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PHYLOGENETIC SIGNIFICANCE, TAXONOMIC STATUS AND THE SCIENTIFIC NAMES OF THE BRAZILIAN OYSTERS

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ABSTRACT

The paper briefly discusses the systematic position of the Brazilian Oysters, together with their phylogenetic significance. The diagnostic generic features of the three commonly known oysters are described. Taxonomically, the three common species of Brazilian oysters can be assigned to the genus *Crassostrea* while the fourth less common species should be placed in the genus *Ostrea*. Available evidence indicates that oysters might have originated diphyletically, during the Triassic period, from two different genera, *Gryphaea* and *Lopha*. Among the species of the genus *Crassostrea*, the largest type, *Crassostrea paraibanensis* shares much of the generic features with the ancestral stock of *Cassostrea gryphoides* and most probably has descended from it. Genetical experiments, so far, negate the idea that *Crassostrea brasiliana* is phylogenetically derived from the Atlantic-Pacific stock from which the two North American species have derived, and hance it also might have descended from the stock of *gryphoides*. The position of *Crassostrea* sp is still uncertain as much more research is required, especially into its anatomy and physiology to arrive at any conclusion.

INTRODUCTION

Oyster taxonomy has been one of the most intricate and difficult problems among the animal kingdom. The task has been complicated further by the great variabilites of shell characteristics which seem the only source of evidence for palaentologists. Even conchologists and malacologists too tend to rely almost exclusively on the shells for key

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features as basis for sound classification. Consequently, phylogenetic sequences of oysters, as fact of nature, remain incomplete.

HISTORICAL REVIEW

Although the earliest oysters can be traced to the Late Triassic (STENZEL, 1971) no fossil record is available concerning Brazilian oysters. However, archaeological studies on shell middens using radiocarbon dating (FAIRBRIDGE, 1976) suggest that the principal food of the Indians, who settled along the coastal belts and estuaries of Brazil during Holocene period, about 7,000 years ago, consisted at least four species of oysters. Possibly, some of these specific names are repetitious and are synonyms (see Table I). The detailed descriptions of the three known Brazilian species of Ostreidae have been recently reported (SINGARAJAH, 1980). Because the systematic position is rather ambiguous and the scientific names are confusing, this paper briefly clarifies the relationship of the Brazilian oysters, particularly of the genus *Crassostrea.*

VALID GENERA AND SCIENTIFIC NAMES

There has been considerable overlap in the generic and specific names of the living oysters within the family Ostreidae. At least 100 species have been listed throughout the world, but the vast majority of these appear to be synonyms or repetitious. STENZEL (1974) recognizes some eleven valid generic names, some of them were, no doubt, synonyms. On the other hand, GUNTHER (1950) considers that there are only three definite genera, namely: *Ostrea*, *Crassostrea* and *Pycnodonte*, besides three other rather doubtful genera such as *Alectryonia*, *Dendostrea* and *Striostrea*, but he admits that the last two might be synonyms.

RANSON (1941, 1943, 1948, 1960, 1967), who contributed much to the understanding of the taxonomic relationship between fossil and living oysters, placed oysters broadly into three definite genera, but he combined the three genera of doubtful validity with *Ostrea.* Ranson's system of classification was based on the peculiar differences of prodissoconch, structure of shell (ORTON, 1928), promyal chamber (KELLOGG, 1892; NELSON, 1938), and other variable anatomical features. Ranson characterised his classification of genera briefly as follows:

1. *Pycnodonte:* the phylogenetically oldest ones which could be recognised by the presence of "chalky vacuolar" larval shell, with equal valves and the hinge carries an unbroken series of five interlocking teeth, and the presence of promyal chamber.

2. *Ostrea :* with lamellated flat larval shell and unequal valves, with interlocking teeth reduced to two on each side of provinculum, and presence of promyal chamber.

3. *Gryphaea :* with "chalky deposits lamellated larval shell" and unequal and asymetric valves, with teeth reduced to two on each side of provinculum and presence of promyal chamber.

However, GUNTHER (1950) preferred the generic name *Gryphaea* for the fossil types and assigned the most recent types of oysters to *Crassostrea.* KORRINGA (1952), in his extensive review, following Ranson's view, was not only reluctant to separate the two genera but identified them both as *Gryphaea.* Nevertheless, in his subsequent works, since accepting the ruling of the ICZN (1955), he discontinued the name *Gryphaea* and used the generic name *Crassostrea* for nonincubatory or "viviparous" oysters (KORRINGA, personal communication). Others (STENZEL, 1947, 1971; ABBOTT, 1974; GALTSOFF, 1951; WARMKE & ABBOTT, 1961) regarded *Crassostrea* as a separate genus and restricted *Gryphaea* to the fossil genus (STENZEL, 1971; ABBOTT, 1974).

Despite much controversy, it would be only logical to retain the generic name *Crassostrea* for large deeply cupped oysters as originally used (SACCO, 1897) and validated in accordance with the rules of the ICZN (1955) since the genus *Ostrea* is applied to the true flat incubatory or "larviparous" oysters. On the basis of our present state of scientific knowledge, the living family Ostreidae consists mainly of three genera:

1. *Ostrea* Linnaeus, 1758
2. *Crassostrea* Sacco, 1897
3. *Pycnodonte* Fisher de Waldheim, 1835

The genus *Lopha* Roding, 1798 and later described as subgenus by DALL (1898), though conceded to be synonym of *Ostrea* (GALTSOFF, 1964), is kept at the rank of subgenus to include two ecomorphs and the doubtful names referred above.

PHYLOGENETIC SIGNIFICANCE

Oysters on earth probably originated during Triassic period, about 200,000,000 years ago. In view of the uncertainity of the fossil evidence of early forms, the very first oyster seems speculative although a common ancestry of *Pseudomonotis* has been suggested (NEWELL, 1960). According to STENZEL (1971), all species, fossil and living, are traceable from their very first appearence in the Late Triassic to today, and all available evidence indicates that oysters might have evolved from two phylogenetic stems, each derived from a different genus: *Gryphaea* and *Lopha.* The important contributory factors which strengthen the diphyletic origin are:

1. that the oysters were anatomically different,
2. that they were contemporary, and
3. that they were geographically separated wide apart from each other in the beginning.

GRYPHAEA: The Triassic arctic sea was the place of origin and natural abode for Gryphaeas. This sea basin was apparently landlocked on all sides except for a narrow passage which connected the Pacific ocean basin on the western coast near the border between Canada and the U.S.A. At the same time, palaeogeographers agree with the existance of an isthmus which separated this arctic sea from the ancient Tethys sea covering the western and central Europe. The first *Gryphaea* probably evolved in the ancient arctic sea from a genus within the subfamily Pseudomonotinae and had its dominance and decline during the late Triassic. Due to the geological changes when the isthmus broke out during the early Liassic there was a mass interchange of marine organisms between the Mesogeean and the Arctic realms. It was then that *Gryphaea arcuata* and the closely allied species immigrated into the European (Mesogeean) sea (HALLAM, 1962). There the conditions were more favourable and the salinity was relatively high and they once again became so prolific and abundant and gave rise to many species. Some of the direct descendants of *Gryphaea arcuata* Lamarck, 1801 were:

Gryphaea dilata Sowerby, 1816
Gryphaea lituola Lamarck, 1819
Texigryphaea romeri Marcou, 1862
Pycnodonte (costeina) wardi Hill & Vaughan, 1898
Pycnodonte vessiculosa Sowerby, 1822

Of these direct descendants, the last two genera appeared to have shown some traits of transition during the Jurassic. However, after their rise and dominance *Gryphaea* encountered a period of decline. For reasons still obscure, these oysters developed recurved left beaks which impaired the opening of the valves, and consequently feeding and spawning became difficult thus caused their exinction, though adverse changes in climatic and environmental conditions and competition with other species could not be ruled out. While *Texigryphaea* also had only a limited success in number and species, *Pycnodonte* became prolific in species and world wide in distribution. During Miocene time it gave rise to *Neopycnodonte.* From the Triassic *Gryphaea* to their descendants living today are: *Neopycnodonte cochlear* Poli, 1795 and *Hyotissa hotis* (= *Mytilus hyotis* Linné, 1758), and probably a couple of other species all living in warm euhaline waters.

LOPHA: the oldest representative of the family Ostreidae, whose place of origin and natural habitat were the Triassic "Mesogeean and Pacific realms". Their direct descendants living today are: *Lopha folium (Mytilus cristagalli* Linné, 1758) and several

other species which are widely distributed. While Gryphaeidae have had their dominance during the Carnian period and abruptly diminished to only two rather insignificant living genera, the Ostreidae were still prolific and ranged along east-west Mesogeean realm, and speciation continued by succession and by geographic separation during the Miocene and Pliocene. Tectonic or other similar events which brought about barriers to their natural habitats, and consequently geographic separation, possibly contributed more for the speciation of the genus *Crassostrea*. The stock of *Crassostrea* of Tethys sea origin was *Crassostrea gryphoides* von Schlotheim, 1813, a giant oyster of the east-west range of Miocene time. Sometime towards the end of Miocene tectonic movements synchronously produced several land barriers across the former Tethys sea dividing it into a number of separate sea basins and bays. The discrete populations left behind in these broken remnants of Tethys sea simultaneously gave rise to many present day species:

Crassostrea angulata Lamarck, 1819 which is now spread out in Spanish, Portugal, French and Morroccoan coasts.

Crassostrea cucullata (= *Madrasensis* Preston, 1916) distributed along Indian coast, and.

Crassostrea gigas Thumberg, 1793 found along Japanese and Chinese coasts. Some of these have retained the remarkable capacity to grow to greatar size, a feature that is so reminiscent to their ancestor *Crassostrea gryphoides*.

Similarly, the two genera of *Crassostrea corteziensis* Hertlein, 1951 and *Crassostrea virginica* Gmelin, 1791 were daughter species of the common Pacific-Atlantic ancestor (STENZEL, 1971) of Miocene and Pliocene age. These were species formed as a result of geographic separation when the tectonic movements closed the gap which once existed between the two oceans through the straights of central America. Both *Crassostrea corteziensis* and *Crassostrea virginica* are very prolific and the former extends from Panama to gulf of California on the west coast while the latter from Virginia to gulf of Mexico on the east coast while the latter from Virginia to gulf of Mexico on the east coast of North America.

REMARKS

Concerning Brazilian oysters, there is no uniformity in the use of either generic or specific names. Despite clearly defined generic differences (ORTON, 1937 ; GUNTHER, 1950), the genus *Ostrea* is invariabily applied to *Crassostrea* and the specific names are so repetitious and have led to much confusion.

In my extensive collection and close examinations of oysters from Brazil, including the ones from other countries, the only species which could be correctly assigned to the generic name *Ostrea* is *Ostrea cristata* Born, 1778 and all the other known species of Brazilian oysters must be included into the genus *Crassostrea*. Therefore, in the interest of taxonomic revision, abiding by the ruling of the ICZN (1955), the practice of naming all oysters in Brazil as *Ostrea* must be discontinued.

GENERIC AFFINITIES:

Some of the generic features that are common to the three species of the genus *Crassostrea: Crassostrea paraibanensis*, (See Singarajah, in press), *Crassostrea brasiliana* Lamarck and *Crassostrea* sp are:

> shell variably thick, elongated to oval; left valve deeply cupped or concave, right shallow to flat; muscle scar farther removed from the hinge axis, Quenstead muscle recognizable; promyal chamber large; branchial ostia small; eggs relatively small and numerous; nonincubatory; prodissoconch valves unequal, with well developed umbo on left valve; hinge teeth indistinct; intestine bypasses the pericardium and does not pierce through the heart; euryhaline.

Ist should be noted that the differences between these species are more striking (see SINGARAJAH, 1980) than their similarities of generic features. From the phylogenetic point of view, *Crassostrea paraibanensis* shares many features with the ancestral stock of *Crassostrea gryphoides*. The remarkable capacity which this oyster has retained to grow to such an enormous size strongly suggests that it is more likely to have descended from the giant oyster *Crassostrea gryphoides* of Tethys sea origin (Fig. 1). However, the phylogenetic relatioship of *Crassostrea brasiliana* and *Crassostrea sp* is not very clear. *C. brasiliana* is comparatively smaller in size and often claimed to be an ecological variant of *Crassostrea virginica*. But, genetical experiments have shown that when *C. brasiliana* were allowed to crossbreed with a population of *C. virginica*, they failed to interbreed (Menzel, personal communication to Hopkins) and these results negate the idea that *Crassostrea brasiliana* might have derived from the "Pacific-Atlantic of Miocene" ancestor which gave rise to the two North American species. To ascertain the phylogenetic significance of *Crassostrea sp* is not so easy as much more work is required especially on its soft anatomy and physiology although this species differs in many respects from those of the other two Brazilian oysters.

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RESUMO

A posição sistemática das Ostras brasileiras é discutida assim como o seu significado filogenético.

Taxinomicamente, as três espécies comuns podem ser referidas ao gênero *Crassostrea*, enquanto uma quarta, menos comum, pode ser colocada no gênero *Ostrea*.

Evidência válida indica que estas Ostras poderiam haver tido uma origem difilética, durante o Triássico, a partir de dois gêneros diferentes, *Gryphaea e Lopha*. Entre as espécies do gênero *Crassostrea*, o maior tipo, *Crassostrea paraibanensis* compartilha muitos caracteres genéricos com o estoque ancestral de *Crassostrea gryphoides* e, muito provavelmente, é descendente dela. Experiências genéticas negam a idéia que *Crassostrea brasiliana* seja filogeneticamente derivada do estoque Atlântico-Pacífico do qual as duas espécies norte-americanas derivariam e, consequentemente, poderia ser igualmente descendente do estoque *gryphoides*. A posição de *Crassostrea* sp. é ainda incerta e precisa-se de muitas pesquisas anatômicas e fisiológicas para se chegar a melhores conclusões.

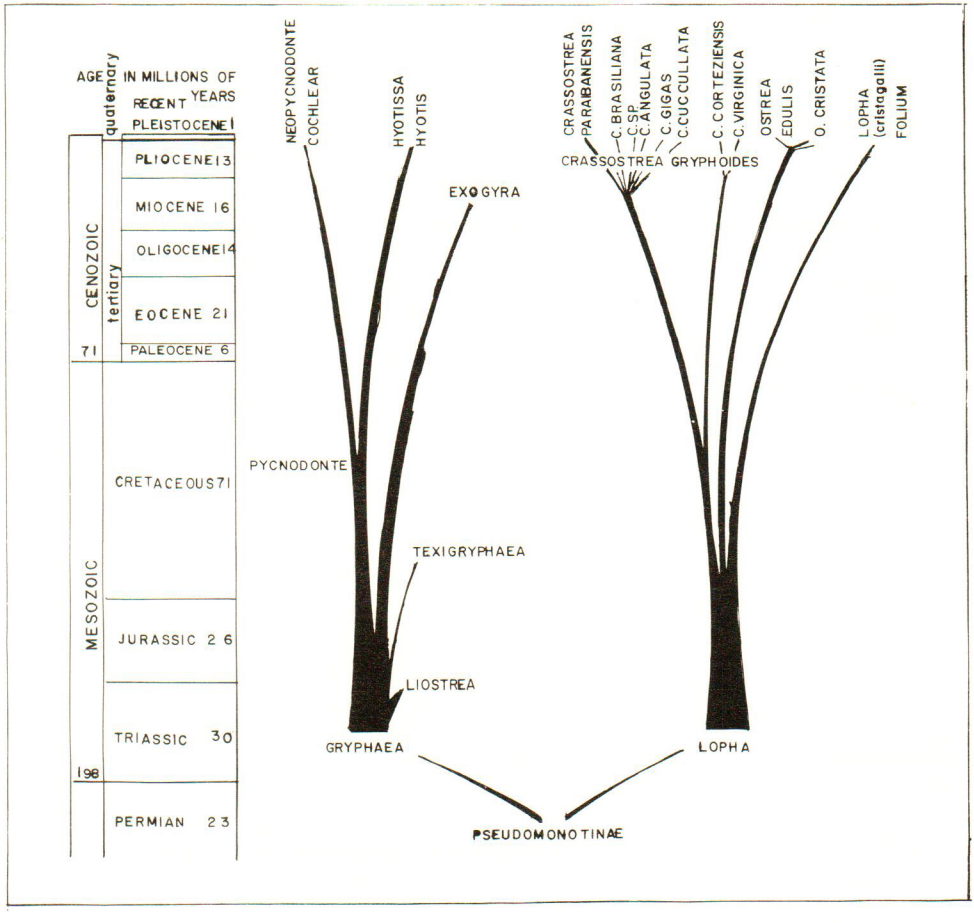

Table I. -- The commonly known living oysters from the Brazilian coast.

Comom names, either synonyms or erroneous	Valid scientific names	Habitat / locality
1. *Ostrea brasiliana* *Ostrea rhizophora* *Ostrea arborea* *Ostrea mangi* *Ostrea borealis* *Ostrea puelchana* *Ostrea adsociata*	*Crassostrea brasiliana* Lamarck, 1919 *(rhizophorae)* Guilding, 1928.	Estuarine, intertidal, widely distributed all along the Brazilian coast.
2. Rock Oyster? *Ostrea lama*	*Crassostrea paraibanensis* Singarajah, 1980	Estuarine, at dephts 2 - 3.5. m., on soft muddy bottom, Paraíba and possibly Northeasterns part of Brazil.
3. *Ostrea parasitica*	*Crassostrea* sp.	Estuaries, at depth 2 – 3 m., prefers high salinity, Rio de Janeiro.
4. *Ostrea spreta* *Ostrea equestris* *Ostrea guntata*	*Ostrea cristata* Born, 1717	Marine, euryhaline, limited in distribution to southern part of Brazil.

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