycnodonte heermanni* (Table 7) and found several uncertain identifications (recognized by the use of ‘cf.’ and ‘aff.’ nomenclature); identifications based on descriptions of Conrad (1855) and Hanna (1926); and a co-occurrence of *Ostrea fischeri* (= *Hyotissa hyotis*) and *O. heermanni* (= *P. heermanni*) in some sites. In most of the reports, there are not descriptions or illustrations. Since taxonomic identifications have been based on comparisons with the Imperial Formation specimens, it is likely that records of *P. heermanni* actually represent *H. hyotis* occurrences.

Moore (1987) list the occurrence of *P. heermanni* in the Pliocene Almejas Formation, Vizcaino Peninsula, Pacific coast of the Baja California Sur, after Minch *et al.* (1976). However, the present authors did not find elements on Minch *et al.* (1976) to support the presence of the species.

The taxonomic revision made here allows extending with certainty the Neogene fossil record of *Hyotissa* in West America until the Early Miocene of southern coastal California (23.03-15.97 Ma) (Table 7). This occurrence coincides with the most extended known record of *Hyotissa* in Eastern America; i.e. fossils of *H. haitensis* have been found from Florida (United States) to Pará (Brazil). It is unknown if *Hyotissa* arrived to northern western America from Asia by crossing the Pacific Ocean, or from eastern America by crossing the ancient Atrato seaway (Figure 10). The possible fossil occurrences of *H. hyotis* in Hawaii (Paulay, 1996, p. 24), and the reports of the same species in Clipperton Island (Keen, 1971) suggest the genus capability to travel 5000 km (Lessios, 2008), which means a double arrived in America.

The type specimens of *P. (P.) howelli* (Wiedey, 1928) (Moore, 1987, p. C20; pl. 14, figs. 1, 3, 5, 7) and *P. (P.) loeli* (Moore, 1987, p. C21; pl. 18, figs. 7, 8), both from southern coastal California (Early Miocene Vaqueros sandstone) (Moore, 1987), might have closer taxonomic relationships with *O. wiedeyi*, given that all specimens share its peculiar oblong, thick, and strongly folded shell. Besides, specimens share the outline and position of the adductor muscle scar, and the narrow commissural shelf. However, an exhaustive examination is needed to elucidate their taxonomic identity. In the meanwhile, the new genus *Orrstreidi* represents a new enigmatic Pycnodonteinae, only known from Channel Islands. Nevertheless, a strongly similar but smaller specimen, identified as *Parahyotissa* sp., had been described from Miocene rocks from Palenque, Chiapas, Mexico (Velasquillo, 2011).

For the Middle Miocene, two West America species are known from La Culebra Cut rocks (Table 7), units that have been related to the ancient Culebra strait (Kirby *et al.* 2008). From the same area and rock unit, specimens of “*Hyotissa*” *tryoni* (Gabb, 1881) were retrieved. It is a Caribbean-Pacific taxon, being also reported in the Early and Middle Miocene rocks of Venezuela and Carriacou Island (Woodring, 1982).

The fossils from La Culebra Cut are much more similar to *Pycnodonte* specimens than *Hyotissa* ones (Woodring, 1982, p. 607). Indeed, the illustrated specimen USNM 647278 of Woodring (pl. 94, figs. 7, 8) seems to show more typical features of *Pycnodonte* than type specimens of *P. (P.) howelli* or *P. (P.) loeli*. USNM 647278 is a poorly folded, strongly convex left valve; which apparently has a radial posterior sulcus, and a posterior flange. Besides it exhibits a marked geniculated commissural shelf, and a prominent umbo incurvature. This association of features are not observed in the Vaqueros specimens, but they are present in many Mesozoic and Cenozoic *Pycnodonte* species.

However, the resemblance between USNM 647278 and the holotype USNM 164966 of *P. (C.) eldridgei* (Arnold, 1907), a third Early Miocene species from Vaqueros sandstone, is very notable. USNM 164966 is an oval, left valve very

Table 7. Late Cenozoic fossil record of *Hyotissa* in Western America. Taxonomic assignments after Moore (1987) (**) or discussed in the systematics section (*). Most reports based on specimens assigned to *Pycnodonte heermanni*. Here they are considered as *Hyotissa hyotis* members, though further examinations are needed to elucidate the actual identity. Updating of ages and geology was based on Simian & Johnson (1997), Oskin (2002), Carreño & Smith (2007), Johnson *et al.* (2007), and Kirby *et al.* (2008).

Taxa	Age	Rock unit	Location		References
<i>H. cf. H. hyotis</i> *	Early Miocene	Vaqueros sandstone	Coyote Creek, California	United States	Loel & Corey (1932)
<i>H. polylopha</i>	Middle Miocene	Pedro Miguel Fm.	Culebra Cut, Panama Canal	Panama	Woodring (1982)
<i>H. haitensis</i>	Middle Miocene	Pedro Miguel Fm.	Culebra Cut, Panama Canal	Panama	Woodring (1982)
<i>H. haitensis</i>	Late Middle Miocene	Isidro Fm.	La Purísima, Baja California Sur	Mexico	Smith (1984)
<i>H. cf. H. hyotis</i> *	Late Miocene	Unit M8c	Isla Tiburón, Sonora	Mexico	Gastil <i>et al.</i> (1999)
<i>H. haitensis</i>	Late Miocene	Unit M8d	Isla Tiburón, Sonora	Mexico	Gastil <i>et al.</i> (1999)
<i>H. hyotis</i>	Late Miocene-Early Pliocene	Infierno Fm.	Northern Península Concepción	Mexico	Wilson (1948)
Hh**	Late Miocene-Early Pliocene	Infierno Fm.	Northern Península Concepción	Mexico	McFall (1968)
Hh**	Early Pliocene	Refugio Fm.	El Refugio, Baja California Sur	Mexico	Hertlein (1957)
<i>H. hyotis</i>	Early Pliocene	Refugio Fm.	El Refugio, Baja California Sur	Mexico	Hertlein (1966)
<i>H. hyotis</i>	Late Pliocene	Infierno Fm.	Boleo Basin, Baja California Sur	Mexico	Wilson (1948)
<i>H. hyotis</i>	Late Pliocene	Infierno Fm.	Boleo Basin, Baja California Sur	Mexico	Wilson & Rocha (1955)
<i>H. hyotis</i>	Late Pliocene	Infierno Fm.	Isla San Marcos, Baja California Sur	Mexico	Durham (1950)
Hh**	Late Pliocene	Unnamed rocks	Bahía Santa Inés, Baja California Sur	Mexico	Hertlein (1957)
Hh**	Late Pliocene	Unnamed rocks	Isla Cerralvo, Baja California Sur	Mexico	Emerson & Hertlein (1964)
Hh**	Late Pliocene	Unnamed rocks	Isla Cerralvo, Baja California Sur	Mexico	Hertlein (1966)
<i>H. hyotis</i> *	Pliocene	Imperial Fm.	Colorado Desert, California	United States	Conrad (1855)
<i>H. hyotis</i> *	Pliocene	Imperial Fm.	Colorado Desert, California	United States	Hanna (1926)
Hh**	Pliocene	Imperial Fm.	Colorado Desert, California	United States	Woodring (1938)
Hh**	Pliocene	Imperial Fm.	Colorado Desert, California	United States	Foster (1980)
Hh**	Pliocene	Imperial Fm.	Colorado Desert, California	United States	Powell (2008)
<i>H. hyotis</i> *	Pliocene	Imperial Fm.	Colorado Desert, California	United States	This paper
Hh**	Pliocene	Unnamed marine conglomerate	San Felipe, Baja California	Mexico	Hertlein (1968)
Hh**	Pliocene	Infierno Fm.	Southern Península Concepción	Mexico	McFall (1968)
<i>H. hyotis</i>	Pliocene	Marquer Fm.	Isla Carmen, Baja California Sur	Mexico	Durham (1950)
<i>H. hyotis</i>	Pliocene	Marquer Fm.	Isla Carmen, Baja California Sur	Mexico	Hertlein (1957)
<i>H. hyotis</i> *	Early Pleistocene	San Juan Limestone	Loreto Basin, Baja California Sur	Mexico	Gabb (1869)
<i>H. hyotis</i>	Early Pleistocene	Piedras Rodadas Fm.	Loreto Basin, Baja California Sur	Mexico	Durham (1950)
<i>H. hyotis</i> *	Early Pleistocene	San Juan Limestone	Loreto Basin, Baja California Sur	Mexico	Piazza & Robba (1994)
<i>H. hyotis</i> *	Early Pleistocene	Piedras Rodadas Fm., El Troquero Fm., San Juan Limestone	Loreto Basin, Baja California Sur	Mexico	This paper
<i>H. quercina</i>	Early Pleistocene	Piedras Rodadas Fm., San Juan Limestone	Loreto Basin, Baja California Sur	Mexico	This paper
<i>H. hyotis</i>	Late Pleistocene	Coral reef deposits	Isla Coronados, Baja California Sur	Mexico	Durham (1950)
<i>H. hyotis</i> *	Late Pleistocene	Coral reef deposits	Isla Coronados, Baja California Sur	Mexico	This paper
<i>H. quercina</i>	Late Pleistocene	Coral reef deposits	Isla Coronados, Baja California Sur	Mexico	This paper
<i>H. hyotis</i>	Late Pleistocene	Unconsolidated sand	Isla Carmen, Baja California Sur	Mexico	Durham (1950)
<i>H. hyotis</i>	Pleistocene	Santa Rosalía Fm.	Boleo Basin, Baja California Sur	Mexico	Wilson (1948)
<i>H. hyotis</i>	Pleistocene	Santa Rosalía Fm.	Boleo Basin, Baja California Sur	Mexico	Wilson & Rocha (1955)
<i>H. quercina</i>	Pleistocene (?)	Unnamed rocks	San Basilio, Baja California Sur	Mexico	This paper
<i>H. hyotis</i>	Pleistocene	Reef Suite deposits	Punta San Telmo, Baja California Sur	Mexico	Squires (1959)
<i>H. hyotis</i>	Pleistocene	Unnamed rocks	Isla Santiago, Galápagos Islands	Ecuador	Hertlein & Strong (1939)

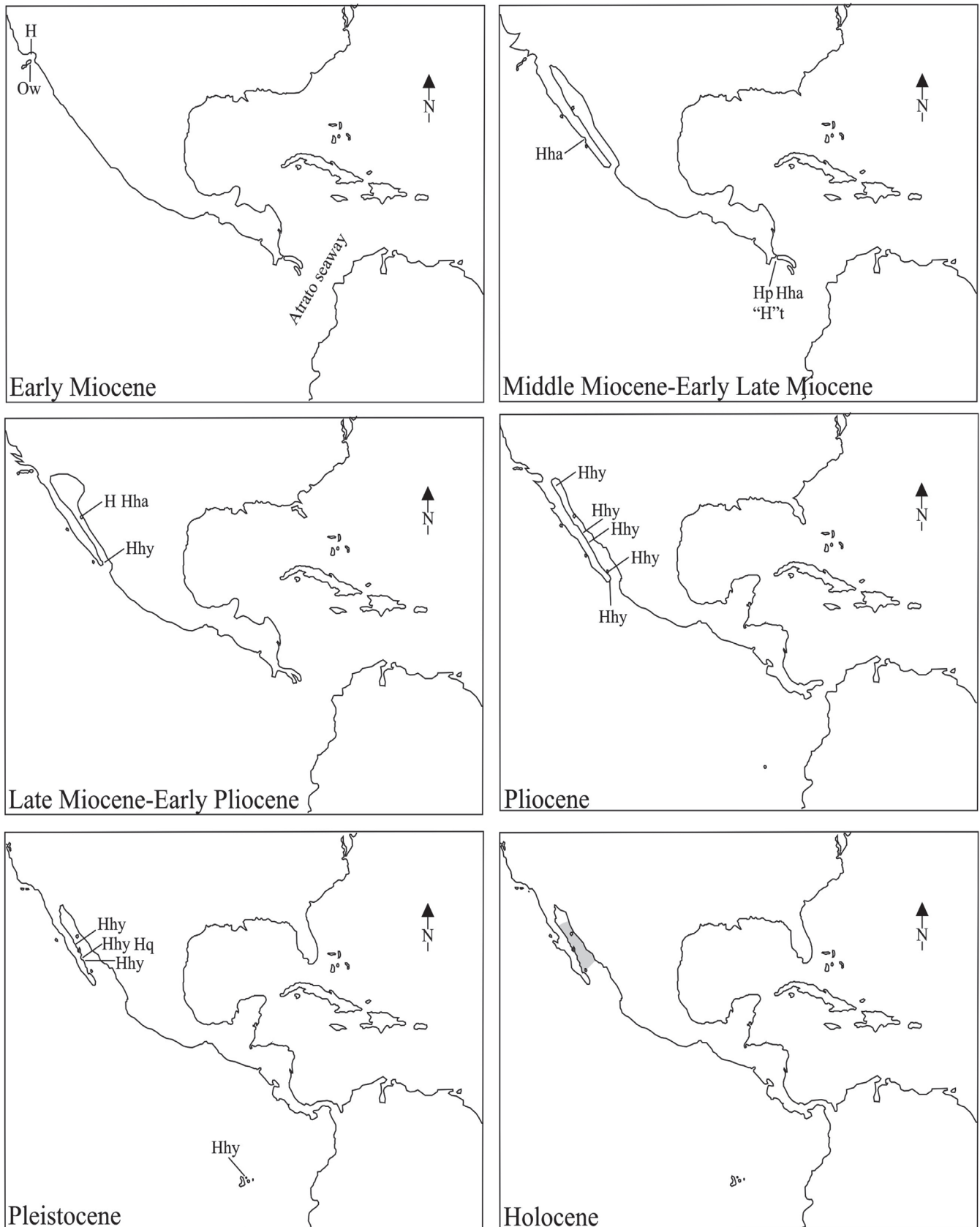


Figure 10. Late Cenozoic records of *Hyotissa* in Western America. **H**, *Hyotissa* cf. *hyotis*; **Hha**, *H. haitensis*; **Hp**, *H. polylopha*; **Hq**, *H. quercina*; **Hhy**, *H. hyotis*. Shaded area represents the current distribution of *H. hyotis* inside the Gulf of California. Additionally, it is represented the occurrences of *Hyotissa*-like oysters *O. wiedeyi* (**Ow**) and "*H. tryoni*" ("**H"t**"). Fossil occurrences according with Table 7. Paleogeography after Carreño & Smith (2007), Kirby *et al.* (2008), and Ledesma-Vázquez & Carreño (2010).

convex, with an umbo incurvature prominent. Moore (1987, p. C21) mentioned the existence of the radial posterior sulcus, which bounded a narrow and elongate posterior flange (see Moore, 1987, pl. 21, figs. 1, 4). “*H.* tryoni is considered by Woodring (1982) as a “link between *Pycnodonte* and *Hyotissa*”; but the present authors think this species along with *P. (C.) eldridgei* are closer to *Pycnodonte*.

The fossils found in La Purísima, and particularly in Isla Tiburón (deposits younger than 5.6 Ma after Oskin, 2002) (Table 7) prove the presence of *Hyotissa* in the ancient Gulf of California. By that time, the ‘tectonic protogulf’ has a P-like shape, elongate and narrower in the south, and largely extended in the north (Karig & Jansky, 1972; Fenby & Gastil, 1991; Ledesma-Vázquez & Carreño, 2010) (Figure 10). Certainly, oceanographic conditions were completely different (Ledesma-Vázquez & Carreño, 2010; Álvarez-Borrego, 2010), which suggests the capacity of *Hyotissa* to face harder conditions of semi-closed marine systems.

It was discarded the Late Miocene occurrence of *P. (C.) veracruzana* in the Gulf of California, by which it remains as a Middle Miocene Atlantic species (Perrilliat, 1994).

The best fossil record of *Hyotissa* is centered in the Pliocene of the Gulf of California only involved *H. hyotis*. This species lived through the entire gulf, from the gulf’s mouth to its head, as is revealed by the fossils found along the Baja California peninsula and southern California (Figure 10). In contrast, the populations nowadays are distributed from the Bahía of San Luis Gonzaga, Baja California to Bahía de La Paz, Baja California Sur (Brusca & Hendrickx, 2008) (Figure 10). This more restricted distribution is not continuously connected to Pacific Ocean; even though the current Gulf of California is a more ‘open’ marine system than it was in the Pliocene (Umhoefer *et al.* 1994; Ledesma-Vázquez & Carreño, 2010).

It was re-considered the Loreto Basin as the place with the best fossil record of *Hyotissa* for the Early Pleistocene in all West America. On one hand, the present authors found several fossils of *H. quercina* (G. B. Sowerby II, 1871) in two formations of the Loreto Basin (Table 7); though the species the present authors not treated here because their distinctive morphology from southern California specimens. The treatment of the species as a member of a *Parahyotissa* genus remains controversial (see Harry, 1985; Kirkendale *et al.* 2004; Huber, 2010; Coan & Valentich-Scott, 2012), but the present authors opted to consider it as *Hyotissa*. The present authors additionally found specimens of *H. quercina* in the Late Pleistocene coral-reef deposits of the Isla Coronados.

Today, the species of this form, *Hyotissa mcgintyi* (Harry, 1985) is distributed in the tropical eastern and western Atlantic Ocean; and *H. imbricata* (Lamarck, 1819) and *H. numisma* (Lamarck, 1819) are distributed in the Indo-West Pacific tropics. Velasquillo (2011) reports one left valve of *Parahyotissa* from Miocene of Chiapas, and although this and Loreto fossils are the only fossil occurrences of this form known in Mexico, it is enough to inquire when, how, and how many times this form arrived to western America.

On the other hand, the present authors study just a small fraction of specimens of *Hyotissa hyotis* from Loreto,

about 80 specimens; but in the basin, the fossils are largely abundant in well exposed and huge outcrops. Besides, fossils are related to several facies, widely described and related to different depositional settings. It allows realizing that ancient populations established here faced conditions of small-scale open marine systems (horizons 1, 2, Figure 2), or small-scale closed-marine systems (horizons 3-8) without underwent important morphological modifications in the shell. These observations imply that reduction of folds specimens from southern California and Isla Tiburón can be related to specific growth conditions (*e.g.* some fossils from Coronados island), or extreme environment.

The dating of the tuff horizons made by Umhoefer *et al.* (1994) and Gillot (in Bigioggero *et al.*, 1995) constraint the age of the deposits, and rule out the traditional vision in which the basin is associated to the Pliocene period. It is possibly that deposits in the Carmen Island from the Marquer Formation, and the Carmen-Marquer Formation (Carreño & Smith, 2007) belong to the Pleistocene; since it has been found the same fossil fauna (see Durham, 1950 and Piazza & Robba, 1994, 1998).

Finally, Ranson (1941) and recently Huber (2010), considered the Recent populations in west America as members of a different species (*Hyotissa fisheri*). For Ranson (1941), populations are morphologically similar to Indo-Pacific populations of *H. hyotis*; but for Huber (2010, p. 614) “*H. fisheri* is the most fragile, moderately plicate, generally found in purplish-brown or deep red juveniles. *H. fisheri* is only known from Panamic water. It has been well depicted by Keen (1971). *H. fisheri* is marked distinct from [*H.*] *hyotis* and barely confoundable when both species are at hand. Easiest for distinction in *Hyotissa* are the muscle scars in adults, not particularly colored, flat in [*H.*] *fisheri*, yellowish brown, marked elevated in [*H.*] *hyotis* and generally smaller, dark purple-black and flat in [*H.*] *sinensis*.”

No doubt, Ranson (1941) and Huber (2010) faced the same problems the present authors faced when they tried to identify for first time the fossils, mirrored when these authors partially compared the descriptions of *Hyotissa haitensis* with the studied specimens of *H. hyotis*. Based on Huber (2010) statement, the observations seem to reveal a third form, in which the distinctive features of the adductor muscle scar in two Recent populations are rare among the fossils. It is probably that Ranson (1941) and Huber (2010) are right; but also, it is equally probably that differences observed in the both forms are just little variations of some few features.

This study reveals that *Hyotissa* species exhibits a little variation in morphology, contrary to many claims on the wide variation of oysters. Paradoxically, it represents serious problem that taxonomists need to resolve in order to understand and document in a reliable way the Pycnodontinae diversity. The issue might be resolved with further acquisition of information on morphology variation, and here the present authors did the first step. Studies on morphological variation are as important as genetical (Bieler *et al.*, 2004; Kirkendale *et al.*, 2004); anatomical (Harry, 1985; Sevilla-H. *et al.*, 1998); and even biochemical (Rodríguez-Astudillo *et al.* 2007) ones.

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