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SYSTEMATICS AND PALEOGEOGRAPHICAL STUDIES OF SOME SPECIES OF BRYOZOA (CHEILOSTOMATA) FROM THE GULF OF MEXICO

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ABSTRACT

Two groups of problematic species of bryozoans (Cheilostomata) from the Gulf of Mexico were analized. The first group contains species of the Genus *Stylopoma* Levinsen, 1909. The following species, which were usually confused, were distinguished by statistical methods: *Stylopoma spongites* (Pallas, 1766); *Stylopoma informata* (Lonsdale, 1845), a variety of *Stylopoma spongites* and a synthetic form called here *Stylopoma* sp. *5*.

The second group is represented by the species of the Family Smittinidae Levinsen, 1909. The most important genus with six species is *Parasmittina* Osburn, 1952, which contains the newly defined species *Parasmittina mexicana*. We have observed at least five evolutionary trends in this family, and the most important trend is found in the group called *trispiniformis* (without taxonomic significance).

A study of their paleobiogeographical, biogeographical and phyletical relationships was made for all the species. Both groups show the repercussions of the geological phenomenon of formation of the Isthmus of Panama (Pliocene-Pleistocene) in speciation and distribution of Recent species.

RESUMEN

Se analizaron dos grupos de especies con problemas sistemáticos del Phylum Bryozoa (Cheilostomata) del Golfo de México. El primer grupo pertenece al Género *Stylopoma* (Levinsen, 1909). Se distinguieron por métodos estadísticos las siguientes especies que comúnmente se habían confundido: *Stylopoma spongites* (Pallas, 1766), *Stylopoma informata* (Londsdale, 1845), una variedad de *Stylopoma spongites* y una forma sintética que llamamos *Stylopoma* sp. *5*.

El segundo grupo está constituido por ocho especies de la Familia Smittinidae Levinsen 1909. El género más importante es *Parasmittina* Osburn 1952, representado por seis especies, entre ellas una nueva especie descrita *Parasmittina mexicana*. En esta familia se distinguieron al menos cinco tendencias evolutivas diferentes, la más importante está representada por el grupo llamado *trispiniformis* (sin significado taxonómico).

En los dos grupos de especies se realizaron estudios sobre las relaciones paleobiogeográficas, biogeográficas y filéticas y ambos mostraron la repercusión de un fenómeno geológico como la formación del Istmo de Panamá (Plioceno-Pleistoceno) en el desarrollo y distribución de las especies actuales.

INTRODUCTION

The bryozoa is a very complex group, its systematics is very difficult due to the great genetical and phenotypical variability and their phyletic relationships are not clearly understood. Old determinations resulted in the formations of heterogeneous groups with an unnatural classification. Systematic confusion has caused erroneous deductions which have been used in the interpretation of the ecology, biogeography, paleoecology and paleogeography of Recent and fossil communities.

It is necessary to make a systematic revision of the group, not only in isolation. This revision intends the formation of faunistic inventories and communities and to show their relationships with the environment. On the other hand, it is also very important to use this knowledge in a view of the past to be able to infer their organic, distributional and environmental evolution, to understand the phyletical, paleoecological and paleobiogeographical aspects and their implications.

The bryozoan fauna of the Gulf of Mexico has been well studied and it is considered among the better known. Lagaaij (1963) mentioned 216 species of bryozoans reported in this area; however, there are some species that have never been recorded before from the area; others are new species, and some are species which have been taxonomically confused with others.

In September 1977, S. Pouyet and L. David, with the cooperation of the Hernán Cortés Cruise of the U. S. Navy, collected material dredged in two places of the Gulf (Figure 1):

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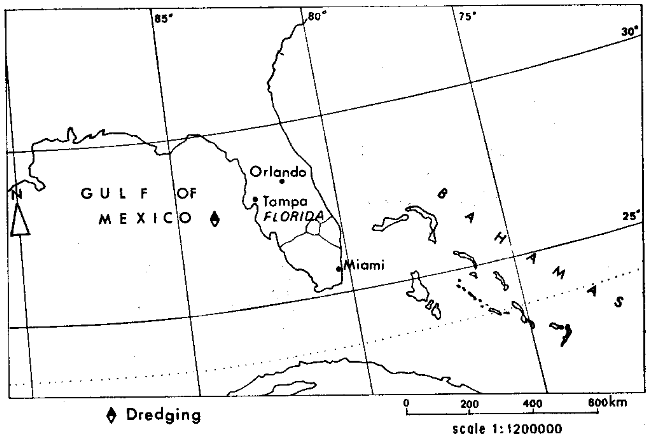

Figure 1.- Location of dredgings.

1. Vicinity Hourglass station D; depth 55 m; about 65 nautical miles due west Egmont Key (27°37′ N - 83°59′ W).

2. Vicinity Hourglass station C; depth 37 m; about 38 nautical miles due west Egmont Key (27°36′ N - 83°30′ W).

A total of 67 species of Cheilostomata was recognized, most of which have been recorded in earlier works (Smitt, 1873; Canu and Bassler, 1929; Lagaaij, 1963; Cheetham and Sandberg, 1964). Two groups of species were specially interesting because they pose systematic problems, and this study is an analysis of these two groups:

The first group is the Family Smittinidae Levinsen, 1909. Eight species were recognized in the Gulf of Mexico, belonging to three genera: the most important in number of species as in number of specimens is *Parasmittina* Osburn, 1952. It includes well known forms like *P. spathulata* (Smitt, 1873), and others which were confused as *P. trispinosa* (Johnston, 1838) and *P.* cf. *P. crosslandi* (Hastings, 1930). There is also a new species *P. mexicana*. The Genus *Smittina* Norman 1903 is represented only by a single species. The last species was named *Rimulostoma signatum* by Cheetham and Sandberg (1964, p. 1038-1039), but we consider this species belonging to the Genus *Pleurocodonellina* Soule and Soule, 1973.

The second group belongs to the Genus *Stylopoma* Levinsen, 1909 of the Family Schizoporellidae Jullien, 1903. This genus is defined by a granular tremocyst with small pores. The primary orifice is orbicular with a narrow and deep rimule on the proximal border. The peristome is thin. There are always one or two oral avicularia, several frontal avicularia and also interzooecial avicularia. The ovicell is large, rounded, porous and frequently with frontal avicularia. The genus is reported from the Miocene to Recent.

To differentiate species, both qualitative and quantitative data were considered. Morphological features were observed from photographs made with the scanning electron microscope using a Stereoscan 600 from the Centre de Microscopie Electronique Appliquée à la Biologie et à la Géologie of the Claude Bernard University in Lyon.

Statistical analysis were measured with an automatic Wild Censor. For each species 30 or 50 zooecia on one or two zooaria have been measured. The measurements are given in millimeters. We have used the classical abreviations (Figure 2A–C): Lz = length of zooecium; lz = width of zooecium; Lo = length of primary orifice; lo = width of primary orifice; Lav = length of adventitious avicularium; lav = width of adventitious avicularium; Lavg = length of interzooecial avicularium; lavg = width of interzooecial avicularium; ll = width of lyrula; Lov = length of ovicell; lov = width of ovicell.

Two new characters are defined for the problematic species of the Genus *Stylopoma*: D = distance between the aperture base and the distal wall; and Lan = length of anter (Figure 2C).

For all parameters were obtained the mean X, the variance S^2, the extreme values and (r) coefficient of correlation.

A multivariance analysis of each parameter was required to distinguish the species of the Genus *Stylopoma*.

All specimens were deposited in the collections of the Department of Earth Sciences of the Université Claude Bernard at Lyon, and paratypes in the collections of the Instituto de Geología, UNAM at Mexico City. They have a number preceded by the siglum FSL corresponding to the catalogue of collections. We do not give the list of material through it may be obtained by writing to the authors. Only the numbers of figures and type material may be obtained.

SYSTEMATICS

Order Cheilostomata
Suborder Ascophora
Family Smittinidae Levinsen, 1909

This family was defined by G. M. R. Levinsen in 1909; in 1952 Osburn (p. 390) gave a new definition; the main characters taken in consideration for the generic delimitation are: nature of the frontal wall (tremocyst or pleurocyst); presence or lack of lyrula and cardelles in the primary orifice; position and origin of avicularia; ovicell, position and perforation of its frontal.

Definition of this family has been confusing and it makes a heterogeneous group constituted by few parallel and convergent evolutionary lineages. Probably all genera included in the family do not belong to it.

Osburn (*op. cit.*) divided *Smittina* into three genera:

Smittina sensu stricto with a porous frontal and a median symmetrical suboral avicularium. Type-species: *Lepralia landsborovii* Johnston.

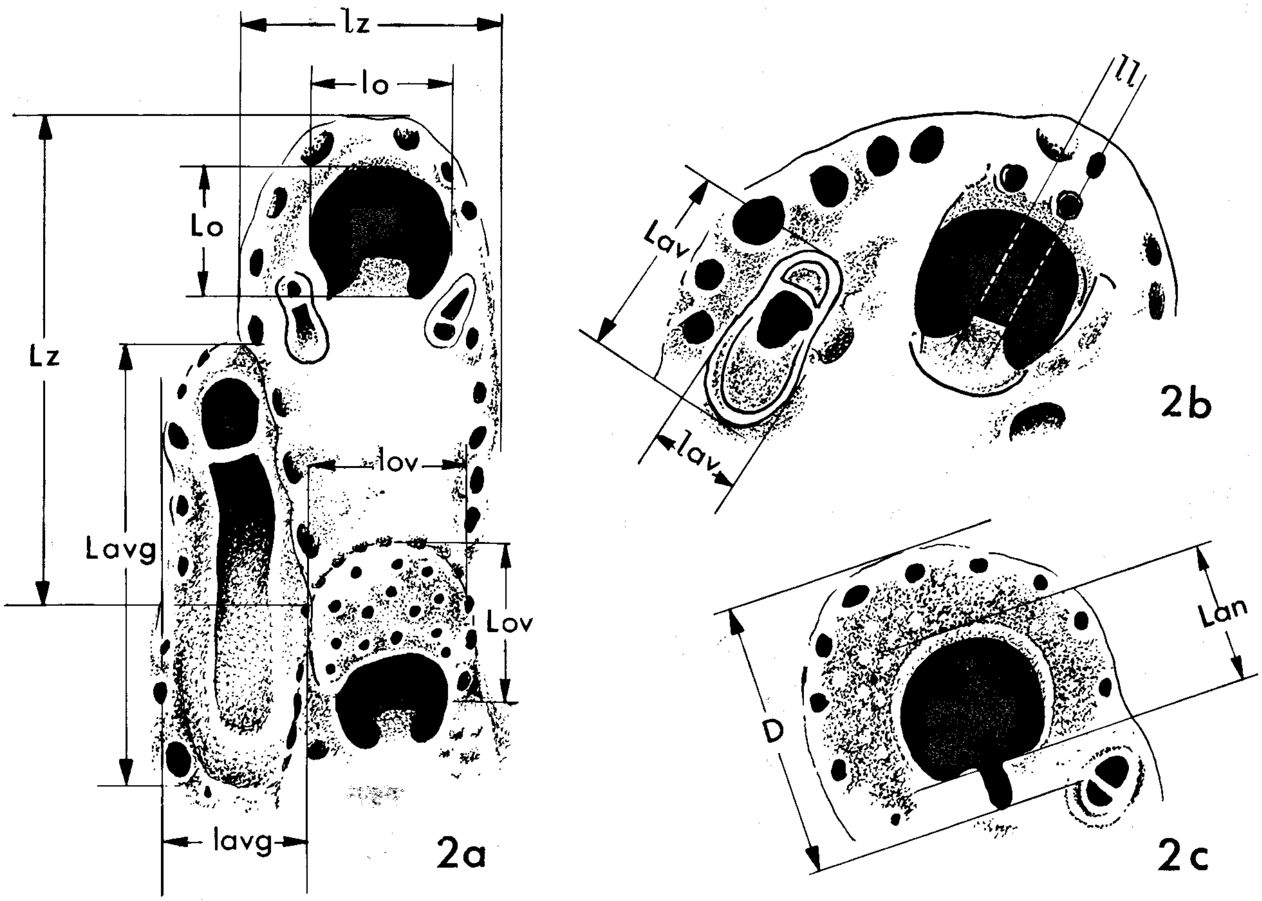

Figure 2.- Sketch of the measured morphological features.

Smittoidea with a pleurocyst (imperforate frontal), a median suboral avicularium and perforate ovicell. Type-species: *S. prolifica* Osburn.

Parasmittina with a pleurocyst frontal and avicularia which are variously distributed but never median and suboral. Type-species: *Lepralia jeffreysi* Norman.

Soule and Soule (1973) mentioned two new genera:

Hemismittoidea with an imperforate frontal, one median avicularium; type-species: *H. corallinea* Soule and Soule.

Pleurocodonellina with a pleurocyst, no lyrula, a single frontal avicularium. Type-species: *P. lahainae* Soule and Soule.

In the Gulf of Mexico we have found three genera and eight species of this family: *Parasmittina anderseni*, *P.* cf. *crosslandi*, *P. spathulata*, *P. nitida* morphotype A, *P. trispinosa*, *P. mexicana* new species; *Smittina nitidissima; Pleurocodonellina signata.*

Table 1 shows measurements and statistical values of the different parameters of the species of Smittinidae.

Genus *Parasmittina* Osburn, 1952

Parasmittina anderseni Cheetham and Sandberg, 1964

(Figures 3 and 4)

1964 - *Parasmittina anderseni* Cheetham and Sandberg, p. 1037, fig. 48.

Description.- Zoarium encrusting. Zooecia arranged in longitudinal rows, alternating in position. Zooecia rectangular to polygonal, separated by thin, salient threads.

The frontal is a thick granular pleurocyst with rudimentary interareolar costules; there is one row of large areolae.

Aperture circular with a short lyrula and very thin condyles. Peristome lacking. One spine cicatrix placed distally.

Avicularia rarely present, single, frontal, lateral to the orifice and very distally placed, mandible acutely rounded, directed transversely outwards.

Ovicell hyperstomial, globular with thin pores, it seems to be closed by the operculum.

Measurements.- 30 zooecia measured.

Lz = 0.44 - 0.85	$L\bar{z}$ = 0.59
lz = 0.25 - 0.45	$l\bar{z}$ = 0.37
Lo = 0.10 - 0.16	$L\bar{o}$ = 0.13
lo = 0.12 - 0.17	$l\bar{o}$ = 0.14

Remarks.- The only previous report of this species was made by Cheetham and Sandberg (1964), who found it in the Louisiana mudlumps.

Table 1.- Statistical values of the parameters measured in the species of the Family Smittinidae. X: mean, S^2: variance, V.E.: extreme values. r: correlation coefficient.

		Lz	lz	Lo	lo	Lav	lav	Lavg	lavg	ll
Smittina nitidissima	$\bar{X}$	0.393	0.283	0.139	0.134					
	S^2	0.0023	0.0012	0.0002	0.0002					
	V.E.	0.5-0.3	0.37-0.21	0.16-0.11	0.16-0.11					
(50)	r	-0.0009		0.292						
Parasmittina nitida morphotype A	$\bar{X}$	0.503	0.391	0.125	0.133	0.167	0.095			0.073
	S^2	0.0054	0.0029	0.0002	0.0001	0.001	0.0003			0.0001
	V.E.	0.65-0.41	0.55-0.28	0.18-0.10	0.16-0.11	0.28-0.12	0.12-0.07			0.09-0.06
(50)	r	0.156		0.475		0.469				
Parasmittina trispinosa	$\bar{X}$	0.603	0.393	0.156	0.138	0.231	0.065			0.069
	S^2	0.0071	0.0021	0.0005	0.0003	0.0032	0.0003			0.00005
	V.E.	0.71-0.49	0.28-0.47	0.21-0.12	0.19-0.10	0.36-0.14	0.12-0.04			0.08-0.06
(30)	r	0.138		0.501		0.524				
Parasmittina spathulata	$\bar{X}$	0.552	0.389	0.146	0.134	0.145	0.087	0.473	0.253	0.048
	S^2	0.0079	0.0059	0.0002	0.0002	0.0001	0.0001			0.00005
	V.E.	0.71-0.41	0.58-0.26	0.18-0.12	0.17-0.11	0.16-0.13	0.10-0.07	0.57-0.39	0.28-0.23	0.04-0.06
(30)	r	0.615		0.568		0.078				
Parasmittina mexicana	$\bar{X}$	0.733	0.490	0.166	0.159	0.205	0.058	0.104*	0.066*	0.073
	S^2	0.0139	0.0097	0.0003	0.0003	0.0014	0.0001	0.0003	0.0001	0.0001
	V.E.	0.95-0.53	0.69-0.31	0.21-0.14	0.20-0.14	0.32-0.15	0.07-0.04	0.14-0.07	0.08-0.05	0.09-0.06
(50)	r	0.127		0.323		-0.343		0.1969		0.246
Parasmittina cf. *P. crosslandi*	$\bar{X}$	0.474	0.324	0.132	0.126	0.139	0.081			0.0641
	S^2	0.0039	0.0028	0.0001	0.0001	0.0004	0.0002			0.00006
	V.E.	0.66-0.32	0.42-0.21	0.16-0.11	0.15-0.11	0.19-0.09	0.14-0.07			0.05-0.09
(50)	r	-0.021		0.150		0.388				0.292
Parasmittina anderseni	$\bar{X}$	0.588	0.368	0.131	0.144					
	S^2	0.1248	0.0029	0.0002	0.0003					
	V.E.	0.85-0.44	0.45-0.25	0.16-0.10	0.17-0.12					
(30)	r	0.063		0.024						
Pleurocodonellina signata	$\bar{X}$	0.545	0.306	0.146	0.142					
	S^2	0.0059	0.0062	0.0008	0.0008					
	V.E.	0.71-0.47	0.41-0.12	0.18-0.08	0.17-0.06					
(17)	r	0.5212		0.6781						

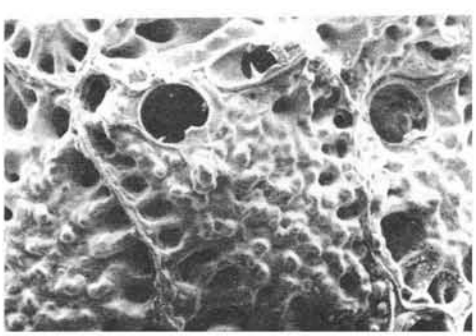

Figure 3.- ***Parasmittina anderseni*** **Cheetham and Sandberg. FSL 117 115. One zooecium showing granular pleurocyst and lateral oral avicularia, x 40.**

Figure 4.- ***Parasmittina anderseni*** **Cheetham and Sandberg. FSL 117 115. Detail of the aperture showing fine condyles and short lyrula, x 100.**

Distribution.- Atlantic Ocean, Gulf of Mexico, 55 m.

Parasmittina spathulata (Smitt, 1873)
(Figures 5, 6, and 7)

1873 - *Escharella jacotini* var. *spathulata* Smitt, p. 59, pl. 10, fig. 199-200.
1914 - *Smittina trispinosa* var. *spathulata* Smitt, Osburn, p. 435.
1929 - *Smittina trispinosa spathulata* (Smitt), Canu and Bassler, p. 114, pl. 15, fig. 9-13.
1952 - *Parasmittina spathulata* (Smitt), Osburn, p. 415, pl. 49, fig. 12-14.
1961 - *Parasmittina spathulata* (Smitt), Kataoka, p. 258, pl. 35, fig. 4.
1964 - *Parasmittina spathulata* (Smitt), Cheetham and Sandberg, p. 1037, text-fig. 44-47.
1967 - *Parasmittina spathulata* (Smitt), Rucker, p. 830, fig. 16a.
1971 - *Parasmittina spathulata* (Smitt), Hayami, p. 89, pl. 2, fig. 2.

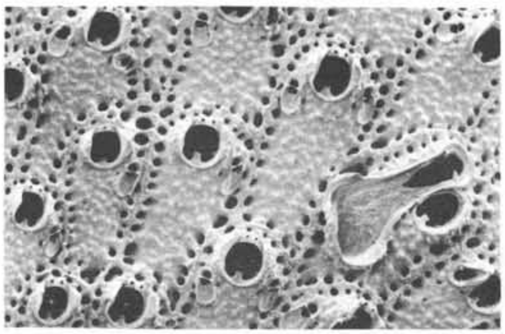

Figure 5.- *Parasmittina spathulata* (Smitt). FSL 117 113. Part of zoarium showing one zooecium wih a spatulate avicularium, x 20.

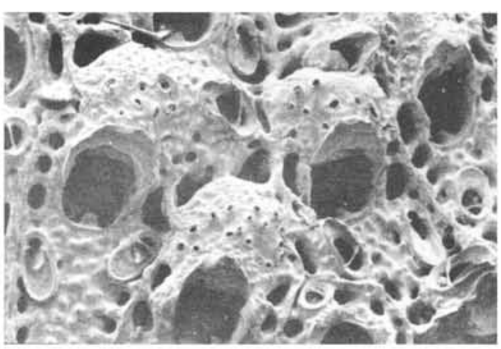

Figure 6.- *Parasmittina spathulata* (Smitt). FSL 117 113. Three ovicelled zooecia, x 40.

Description.- Zoarium encrusting in one or more layers. In the first layer, the zooecia are regularly disposed and rectangular, but in the plurilaminar colonies, zooecia are polygonal and without a preferential orientation. A salient thread separates the zooecia. The frontal is a granular pleurocyst with a row of areolar pores of moderate size.

The primary orifice is rounded with a small lyrula which is placed previously anteriorly to the short hooked cardelles. The peristome is only developed in both sides of the aperture and forms two triangular lappets. There are two spines in the distal gap.

Generally every zooecium has one or two oral, oval avicularia directed proximally. In some cases, one of these oval avicularia can be replaced by a triangular one distally directed. In addition some zooecia show one to three small frontal avicularia. But the most characteristic avicularium is large, spatulate, at one side of the aperture, directed proximally.

There are no interzooecial avicularia.

The ovicell is globular, with small pores and a basal collar; the peristome is connected with it and is continued across the border on the orifice.

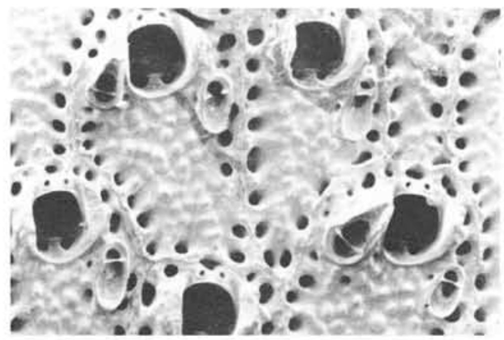

Figure 7.- *Parasmittina spathulata* (Smitt). FSL 117 113. Zooecia with two different oral avicularia, x 40.

Measurements.- 50 zooecia measured.

Lz = 0.41 - 0.70	$L\bar{z}$ = 0.55
lz = 0.29 - 0.48	$l\bar{z}$ = 0.39
Lo = 0.11 - 0.17	$L\bar{o}$ = 0.14
lo = 0.11 - 0.16	$l\bar{o}$ = 0.13
Lav = 0.13 - 0.16	$L\overline{av}$ = 0.14
lav = 0.07 - 0.11	$l\overline{av}$ = 0.09
Lavg = 0.39 - 0.57	$L\overline{avg}$ = 0.47
lavg = 0.23 - 0.28	$l\overline{avg}$ = 0.25
ll = 0.04	

Discussion.- This is a species which has been confused with others for a long time. It was described as a variety of *P. trispinosa*. It was only in 1952 that Osburn (p. 415) considered it as a true species. At the British Museum (Natural History) we have seen the specimens described by Cheetham and Sandberg in 1964 (n° 1961.11.2.21); our specimens are identical.

It is difficult to identify the specimens described by Kataoka (1961), Rucker (1967) and Hayami (1971) really as *P. spathulata*, figures are not adequate and we keep our opinion until we can see the material.

Distribution.- Pliocene of Mexico; Pleistocene of Japan ?; Recent: Gulf of Mexico, Caribbean Sea, Brazil. From the shore to 55 m depth in tropical waters.

Parasmittina nitida morphotype A (Verrill, 1875)
(Figure 8)

1875 - *Discopora nitida* Verrill, p. 415, pl. 7, fig. 3.
1968 - *Discopora nitida* Verrill morphotype A, Maturo and Schopf, p. 41-48, fig. 13 A-B.

1975 - *Parasmittina nitida* (Verrill) morphotype A, Humphries, p. 19-35, pl. 1, fig. A1-A3, pl. 2, fig. A1, A2, A5-A7, pl. 3, fig. 1-12.

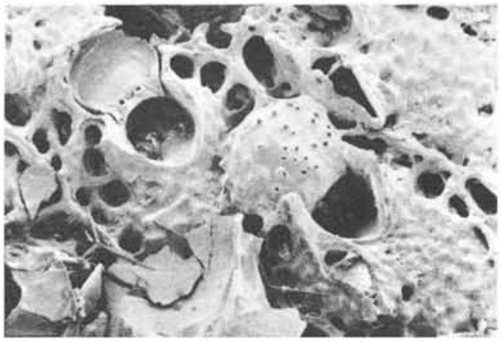

Figure 8.- *Parasmittina nitida* morphotype A. FSL 117 114. Two ovicelled zooecia, x 40.

Description.- Zoarium encrusting. Zooecia rectangular or polygonal. The frontal is a thick and granular pleurocyst with a single row of large areolar pores. The aperture is more or less round with a well developed anvil-shaped lyrula and very fine cardelles. The peristome has a proximal notch with lateral lappets not distally jointed. There are two spines in the distal gap.

There is always one frontal avicularium which is larger than the normal oral avicularia; it has a triangular mandible extending proximally with a bar and a very well developed chamber which arises in one side of the peristome at the cardelles level.

The ovicell is hyperstomial with about twenty-four pores, it is surrounded by a ring formed by the adjacent frontal.

Measurements.- 50 zooecia measured.

Lz = 0.41 - 0.65	$L\overline{z}$ = 0.50
lz = 0.31 - 0.50	$l\overline{z}$ = 0.39
Lo = 0.10 - 0.18	$L\overline{o}$ = 0.13
lo = 0.11 - 0.16	$l\overline{o}$ = 0.13
Lav = 0.12 - 0.28	$L\overline{av}$ = 0.17
lav = 0.08 - 0.13	$l\overline{av}$ = 0.095
ll = 0.07	

Discussion.- Our specimens differ slightly from the type: the oral avicularia are not paired. They differ from *P. crosslandi* in the texture of the frontal, the type and the distribution of the avicularia.

Parasmittina trispinosa (Johnston, 1838)
(Figure 9)

1838 - *Discopora trispinosa* Johnston, p. 280, pl. 24, fig. 5.
1847 - *Lepralia trispinosa* (John.), Johnston, p. 324, pl. 57, fig. 7.
1867 - *Escharella jacotini* Smitt, p. 11, pl. 24, fig. 53-58.
1880 - *Smittia trispinosa* (John.), Hincks, p. 353, pl. 49, fig. 1-8.
1923 - *Smittina trispinosa* (John.) Canu and Bassler, p. 143, fig. 7-14.
1929 - *Smittina trispinosa* (John.), Canu and Bassler, p. 340, pl. 41, fig. 1-3.
1952 - *Parasmittina trispinosa* (John.), Osburn, p. 412, pl. 49, fig. 7-8.
1962 - *Parasmittina trispinosa* (John.), Gautier, p. 200.

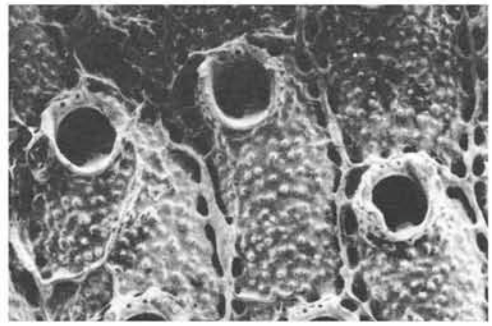

Figure 9.- *Parasmittina trispinosa* (Johnston). FSL 117 116. Part of zoarium; on the left, one zooecium with a small lateral avicularium, x 40.

Description.- Zoarium encrusting. Zooecia more or less rectangular, varying greatly in both size and form. Our specimens are not very calcified and the frontal is a thin granulated pleurocyst with a row of areolar pores and fine lateral walls.

The primary aperture is round with a moderately developed lyrula and two hooked condyles. The peristome is well developed, specially in the older zooecia where it can take a tubular form. More generally there are two lappets and in the distal gap two or rarely three spines.

Frequently, there is only one small avicularium located proximally and to one side of the peristome, the rostrum directed distally toward the median axis. Sometimes there are two paired avicularia.

No vicarious avicularia.

Ovicell not seen.

Measurements.- 30 zooecia measured.

Lz = 0.49 - 0.71	$L\overline{z}$ = 0.60
lz = 0.28 - 0.47	$l\overline{z}$ = 0.39
Lo = 0.12 - 0.21	$L\overline{o}$ = 0.16
lo = 0.10 - 0.19	$l\overline{o}$ = 0.14
Lav = 0.14 - 0.36	$L\overline{av}$ = 0.23
lav = 0.04 - 0.12	$l\overline{av}$ = 0.065
ll = 0.069	

Remarks.- This is a cosmopolitan species with many varieties which have often been confused. Our material is similar to that described by Osburn (1952). More specimens are necessary to confirm the determination.

Distribution.- Miocene: North Carolina (USA), Australia; Pliocene: Florida (USA), Japan; Pleistocene: California, Florida, South Carolina (USA), Sicily; Recent: cosmopolitan, eastern and western North Atlantic, western South Atlantic, Indian Ocean, Pacific (Japan, Galapagos), Adriatic.

Parasmittina cf. *P. crosslandi* (Hastings, 1930)
(Figures 10, 11 and 12)

1930 - *Smittina crosslandi* Hastings, p. 726, pl. 13, fig. 75-79; pl. 17, fig. 122.
1952 - *Parasmittina crosslandi* (Hastings), Osburn, p. 418, pl. 48, fig. 12.

1973 - *Parasmittina crosslandi* (Hastings), Soule and Soule, p. 382, fig. 2 E-F.
1976 - *Parasmittina crosslandi* (Hastings), Hayami, p. 44, pl. 4, fig. 4.
1977 - *Parasmittina crosslandi* (Hastings), Banta and Carson, p. 408, fig. 6 D-F, pl. 4, fig. 24-25.

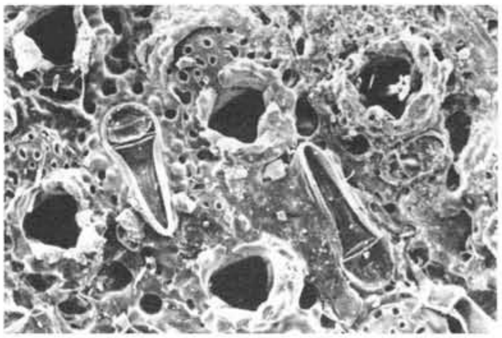

Figure 10.- *Parasmittina* cf. *crosslandi* (Hastings). FSL 117 117, x 40. Zooecia with a great frontal avicularium distally directed. On the left, one interzooecial avicularium, x 40.

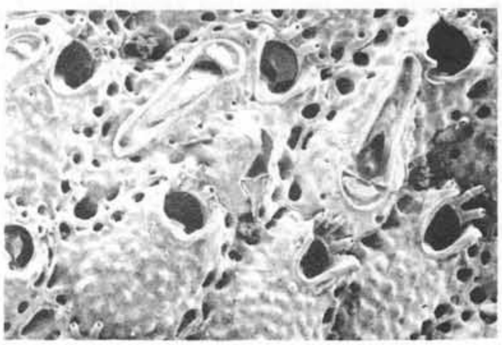

Figure 11.- *Parasmittina* cf. *crosslandi* (Hastings). FSL 117 118. Some zooecia and one interzooecial avicularium, x 40.

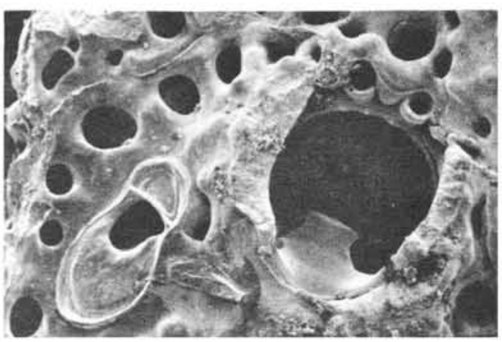

Figure 12.- *Parasmittina* cf. *crosslandi* (Hastings). FSL 117 118. Distal part of zooecia, x 100.

Description.- This is a species which presents great variations in its astogeny. In the first stages, it is an encrusting, unilaminar zoarium, later it becomes irregular multilaminar colonies.

The youngest zooecia are rectangular, irregular, with granular frontal wall bordered by a row of well developed areolar pores. Primary orifice rounded or square bearing large triangular oral lappets and two or three strong distal spines; the inner distal edge is crenulated; inside the aperture, a short, wide lyrula and two lateral acute, small cardelles. The lappets can be proximally connected and form a pseudorimule.

There are three kinds of avicularia:

1) Oval, small avicularia at one side of the aperture and proximally directed; 2) small triangular avicularia proximally directed, situated at one side of the aperture; 3) long triangular or shoulder avicularia with an independent chamber.

Ovicell hyperstomial with large pores.

In the older zooecia, we have observed several modifications: the frontal wall is thick and the areolar pores form costulae and ridges. In the zooecia without ovicell, the aperture can be totally surrounded by the proximal connection of the lappets which develop curls and projections. These curls can be joined with the proximal wall of the distal zooecium or they can stay without the distal welding and holding the spines.

In the fertile zooecia, the increasing calcification results in the union of the processes and flaps which make a great tubular peristome; the calcareous layer never covers totally the ovicell but it forms great curls in the peristome.

The avicularia also change when the calcification is increasing, the oval one disappears; the number of small triangular avicularia increases with a random distribution. The great shoulder avicularia are directed proximally and there are interzooecial avicularia with a triangular or duckbilled rostrum variable in size but more often large.

Measurements.- 100 zooecia measured.

Lz = 0.32 - 0.67	$L\bar{z}$ = 0.50
lz = 0.21 - 0.48	$l\bar{z}$ = 0.34
Lo = 0.08 - 0.14	$L\bar{o}$ = 0.11
lo = 0.10 - 0.15	$l\bar{o}$ = 0.13
Lav = 0.09 - 0.18	$L\overline{av}$ = 0.12
lav = 0.04 - 0.09	$l\overline{av}$ = 0.07
Lavg = 0.22 - 0.45	$L\overline{avg}$ = 0.31
lavg = 0.10 - 0.19	$l\overline{avg}$ = 0.12
	$L\overline{ov}$ = 0.23
	$l\overline{ov}$ = 0.16
ll = 0.06	

Discussion.- This species is difficult to determine. We examined the holotype of *P. crosslandi* at the British Museum (Natural History), St. George Collection number 1929.4.26.162 as well as the paratype figured by Hastings (1930, pl. 13, fig. 75, number 1929.4.26.256). The lyrula is less narrow on the holotype and the inner distal part of the anter does not seem crenulate. Moreover, the interzooecial avicularia has never been described in *P. crosslandi*, but this is not enough to create a new species.

On the Hawaiian Islands, Soule and Soule (1973) described a new species *P. raigiformis* showing interzooecial avicularia similar to those from our specimens but the frontal avicularia are different in number and shape.

Distribution.- Hayami named a species *P. crosslandi* from the Pliocene of Japan, but we think that it is a different species.

Pacific: Hawaiian Islands ?, Panama, Galapagos, Gulf of California.

Parasmittina mexicana new species
(Figures 13 and 14)

Holotype: FSL 117 119
Paratype: Instituto de Geología, UNAM
Type locality: Gulf of Mexico, Atlantic Ocean.
Etymology: named from the type locality.

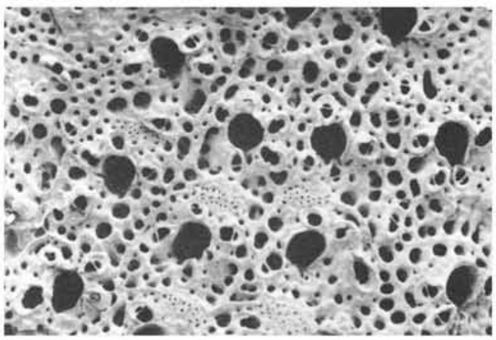

Figure 13.- *Parasmittina mexicana* new species. Holotype FSL 117 119. Zooecia with several small avicularia around the aperture, x 20.

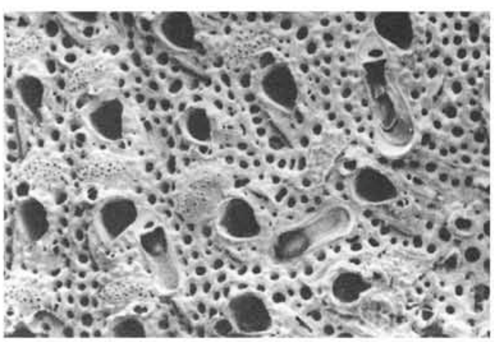

Figure 14.- *Parasmittina mexicana* new species. Holotype FSL 117 119. Part of zoarium with ovicells and large frontal avicularia, x 20.

Description.- Zoarium encrusting, forming multilamellar crust on shells, sponges or corals. It is peach pink and clear colored. Zooecia are elongate, polygonal with a round distal part and a strong wall. The frontal is a pleurocyst in which the increasing calcification makes it rugose. There are laterally and proximally two rows of areolar pores which form tubules in the well calcified frontal wall, finally producing the appearance of a tremocyst.

The primary aperture is orbicular (rounded) with two spines in the very young zooecia. Inside the aperture on the proximal part there is a strong, wide, anvil-shaped lyrula and two lateral, hooked condyles (cardelles). The peristome is developed very early and it forms a tube with a distinct sinus. Just below the orifice, in one side, there is a little drop-shaped avicularium with a chamber which arises from an areolar pore; this avicularium is distolaterally directed more or less obliquely.

Several kinds of avicularia are found within the same zoarium: long and narrow paired avicularia on each side of the aperture, directed proximally; frontal, drop-shaped avicularia with complete pivot and triangular mandible; irregularly distributed on the zooecia. Sometimes they are on the peristome or ovicell; large vicarious spatulate avicularia.

Ovicell hyperstomial with numerous scattered pores, immersed when it is thickly calcified, opening into the peristome.

Operculum rounded distally and with straight proximal rim with a peripherical sclerite; it is inserted above the cardelles.

Measurements.- 50 zooecia measured.

Lz = 0.53 - 0.93	$L\bar{z}$ = 0.73
lz = 0.31 - 0.69	$l\bar{z}$ = 0.49
Lo = 0.14 - 0.21	$L\bar{o}$ = 0.17
lo = 0.14 - 0.20	$l\bar{o}$ = 0.16
Lav = 0.15 - 0.32	$L\overline{av}$ = 0.20
lav = 0.04 - 0.08	$l\overline{av}$ = 0.06
ll = 0.07	

Median avicularia:

L = 0.07 - 0.14	$\bar{L}$ = 0.10
l = 0.05 - 0.08	$\bar{l}$ = 0.07

Remarks.- This species is characterized by the great number of avicularia, the peristomial form, the thick calcification and particularly by the constant presence of the median avicularium. That presence makes us think that this species may not belong to *Parasmittina*, since it is the genus defined by the absence of a median avicularium. A comparison with other similar Genus *Hemismittoidea* Soule and Soule 1973, shows that there are several differences and that the nature, form and direction of the median avicularium are not the same. There are more features in common with the Genus *Parasmittina* than with *Hemismittoidea* and this is confirmed by comparison with species like *Parasmittina rouvillei*. We think that the existence of the median avicularium is a secondary character, later acquired and convergent with *Hemismittoidea*. On the other hand, this feature is constant enough in our specimens to be considered like a distinct character of the species.

One species is very similar to our specimen: *Parasmittina rouvillei* (Calvet, 1902) reported from the Mediterranean Sea (France, Tunisia, Turkey). Nevertheless, there are several differences between the two species.

Parasmittina mexicana

1 - Peristome well developed, with tubular form, pyriform aperture without lappets.

2 - Suboral avicularia constant and in a transversal position. The spatulate avicularia are longer and greater. The frontal avicularia are more abundant and also around the peristome.

3 - Median denticle (lyrula) wider and cardelles well developed.

4 - Ovocell more submerged and covered by the calcification of lateral walls.

Parasmittina rouvillei

1 - There is a well developed peristomial tube but never like that of the specimen of the Gulf of Mexico, it is formed by the fusion of the lappets and the distal edge.

2 - The median avicularium is not constant; the spatulate avicularia are narrower and less developed, frontal avicularia are fewer.

3 - Median denticle (lyrula) narrower.

4 - Ovicell less submerged and less calcified.

On the other hand, the specimen figured by Cheetham and Sandberg (1964, text-fig. 46, p. 1034) is probably *P. mexicana* and not *P. spathulata*.

Distribution.- Recent: western Atlantic, Gulf of Mexico.

Genus *Smittina* Norman, 1903

This genus is now limited to species with a perforate frontal, a median suboral avicularium and a perforate ovicell.

Type-species: *Lepralia landsborovii* Johnston 1838.

Smittina nitidissima (Hincks, 1880)
(Figures 15 and 16)

1880 - *Porella nitidissima* Hincks, p. 78, pl. 10, fig. 2.
1947 - *Smittina smittiella* Osburn, p. 37, pl. 6, fig. 1-2.
1952 - *Smittina smittiella* Osburn, Osburn, p. 404, pl. 47, fig. 11-12.
1964 - *Smittina smittiella* Osburn, Cheetham and Sandberg, p. 1036, text-fig. 43.
1968 - *Smittina nitidissima* (Hincks), Cook, p. 213.

Description.- Zoarium encrusting. Zooecia polygonal, irregular, separated by distinct threads. Frontal wall tremocystal with tremopores separated by ridges, from which it has a reticulate appearance.

Primary orifice subcircular with a broad lyrula. Single avicularium median, oral, proximal, projecting into secondary orifice.

Ovicell large, moderately convex, regularly perforated.

Measurements.- 50 zooecia measured.

Lz = 0.30 - 0.50	$L\bar{z}$ = 0.39
lz = 0.21 - 0.37	$l\bar{z}$ = 0.28
Lo = 0.11 - 0.16	$L\bar{o}$ = 0.14
lo = 0.11 - 0.16	$l\bar{o}$ = 0.13

Figure 15.- *Smittina nitidissima* Hincks. FSL 117 120. Part of zoarium, ovicell, median avicularia, x 40.

Figure 16.- *Smittina nitidissima* Hincks. FSL 117 120. Part of zoarium, ovicell, median avicularia, x 20.

Discussion.- There is no doubt about the identification of our specimens. On the figured specimens (Osburn, 1952; Cheetham and Sandberg, 1964) it is very difficult to observe the rostrum of the median avicularia but this feature was seen in other specimens with good preservation.

Cook (1968) considered that *S. smittiella* was a junior synonym of *S. nitidissima*. This species is very variable specially in number and distribution of avicularia; calcification of the frontal wall is the most constant character.

Distribution.- Recent: western Atlantic, Gulf of Mexico, Caribbean Sea; eastern Atlantic, coasts of Africa; eastern Pacific, Galapagos 14 to 180 m depth.

Genus *Pleurocodonellina* Soule and Soule, 1973

The frontal is a pleurocyst with a single row of areolar pores. Orifice without lyrula. One frontal avicularium. Ovicell with crescent of small pores.

Type-species: *P. lahainae* Soule and Soule, 1973.

Pleurocodonellina signata (Waters, 1889)
(Figures 17 and 18)

1889 - *Smittia signata* Waters, p. 17, pl. 3, fig. 4-6.
1927 - *Schizopodrella horsti* Osburn, p. 127, text-fig. 3-5.
1957 - *Smittina signata* (Waters), Harmer, p. 98, pl. 63, fig. 27-29.
1963 - *Parasmittina signata* (Waters), Lagaaij, p. 197, pl. 6, fig. 2.
1964 - *Rimulostoma* ? *signatum* (Waters), Cheetham and Sandberg, p. 1038, text-fig. 49.
1967 - *Rimulostoma signatum* (Waters), Rucker, p. 839, fig. 14K.

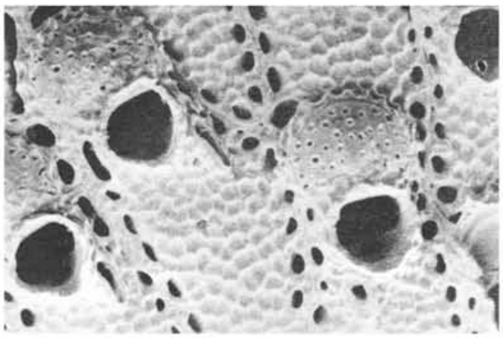

Figure 17.- *Pleurocodonellina signata* (Waters). FSL 117 121. Ovicelled zooecia, x 40.

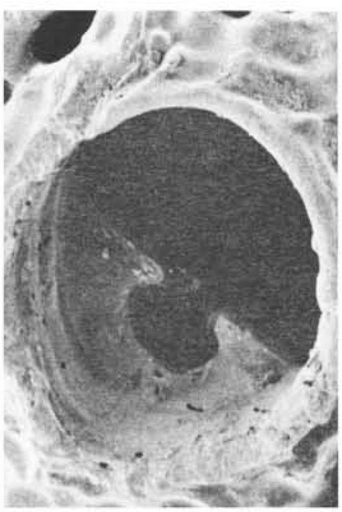

Figure 18.- *Pleurocodonellina signata* (Waters). FSL 117 121. Aperture x 200.

Description.- Zoarium encrusting; zooecia elongate rectangular or polygonal. The frontal wall is a reticular pleurocyst with a row of areolar pores. Primary orifice with a round sinus. Peristome thin, irregular. There is a single frontal avicularia proximal to the orifice, it is thin and directed proximally. Ovicell globular with small pores, opening into the peristome.

Measurements.- 17 zooecia measured.

Lz = 0.47 - 0.71	$L\bar{z}$ = 0.54
lz = 0.12 - 0.41	$l\bar{z}$ = 0.31
Lo = 0.08 - 0.18	$L\bar{o}$ = 0.15
lo = 0.06 - 0.17	$l\bar{o}$ = 0.14

Discussion.- Soule and Soule (1973, p. 430) think that this species belongs to their new Genus *Pleurocodonellina*. We compared our specimens with one specimen from Cheetham's collection in BMNH, number 1961.11.2.17, dredged near Panama and established their identity. The Genus *Rimulostoma* Vigneaux, 1949 is not well defined and not well enough figured to afford clear comparison; consequently we agreed with Soule and Soule's opinion and places this species in their Genus *Pleurocodonellina*.

Distribution.- Recent: eastern Atlantic, Guinea coast of Africa; western Atlantic, Caribbean Sea, Gulf of Mexico, Pacific, Australia (New South Wales, Adelaide), Philippines, Malay Archipelago, Japan.

Family Schizoporellidae Jullien and Calvet, 1903

Genus *Stylopoma* Levinsen, 1909

The frontal wall is a tremocyst smooth or granular. The ovicell is hyperstomial and covers the aperture entirely. The primary orifice is provided with a small linear rimule.

Type-species: *Stylopoma spongites* Pallas, 1766

Stylopoma spongites (Pallas, 1766)
(Figures 19 and 20)

1766 - *Eschara spongites* Pallas, p. 45.
1873 - *Hippothoa spongites* (Pallas), Smitt, p. 42, fig. 161.
1900 - *Hippothoa spongites* (Pallas), Verrill, p. 593.
1964 - *Stylopoma spongites* (Pallas), Cheetham and Sandberg, p. 1031, text-fig. 37.

The identities of the species described in the following references are not certain and we do not included them in synonymy until we have seen the material described.

1914 - *Schizoporella spongites* (Pallas), Osburn, p. 207.
1923 - *Stylopoma spongites* (Pallas), Canu and Bassler, p. 102, pl. 17, fig. 1-12.
1928 - *Stylopoma spongites* (Pallas), Canu and Bassler, p. 91, pl. 4, fig. 8-10; pl. 33, fig. 9.
1967 - *Stylopoma spongites* (Pallas), Rucker, p. 102-103, pl. 17, fig. 1-2.

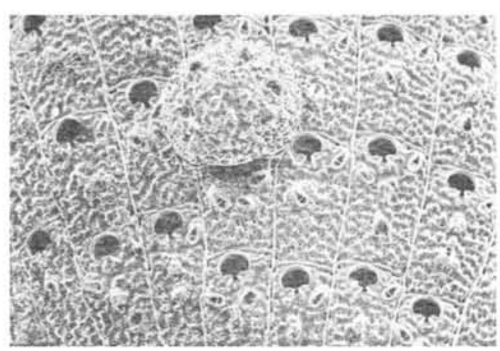

Figure 19.- *Stylopoma spongites* (Pallas). FSL 117 122. Part of zoarium with regular rectangular zooecia and prominent ovicell, x 20.

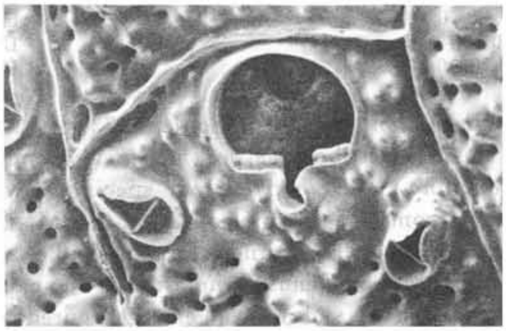

Figure 20.- *Stylopoma spongites* (Pallas). FSL 117 122. Distal part of a zooecium, x 100.

Description.- Zoarium encrusting unilaminar. In some specimens, the zoarium is multilaminar or forms tubular fronds. Zooecia generally rectangular; the frontal is a tremocyst without areolar pores. The aperture is almost contiguous to the distal wall and over the middle axis; the anter is semicircular, the proximal part is straight, notched by a small drop-shaped rimule. Sometimes there is a median umbo just below the sinus.

Every zooecium has one or more often two oral avicularia, more or less triangular, directed obliquely and distally. They arise between the rimule and the umbo and when there are two, one is generally placed lower than the other and they are never adjacent to the aperture. Sometimes this kind of avicularium occurs on the frontal wall or on the ovicell.

The interzooecial avicularia are of the same size as the zooecia, they are rectangular with a keyhole orifice surrounded by a granular rim, they have a transverse bar.

The ovicell is globular, prominent, perforate like the frontal, with avicularia.

Distribution.- Miocene and Pliocene of Florida and Virgina (USA); middle Pliocene of Veracruz, Mexico; Recent: western Atlantic (Gulf of Mexico, Florida, Caribbean Sea, Puerto Rico, Yucatan).

We are not certain of its presence in the Pacific coast of America.

Stylopoma informata (Lonsdale, 1845)
(Figures 21 and 22)

1845 - *Cellepora informata* Lonsdale, p. 505, fig. 1b.
1914 - *Schizoporella informata* (Lonsdale), Osburn, p. 207.
1937 - *Stylopoma informata* (Lonsdale), Marcus, p. 91, pl. 18, fig. 48.
1940 - *Stylopoma informata* (Lonsdale), Osburn, p. 424, pl. 7, fig. 58.
1952 - *Stylopoma informata* (Lonsdale), Osburn, p. 336, pl. 38, fig. 11-12.
1982 - *Stylopoma spongites* (Pallas), Winston, p. 145 and 147, fig. 78.

Description.- Zoarium encrusting on shells and seaweed, unilaminar in the first stages but it becomes frequently an irregular multilaminar mass.

Zooecia are rather regularly rectangular in young stages but later they are polygonal and convex. The frontal is strongly calcified with large tremopores and it is roughened. The aperture is not always median but placed in one corner of the zooecium, it is semicircular, the proximal border with a narrow V-shaped or enlarged sinus. The peristome is large and granular.

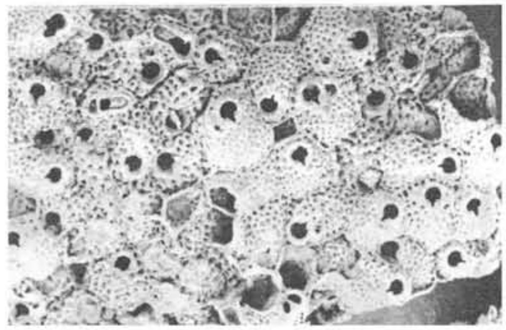

Figure 21.- *Stylopoma informata* (Lonsdale). FSL 117 123. Zooecia irregularly disposed, x 10.

Figure 22.- *Stylopoma informata* (Lonsdale). FSL 117 123. Ovicell, x 20.

Sometimes there is a small oval avicularium which arises just below and on one side of the rimule. This avicularium is not very frequent.

In the old irregular parts of the zoarium large interzooecial avicularia may be present, they are generally straight and spatulate.

The ovicell is huge, globular, perforate, without avicularia on its frontal.

Distribution.- Upper Miocene of Virginia (USA); middle Pliocene of Veracruz, Mexico; Recent: western Atlantic, Florida, Gulf of Mexico, Brazil; eastern Pacific, Galapagos and California.

Stylopoma sp. *3*
(Figures 23 and 24)

Zoarium encrusting on seaweed, corals or gorgonian and producing tubular, unilaminar colonies. Zooecia rectangular with a well calcified tremocyst with small tremopores. Sometimes there is a median umbo below the aperture. The primary orifice is almost always placed in the axis of the zooecia; the peristome is commonly complete, finely granular so that it looks crenulated. The anter is semicircular with a proximal straight edge notched by a pyriform rimule.

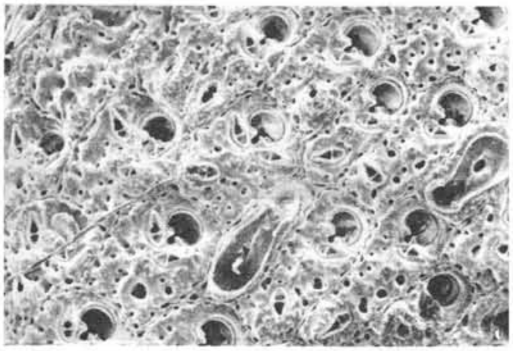

Figure 23.- *Stylopoma* sp. *3*. FSL 117 124. Part of zoarium with interzooecial avicularia, x 20.

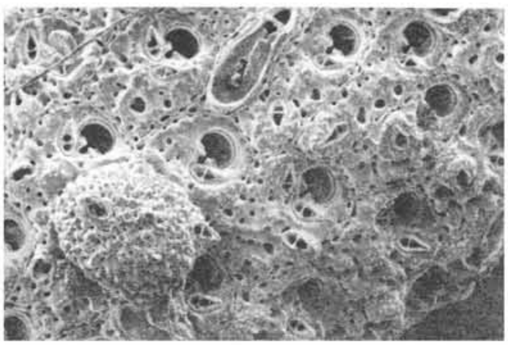

Figure 24.- *Stylopoma* sp. *3*. FSL 117 124. Ovicell, x 20.

On each side of the aperture there are commonly two narrow and long avicularia situated below or on the same level and very close to the rimule; the avicularia makes a 45° angle with the zooecial axis; sometimes they are surrounded by the peristome. More often there are also small avicularia on the frontal wall.

The interzooecial avicularia are rectangular with a keyhole shaped orifice.

Ovicell globular with small pores and fine granulations sometimes with avicularia.

Remarks.- *Stylopoma* sp. *3* is close to *S. spongites*; however, the peristome is larger than in *S. spongites* and more elevated.

The interzooecial avicularia are very similar to those of *S. spongites*.

Stylopoma sp. *4*
(Figures 25 and 26)

This is the same species as *S. informata* but it differs only in the colony form: the zoarium is unilaminar and grows on seaweed.

Stylopoma sp. *5*
(Figure 27)

The following synonymy is based upon the comparison of different figured specimens and on the assumption that they belong to a species different of *Stylopoma spongites*.

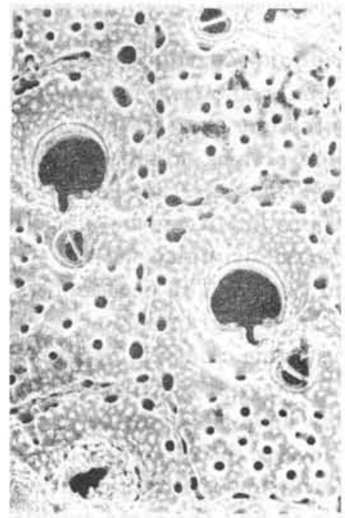

Figure 25.- *Stylopoma* sp. *4*. FSL 117 125. Zooecia, x 40.

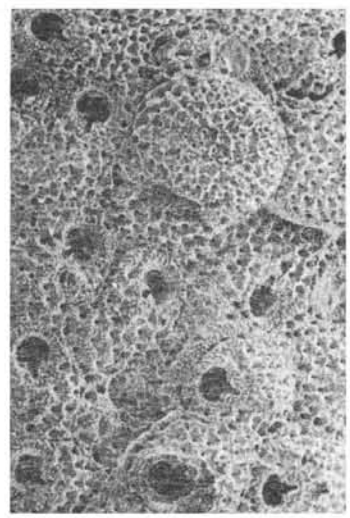

Figure 26.- *Stylopoma* sp. *4*. FSL 117 125. Ovicell, x 20.

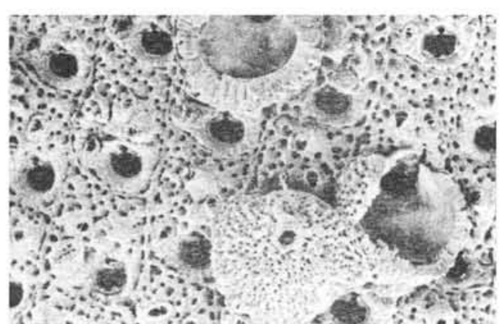

Figure 27.- *Stylopoma* sp. *5*. FSL 117 126. Part of zoarium with ovicell, x 20.

1923 - *Stylopoma spongites* (Pallas), Canu and Bassler, p. 102, pl. 17, fig. 1-12.
1928 - *Stylopoma spongites* (Pallas), Canu and Bassler, p. 91, pl. 10, fig. 8-10, pl. 32, fig. 9.
1964 - *Stylopoma spongites* (Pallas), Rucker, p. 827, fig. 15d.

Description.- Zoarium encrusting on seaweed, generally unilaminar. Zooecia rectangular and larger than in *S. spongites* but shorter than in *S. informata*. The frontal wall is a thick tremocyst with tremopores and areolar pores. The aperture is almost always placed in the median axis but it can be placed to one side of the zooecia; it is semicircular with a straight edge and a drop-shaped rimule. The peristome is complete, raised, narrow and slightly granular.

In the same zoarium, there are two possibilities: one or two oral avicularia or none. If they are present, they have the same form of those of *S. spongites* and they are distolaterally directed. They arise at the level of or below the rimule but never adjacent to it. It is possible to find the same avicularia on the frontal wall.

The interzooecial avicularia are very uncommon and similar to those of *S. spongites*.

The ovicell is globular with a thick porous frontal; sometimes there are one or two avicularia.

Distribution.- Miocene of Virginia and Florida (USA); Pliocene of Florida and Panama; Pleistocene of South Carolina (USA); Recent: if we agree with the synonymy of this species, it has been found in eastern Atlantic: Gulf of Mexico, Florida, Bermudas, Tortugas Islands, Caribbean Sea and Venezuela.

STRATIGRAPHICAL AND BIOGEOGRAPHICAL ANALYSIS OF THE SPECIES OF FAMILY SMITTINIDAE

We have found eight species of the family represented in the Gulf of Mexico material; six of them belong to the Genus *Parasmittina* (Figure 28). The great confusion which exists in this genus is well-known and the bibliographical data are full of contradictions; there is not enough support in the fossil record.

One of the oldest forms is *Parasmittina trispinosa* (Johnston, 1838), which was found in the Miocene of North America, the Pliocene of Florida and Japan, the Pleistocene of California, South Carolina, Florida and Sicily and in all the seas of the world.

The other species which is represented in the fossil record is *Parasmittina spathulata* which we found in the Pliocene of Mexico and in the Quaternary mudlumps. We think that the species found by Hayami (1971) in the Pleistocene of Japan is not *P. spathulata*, because it has different avicularia morphology. On the other hand, according to Soule and Soule (1973), the *P. spathulata* reported by Osburn (1952) in the Galapagos Islands is not this species but *P. dolobrata*; so that *P. spathulata* is an endemic species of the tropical coast of eastern America.

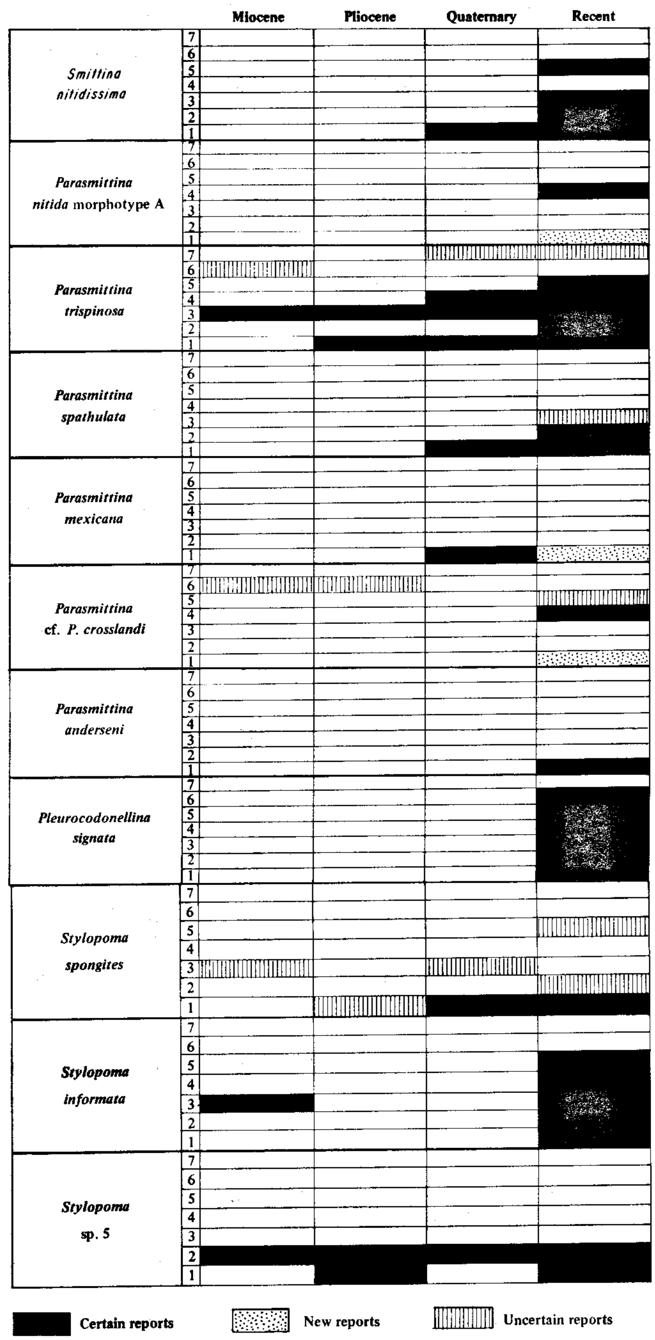

Figure 28.- Geographical and stratigraphical distribution of the species (the stratigraphical series has no time scale). 1 - Gulf of Mexico. 2 - Gulf of Mexico and Caribbean Sea. 3 - Western tropical Atlantic Coast. 4 - Gulf of California. 5 - Eastern tropical Pacific Coast. 6 - Western tropical Pacific waters. 7 - European, African and cosmopolitan species.

One species shows a close relationship with Pacific forms: *Parasmittina* cf. *P. crosslandi* which is very close to the form described by Osburn (*op. cit.*) from the Galapagos Islands and California, but it is also similar to the Hawaiian species *Parasmittina raigiformis* of Soule and Soule (1973).

Parasmittina mexicana new species is defined from the Gulf of Mexico. The nearest species are found in the Mediterranean Sea; *P. rouvillei* and *P. tropica* of the Red Sea, Japan and West Africa. Among the fossil forms, *P. mexicana* is close to an American species from the Quaternary mudlumps and one of the Pliocene forms from Mexico.

One endemic form of the Gulf of Mexico is *Parasmittina anderseni* which was also found in the Quaternary mudlumps.

Pleurocodonellina signata is a cosmopolitan form also present in the Louisiana mudlumps. *Smittina nitidissima* lives both in tropical coasts of America and in the Quaternary Louisiana mudlumps.

All this evidence makes us think that the phenomenon of speciation in these species is very recent and we can recognize at least five different trends.

The first one includes the species which we call the "trispiniformis". In this group, we include *P. trispinosa, P. nitida* and *P. spathulata.* It is possible that *P.* cf. *crosslandi* belongs to this group also. We suppose that in the Miocene there was a generalized form like *Parasmittina trispinosa* which began to diversify in the late Miocene and early Pliocene in the tropical waters of western Atlantic. At that time, North and South America were still separated. In the late Pliocene and early Pleistocene the union of both parts of America was made by the Isthmus of Panama and the incipient populations were totally isolated and continued different evolutionary trends. *Parasmittina spathulata* was probably one of the first species to differentiate, since it was present in the Pliocene of Mexico and it remained in the eastern tropical coast of America. *Parasmittina nitida*, morphotype A is an endemic form of the western Atlantic without fossil forms, its origin must be very recent.

Parasmittina cf. *crosslandi* is very close to *P. crosslandi* and also to *P. raigiformis* from the Pacific coast. We can suppose that the incipient population began to be differentiated after the formation of the Isthmus of Panama, each population developing separately but in a parallel path.

The second trend is represented by *Parasmittina mexicana* which is related to the Mediterranean, African and Red Sea forms like *P. rouvillei* (Calvet).

Parasmittina anderseni represents the third trend, it is an endemic form of the Gulf of Mexico.

The fourth trend is represented by *Smittina nitidissima* which is found in both American tropical coasts and which also has a very close relationship to the species of Hawaii like *Smittina kukuiula* (Soule and Soule), and the Indopacific form like *S. malleolus* (Hincks) = *S. nitidissima* (Hincks).

The last trend is represented by *Pleurocodonellina signata*; this species has a wide distribution in the Indian Ocean and western Pacific, but it is also well known in the Pacific and Atlantic coasts.

Finally, it is important to remark that among the eight species of this family, three have a close relationship with eastern and western Pacific species. *P. trispinosa* is a cosmopolitan form but it is possible that several species have been confused under this name. Two species have only been described in the Gulf of Mexico and *P. mexicana* which has similarities with Mediterranean and Red Sea species.

GEOGRAPHICAL AND STRATIGRAPHICAL ANALYSIS OF THE SPECIES OF *STYLOPOMA*

Due to the great systematic confusion, not all records of geographical and stratigraphical distribution can be considered. We are certain that *Stylopoma spongites* is a western Atlantic species which occurs particularly of the Gulf of Mexico. We are not certain of the reports of the Pacific coast of America as of its presence in the Miocene; however, its presence is certain in the Quaternary mudlumps of Louisiana, USA, and in the Pliocene of Mexico.

Stylopoma informata was recognized in the Pacific coast of America by Osburn (1952), in the western Atlantic on Florida coast and in the Caribbean Sea, perhaps in Brazil too. There is a fossil citation in the Miocene of Virginia, USA (Londsdale, 1845) and it is also present in the Pliocene of Mexico.

On the other hand, *Stylopoma* sp. *5* looks like the upper Miocene forms of Florida and the Pleistocene fossils of Panama; now it is found in the Gulf of Mexico, on the coast of Panama, in the Caribbean Sea and perhaps in Brazil.

All these considerations are very important, since *Stylopoma informata* and *Stylopoma* sp. *5* were discovered in the Miocene before the formation of the Panama Isthmus during the late Pliocene to early Pleistocene (Hallam, 1973). Since then, there has been a divergence between *Stylopoma* sp. *5* and *S. spongites.* Today *S. informata* is present from both tropical coasts while *S.* sp. *5* is present in the Atlantic tropical waters and *S. spongites* is confined to the Gulf of Mexico and perhaps to the Caribbean Sea.

We suppose that the oldest Miocene form was *S. informata* which gave rise to *Stylopoma* sp. *5* in the Miocene which then gave rise to *Stylopoma spongites* during the Pliocene in the Gulf of Mexico.

STATISTICAL ANALYSIS AND DISCUSSION OF THE SPECIES OF *STYLOPOMA*

The group of species of the Genus *Stylopoma* Levinsen, 1909 shows many characteristics in common though there are some different features. The great variability of this group is due to both phenotypical and genotypical factors and it is not easy to distinguish between interspecific and intraspecific variations.

In our material we found several species of *Stylopoma*; morphological observation leads us to subdivide them in five populations, two are well defined *Stylopoma informata* (S-2) and *S. spongites* (S-1), the three others show intermediate features and they are defined as:

- *Stylopoma* sp. *3* (S–3)
- *Stylopoma* sp. *4* (S–4)
- *Stylopoma* sp. *5* (S–5)

We measured eight features on 50 zooecia of two colonies for each population; we obtained the mean (X), the variance (S^2) and the coefficient of correlation (r) (Table 2).

Table 2.- Principal statistical values (50 zooecia measured). X: mean. S^2: variance. r: correlation coefficient. S–1: *Stylopoma spongites*. S–2: *Stylopoma informata*. S–3: *Stylopoma* sp. *3*. S–4: *Stylopoma* sp. *4*. S–5: *Stylopoma* sp. *5*.

		Lz	lz	Lo	lo	Lav	lav	D	Lan
S-1	$\bar{X}$	0.5410	0.3046	0.1270	0.1228	0.9228	0.0564	0.1487	0.0888
	S^2	0.0020	0.0011	0.0001	0.0001	0.0003	0.0001	0.0005	0.0001
	r	0.5214		0.1778		0.0678		0.1369	
S-2	$\bar{X}$	0.5550	0.3950	0.1628	0.1456	0.1105	0.0735	0.1180	0.2460
	S^2	0.0054	0.0046	0.0002	0.0001	0.0002	0.0001	0.0001	0.0003
	r	0.6064		0.4435		0.5700		0.4369	
S-3	$\bar{X}$	0.4956	0.3095	0.1396	0.1303	0.1182	0.0541	0.0926	0.1916
	S^2	0.0037	0.0039	0.0001	0.0001	0.0002	0.0001	0.0001	0.0004
	r	-0.5021		-0.2602		0.2496		0.4145	
S-4	$\bar{X}$	0.5973	0.4179	0.1540	0.1401	0.1088	0.0753	0.1196	0.2370
	S^2	0.0077	0.0032	0.0002	0.0227	0.0010	0.0001	0.0001	0.0005
	r	0.5932		0.1618		0.2400		0.4837	
S-5	$\bar{X}$	0.5196	0.3790	0.1440	0.1330	0.1003	0.0584	0.1004	0.1920
	S^2	0.0033	0.0015	0.0001	0.0001	0.0002	0.0001	0.0001	0.0097
	r	-0.4989		0.2491		0.1223		0.2187	

We employed the student test (t) for the mean comparisons: the variances (S^2) were compared by the Fischer test (Table 3F). This analysis shows that the species (S–1) and (S–3) are not different at a significative level of 99%; it was the same for the species (S–4) and (S–2). We only include the parameters la and Lan.

In the assumption of the great intraspecific variability of the species, it was necessary to prove if the interspecific variations between the species (S–1), (S–2) and (S–5) were greater than the intraspecific variations of the colonies of the same species. With this purpose, we used a multivariance test in which we compared two colonies for each population (Table 4), (C–B, rows), and at the same time we compared each population with the others (line, D–B), for all the parameters (Lz, lz, lo, ...).

This kind of test allows us to estimate which parameter is more significant in differentiation of the species and it also shows which of the interspecific or intraspecific variations are the most significant.

We used a significance testing level of 99%, since our samples are relatively small in comparison with the natural populations.

All parameters, except lav, have a non significant variation between the colonies of the same species. On the other hand, there is a significant variation of all the parameters, except Lav, among the different populations. There is also a great variation of the parameter lav among the colonies of the same population as there is in different populations. Thus, both parameters (Lav, lav) cannot be used for the species definition, with this size of sample, since their qualitative aspects are different.

Table 3.- "t" and "F" analysis for the five groups of species of *Stylopoma* and for the parameters lav and Lan. ddl: freedom degree. : significant difference. =: no significant difference.

	S-1			S-2			S-3			S-4		
		ddl	S		ddl	S		ddl	S		ddl	S
F	1.12	23/16	=									
t	5.07	39	≠									
S-2												
F	1.89	23/16	=	1.69	16/16	=						
t	0.72	39	=	6.15	32	≠						
S-3												
F	1.23	23/15	=	1.09	16/15	=	1.55	16/15	=			
t	5.59	38	≠	0.52	31	=	6.84	31	≠			
S-4												
F	1.78	23/37	=	1.59	16/37	=	1.06	16/37	=	1.45	15/37	=
t	2.85	60	≠	5.83	53	≠	1.82	53	=	6.53	52	≠
S-5												

lav

	S-1			S-2			S-3			S-4		
		ddl	S		ddl	S		ddl	S		ddl	S
F	1.80	29/29	=									
t	17.9	58	≠									
S-2												
F	1.37	29/29	=	1.32	29/29	=						
t	7.05	58	≠	11.1	58	≠						
S-3												
F	1.09	29/29	=	1.65	29/29	=	1.25	29/29	=			
t	14.7	58	≠	1.71	58	=	8.15	58	≠			
S-4												
F	17.5	29/49	≠	31.48	29/49	≠	23.84	29/49	≠	19.08	29/49	≠
t	2.24	78	=	2.94	78	≠	0.02	78	=	2.44	78	≠
S-5												

Lan

The other parameters show that there are enough differences between the species to be used for species definition, and that the most significant differences are the length of the primary orifice (Lo) and the length of the anter (Lan).

Although the multivariance analysis demonstrates that there is a variation between the species in general, it does not allow measurement of the actual variation of one species in comparison with another. It was therefore necessary to consider the mean X and variance tests (F and t) for the species which show the most important differences (S–1, S–2, S–5) (Table 5).

These tests show that species S-1 (*Stylopoma spongites*) is always significantly different from S-2 (*Stylopoma informata*) either in the mean X or in the variance. In the same way, S–2 is significantly different from S–5.

Table 4.- Multivariance analysis for each parameter. (C–B) variation between the colonies of the same species. (D–B) variation between the three groups of compared species (S–1, S–2, S–5). S. V. = variation origin. Va = variability. ddl = freedom degree. S^2 = variance. F = Fischer value. ddlF = freedom degree for F.

	S.V.	Var	ddl	S^2	F	ddl F
Lz	C-B	0.0005	1	0.0005	9.972	1/84
	D-B	0.1535	2	0.07675	15.393	2/84
lz	C-B	0.0048	1	0.00482	3.070	1/84
	D-B	0.0722	2	0.00361	22.993	2/84
Lo	C-B	0.0004	1	0.0004	5.649	1/84
	D-B	0.0171	2	0.0086	120.90	2/84
lo	C-B	0.0001	1	0.0001	2.158	1/84
	D-B	0.0058	2	0.0029	28.723	2/84
Lav	C-B	0.0001	1	0.0001	2.633	1/84
	D-B	0.0007	2	0.0004	1.561	2/84
lav	C-B	0.0009	1	0.0009	25.139	1/84
	D-B	0.0043	2	0.0022	63.450	2/84
Lan	C-B	0.00003	1	0.00003	2.720	1/84
	D-B	0.0148	2	0.0074	90.920	2/84
D	C-B	0.0010	1	0.0010	2.565	1/84
	D-B	0.1352	2	0.0676	26.345	2/84

Stylopoma spongites (S–1) and *Stylopoma* sp. *5* are not different for parameters lav, Lav and Lz. We cannot consider the first two parameters for the reasons shown by the multivariance analysis, but it is not the same for Lz; so, if *Stylopoma* sp. *5* is a different population of *S. spongites*, there is a greater relationship between them than with *S. informata*.

Stylopoma spongites and *S. informata* have enough qualitative and quantitative different features to be considered different species and never more be confused.

The population S–3 (*Stylopoma* sp. *3*) can be considered to be a variety of *S. spongites* in which the oral avicularia are different in form and position; there is also a small variation in the colonial and peristomial forms.

Stylopoma sp. *5* (S–5) is probably either a subspecies of *S. spongites* or a distinct species; the statistical test shows that the second possibility is more feasible, but needs to be confirmed by biological and ecological studies.

Table 5.- a) "t" and "F" analysis for each parameter of the species S–1 compared with S–2 and S–5. b) "t" and "F" analysis for species S–2 compared with S–5. significant difference. = no significant difference. Confidence level 99.9%.

		Lz			lz			Lo			lo		
			ddl	Sig		ddl	Sig		ddl	Sig		ddl	Sig
S-2	F	2.67	49/49	≠	4.56	49/49	≠	2.38	49/49	≠	1.00	49/49	=
	t	1.15	98	=	8.57	98	≠	15.0	98	≠	11.0	98	≠
S-5	F	1.65	49/49	=	1.36	49/49	=	1.42	49/49	=	1.56	49/49	=
	t	2.08	98	=	10.3	98	≠	8.43	98	≠	5.63	98	≠

		Lav			lav			Lan			D		
			ddl	Sig		ddl	Sig		ddl	Sig		ddl	Sig
S-2	F	1.46	23/16	=	1.12	23/16	=	1.53	29/29	=	1.80	29/29	=
	t	3.41	39	≠	5.07	39	≠	12.9	58	≠	17.9	58	≠
S-5	F	1.62	23/37	=	1.78	23/37	=	1.55	29/49	=	17.5	29/49	≠
	t	1.87	60	=	0.85	60	=	5.59	78	≠	2.24	78	=

b

		Lz			lz			Lo			lo		
			ddl	Sig		ddl	Sig		ddl	Sig		ddl	Sig
S-5	F	1.62	49/49	=	3.04	49/49	≠	1.68	49/49	=	1.56	49/49	=
	t	2.64	98	≠	1.45	98	=	7.44	98	≠	6.96	98	≠

		Lav			lav			Lan			D		
			ddl	Sig		ddl	Sig		ddl	Sig		ddl	Sig
S-2	F	1.11	16/37	=	1.59	16/37	=	1.00	29/49	=	31.5	29/49	≠
	t	2.49	53	=	5.83	53	≠	7.92	78	≠	2.94	78	≠

CONCLUSIONS

Among the well known bryozoan fauna of the Gulf of Mexico, we have chosen species with systematic problems, which are also very important in the paleobiogeography, evolutionary and systematic distributional history of the area. The problematic species belong to two different taxonomic groups and they have been analysed in two different ways.

The species of the Genus *Stylopoma* Levinsen, 1909 were distinguished by a statistical analysis of morphological characters. We have definitively differentiated *S. spongites* and *S. informata* for the Gulf of Mexico; we also found a variety of *S. spongites* and a synthetic form named *Stylopoma* sp. *5*. In our opinion *S. informata* gave rise to *S.* sp. *5* in the early Miocene; and later, when the Isthmus of Panama was formed, this species gave rise to *S. spongites* in the Gulf of Mexico.

The species of the Family Smittinidae are distinct and it was not necessary to apply a statistical test. In this family, the most diverse genus is *Parasmittina* Osburn, 1952 with six species. The species of the genera *Pleurocodonellina* (Soule and Soule, 1973) and *Smittina* (Norman, 1903) are also present.

We have observed five different evolutionary trends in this family, the most important is represented by the group of species which have many common features; we call them the *trispiniformis* group. This group contains

Parasmittina trispinosa, *P. nitida*, *P.* cf. *P. crosslandi* and *P. spathulata*. *P. trispinosa* and *P. crosslandi* have close relationship with Pacific forms. *P. nitida* and *P. spathulata* are endemic species of the eastern American tropical coast.

P. mexicana new species is the only one showing affinities with forms of the Mediterranean Sea, Red Sea or western Africa . We think that it is excluded from the *trispiniformis* group and that it has a different evolutionary history in spite of the convergence of characters.

Parasmittina anderseni is an endemic form of the Gulf of Mexico and we are not certain of its relationship with the other species. The last two trends are represented by *Pleurocodonellina signata* and *Smittina nitidissima*, species with a great resemblance with Pacific forms.

Finally, it is very interesting to observe that the analysis of two different taxonomic groups (Genus *Stylopoma* and *trispiniformis* group) reflects a very similar evolutionary and biogeographical behaviour. These species show the consequences of a geological phenomenon in their evolution and Recent distribution. The Isthmus of Panama represented a geographical barrier impeding the free interchanges of populations between the Pacific and Atlantic Oceans. In the *trispiniformis* group there was a synthetic form during the late Miocene living in the tropical waters of America; at that time *Stylopoma* sp. *5* and *S. informata* were different populations but *S. spongites* and the species of the *trispiniformis* group were the incipient populations. When the barrier was formed each population followed its own evolutionary path and reached its present distribution.

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