Reproduction and larval development of the *Strombina*-group (Buccinoidea: Columbellidae) and related gastropods: testing the use of the larval shell for inference of development in fossil species

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ABSTRACT

The primitive planktotrophic mode of larval development of gastropods of the *Strombina*-group was replaced during the closure of the Isthmus of Panama by predominantly direct development in the Caribbean, but remains the predominant mode in the eastern Pacific. As with other gastropods, the inference of larval development in this group is based on the morphology of the larval shell, but the validity of this method has not been tested by direct biological observations. Reproduction was observed for six species of the *Strombina*-group and compared to those for two other species reported previously. These data were then used to infer the mode of development for four additional species for which only preserved egg capsules and eggs were available. In all 10 cases, the results agree with the mode of development inferred on the basis of larval shell dimensions and numbers of whorls.

RIASSUNTO

Il tipo primitivo di sviluppo larvale (planctotrofico) nei gasteropodi dello *Strombina*-group è stato sostituito durante la chiusura dell'Istmo di Panama da uno sviluppo predominantemente diretto nei Caraibi, mentre è rimasto il tipo di sviluppo prevalente nel Pacifico orientale. Come in altri gasteropodi, l'inferenza del tipo di sviluppo in esemplari di questo gruppo è basata sulla morfologia della conchiglia larvale, ma la validità del metodo non è stata verificata per mezzo di osservazioni biologiche dirette. La riproduzione è stata osservata in sei specie dello *Strombina*-group e comparata con quella di due altre specie studiate precedentemente. Tali dati sono stati usati per inferire il tipo di sviluppo in altre quattro specie per le quali erano disponibili solo dati su uova e capsule ovigere. In tutti i 10 casi, i risultati sono in accordo con il modo di sviluppo inferito sulla base della dimensioni e del numero di giri della conchiglia larvale.

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INTRODUCTION

The *Strombina*-group sensu JUNG (1989) is a highly diverse group and appear as extremely well preserved fossils throughout Neogene and Quaternary deposits of Tropical America. Extensively collected, and with their taxonomy recently revised (JUNG, 1989), species of this group have been used as a model system to study temporal and spatial evolutionary consequences of the Pliocene rise of the Isthmus of Panama (JACKSON ET AL., 1993; JACKSON, 1994; JACKSON ET AL., 1996).

Inferences based mainly on the morphology of the protoconch of both fossil and living species of this group indicate that the oldest species (Early and Middle Miocene) were entirely planktotrophic (JACKSON ET AL., 1996). The proportion of non-planktotrophs increased thereafter, but the nature of this change was reversed between the two oceans. Most younger species in the Caribbean exhibited direct development whereas planktotrophic development prevailed in the eastern Pacific with lecithotrophic and direct development combined of roughly equal secondary importance. These striking shifts in the life history of the *Strombina*-group can be used to model the relationships between environmental events and processes of speciation and extinction. In order to do this, however, we need to calibrate modes of development inferred through shell morphology by comparison with the life histories of living species based on observations of larval development.

Gastropod development can be divided into groups based on the number and size of eggs produced, the mode of larval nutrition, and whether later stages of larval development occur within the egg capsule or in the plankton (THORSON, 1946, 1950, 1961; MILEIKOVSKY, 1971; JABLONSKI & LUTZ, 1983; JABLONSKI, 1986; LIMA & LUTZ, 1990). Planktotrophic species lay many small capsules filled with small embryos and without any extra food resources. These embryos develop into veliger larvae, usually with a well developed velum and digestive organs. They swim and feed actively in the plankton where they commonly pass a relatively large period of time before settlement and metamorphosis. In contrast, non-planktotrophic species lay a small number of large capsules containing a few large embryos that may exhibit one of two different modes of development. In the first case, commonly termed direct development, the veliger stage and metamorphosis take place inside the capsule where the embryos develop into fully competent juveniles that crawl away. Direct development is commonly associated with the production of extra nutritive eggs and cannibalism of more slowly developing embryos. In the second case, termed lecithotrophic development, the embryo develops into a 'pediveliger' larva with a small velum and a definitive foot. 'Pediveligers' live in the plankton for a short period of time without feeding, before settling as juveniles.

Table 1. Summary of reproductive aspects for 12 species of the *Strombina*-group and related gastropods.

	Egg Capsule Length (mm)	Egg Capsule Width (mm)	Egg Capsule Aperture Length (mm)	Egg Capsule Aperture Width (mm)	No. Eggs/ Capsule	Egg Diameter (µm)	No. Embryos/ Egg Capsule	Shell Length at Hatching (µm)	Hatching Stage
EASTERN PACIFIC SPECIES									
1- *Bifurcium bicanaliferum*[a]	1.0 ± 0.1	0.8 ± 0.1	0.3 ± 0.01	0.2 ± 0.02	22 ± 2	151 ± 11	20 ± 3	234 ± 10	veliger
	(n = 27)	(n = 27)	(n = 27)	(n = 27)	(n = 24)	(n = 30)	(n = 29)	(n = 40)	1.5 whorls
2-*Sincola gibberula*	1.1 ± 0.1	1.0 ± 0.03	0.3 ± 0.01	0.2 ± 0.01	25 ± 2	150 ± 12	21 ± 2	270 ± 10	veliger
	(n = 25)	(n = 25)	(n = 12)	(n = 12)	(n = 25)	(n = 25)	(n = 17)	(n = 40)	1.75 whorls
3-*Sincola sinuata*	1.5 ± 0.2	1.3 ± 0.2	0.4 ± 0.05	0.3 ± 0.04	ND	ND	ND	ND	ND
	(n = 25)	(n = 25)	(n = 25)	(n = 25)					
4-*Strombina elegans*	3.5 ± 0.3	3.2 ± 0.3	0.9 ± 0.2	0.5 ± 0.1	56 ± 21	304 ± 20	ND	400 ± 73	veliger
	(n = 25)	(n = 25)	(n = 25)	(n = 25)	(n = 11)	(n = 30)	(=17)		1.25 whorls
5-*Strombina lanceolata*	2.1 ± 0.08	1.7 ± 0.09	0.5 ± 0.04	0.4 ± 0.05	30 ± 7	336 ± 30	ND	ND	ND
	(n = 25)	(n = 25)	(n = 25)	(n = 25)	(n = 20)	(n = 44)			
6-*Strombina recurva*	2.4 ± 0.1	2.0 ± 0.3	0.6 ± 0.05	0.5 ± 0.07	27 ± 7	396 ± 75	14 ± 3	423 ± 82[c]	veliger[c]
	(n = 22)	(n = 22)	(n = 22)	(n = 22)	(n = 8)	(n = 21)	(n = 9)	(n = 15)	1.75 whorls
7-*Clavistrombina clavulus*	2.2 ± 0.2	1.7 ± 0.2	0.7 ± 0.08	0.6 ± 0.04	14 ± 2	315 ± 31	ND	470 ± 25	veliger
	(n = 26)	(n = 26)	(n = 26)	(n = 26)	(n = 26)	(n = 58)		(n = 15)	1.5 whorls
8-*Cosmioconcha modesta*	1.9 ± 0.2	1.5 ± 0.2	0.5 ± 0.08	0.4 ± 0.05	22 ± 5	211 ± 27	17 ± 3	312 ± 16	veliger
	(n = 24)	(n = 24)	(n = 24)	(n = 24)	(n = 16)	(n = 25)	(n = 25)	(n = 25)	1.75 whorls
9-*Cosmioconcha parvula*	1.3 ± 0.1	1.1 ± 0.1	0.3 ± 0.07	0.3 ± 0.06	15 ± 2	209 ± 28	4	284 ± 32[c]	veliger[c]
	(n = 22)	(n = 22)	(n = 22)	(n = 22)	(n = 17)	(n = 25)	(n = 12)	(n = 15)	1.25 whorls
10- *Cosmioconcha redheri*	0.6 ± 0.07	0.5 ± 0.04	0.3 ± 0.05	0.2 ± 0.05	ND	ND	ND	ND	ND
	(n = 13)	(n = 13)	(n = 13)	(n = 13)					
CARIBEAN SPECIES									
11- *Strombina pumilio*[b]	2.1-2.4	2.0-2.1	1.3	1.0-1.1	5	616 ± 48	5	947 ± 97	crawling juvenile 1.25-1.5 whorls
12- *Strombina francesae*[b]	2.4 ± 0.3	2.1 ± 0.2	1.3 ± 0.3	0.9 ± 0.1	5	571 ± 35 (n = 22)	5	900 ± 46	crawling juvenile 1.25-1.5 whorls

ND — No data available

a — data from FORTUNATO *et al.*, 1998

b — data from CIPRIANI & PENCHASZADEH, 1993

c — intracapsular veliger

The last decade witnessed an increased interest in the study of the relation between larval ecology and species longevity (HANSEN, 1978; VALENTINE & JABLONSKI, 1986; GILI & MARTINELL, 1994; OLIVERIO, 1996a, 1996b), dispersal capacity (BOUCHET 1981; BOUCHET & WAREN, 1979; 1994; GALLARDO & PERRON, 1982; LEAL & BOUCHET, 1991; OLIVERIO, 1994) and the utility of protoconch morphology in systematic studies (BOUCHET, 1990; OLIVERIO & TRINGALI, 1992; OLIVERIO, 1995). Most of these works deal with wide distributed groups like nassarids and turrids. Despite several studies on the Columbellidae (PETIT & RISBEC, 1929; THORSON, 1940; FRANC, 1941; KNUDSEN, 1950; AMIO, 1955; MARCUS & MARCUS, 1962; SCHELTEMA & SCHELTEMA, 1963; SCHELTEMA, 1969; D'ASARO, 1970; BANDEL, 1974; FLORES, 1978), very little is known about the development of the species of the *Strombina*-group. JUNG (1989) commented on the occurrence of egg masses on adults of several species, but the first direct observations of reproduction were reported by CIPRIANI & PENCHASZADEH (1993) on two Caribbean species, *Strombina pumilio* (Reeve), 1858, and *S.*

francesae J. Gibson-Smith, 1974. I reported on the reproductive modes of two eastern Pacific species, *Bifurcium bicanaliferum* (B. G. Sowerby I, 1832) and *Sincola gibberula* (G. B. Sowerby I, 1832) (FORTUNATO, 1995; FORTUNATO ET AL., 1995; FORTUNATO ET AL., 1998). The purpose of this paper is to present new data on several other eastern Pacific species of the *Strombina*-group and related columbellids, as well as summarize the scattered information given in previous reports.

MATERIALS AND METHODS

Observations were made on seven species of the *Strombina*-group sensu Jung (1989) and three species of the genus *Cosmioconcha* Dall (1913). Identifications follow JUNG (1989) for species of the *Strombina*-group, and KEEN (1971) as modified by RADWIN (1977a, 1977b, 1978) for the genus *Cosmioconcha*.

Adults, masses of egg capsules and juveniles were collected at several localities in the Gulf of Panama (Fig. 1: stn.1-3) from 1994 through 1996, and in the Gulf of Chiriqui in 1995 and 1997 (Fig.1: stn. 4). Collections were made both by hand along the

Table 2. Summary for modes of development based on direct biological observations, inferred from capsular and larval morphology, and protoconch morphology for 12 species of the *Strombina*-group and related gastropods.

| | Type of Larvae | Biological Observations | | | | Protoconch Morphology | |
		No. Eggs/ Capsule	No. Eggs/ Size Capsule	No. Surviving Embryos/Capsule	Size Aperture /Size Capsule	Max Diameter (?m)	Max Number of Volutions
EASTERN PACIFIC SPECIES							
1- *Bifurcium bicanaliferum*[a]	P	22	22	20	0.3	354	2.5
2- *Sincola gibberula*	P	25	22.7	21	0.3	410	3.0
3- *Sincola sinuata*	(P)	ND	ND	ND	0.3	516	3.0
4- *Strombina elegans*	P	56	16	ND	0.3	548	3.0
5- *Strombina lanceolata*	(P)	30	14.3	ND	0.2	505	2.75
6- *Strombina recurva*	(P/L)	27	11.3	14	0.3	465	2.25
7- *Clavistrombina clavulus*	P	14	6.4	ND	0.3	458	3.0
8- *Cosmioconcha modesta*	P	22	11.6	17	0.3	670	2.5
9- *Cosmioconcha parvula*	P	15	11.5	4	0.2	514	2.5
10- *Cosmioconcha redheri*	(P)	ND	ND	ND	0.5	700	3.0
CARIBEAN SPECIES							
11- *Strombina pumilio*[b]	D	5	2.3	5	0.6	660	1.5
12- *Strombina francesae*[b]	D	5	2.3	5	0.5	483	1.5

ND — No data available

a — data from FORTUNATO *et al.*, 1998

b — data from CIPRIANI & PENCHASZADEH, 1993

intertidal zone at low tides, and by dredging offshore. Animals were brought to the Naos Marine Laboratory of the Smithsonian Tropical Research Institute (STRI) in Panama, where they were kept in 15 l outside aquaria with running and aerated sea water. Adults were regularly fed fish scraps. Water temperature was not regulated in any way: aquaria were kept always outside and water was taken directly from the ocean. Observations were made on egg masses laid both in the field and in the laboratory. After hatching, larvae were kept in separated aquaria within the same water system as the adults. No extra food was provided for the larvae.

Measurements and counts of capsules, eggs, embryos, and veligers were made using a Wild M7 stereoscopic microscope. Observations were made on both living and fixed material (3% seawater buffered formaldehyde). A scanning electron microscope EOL 5300LV was used to photograph egg capsules and veliger shells which were cleaned with filtered sea water and kept in a 70% ethanol solution before being coated with gold. Adult specimens, egg capsules and veliger shells of all the species described here were deposited at the Field Museum of Natural History (FMNH), Chicago, at the Academy of Natural Sciences of Philadelphia (ANSP), and at the Muséum d'Histoire Naturelle de Genève (MHNG).
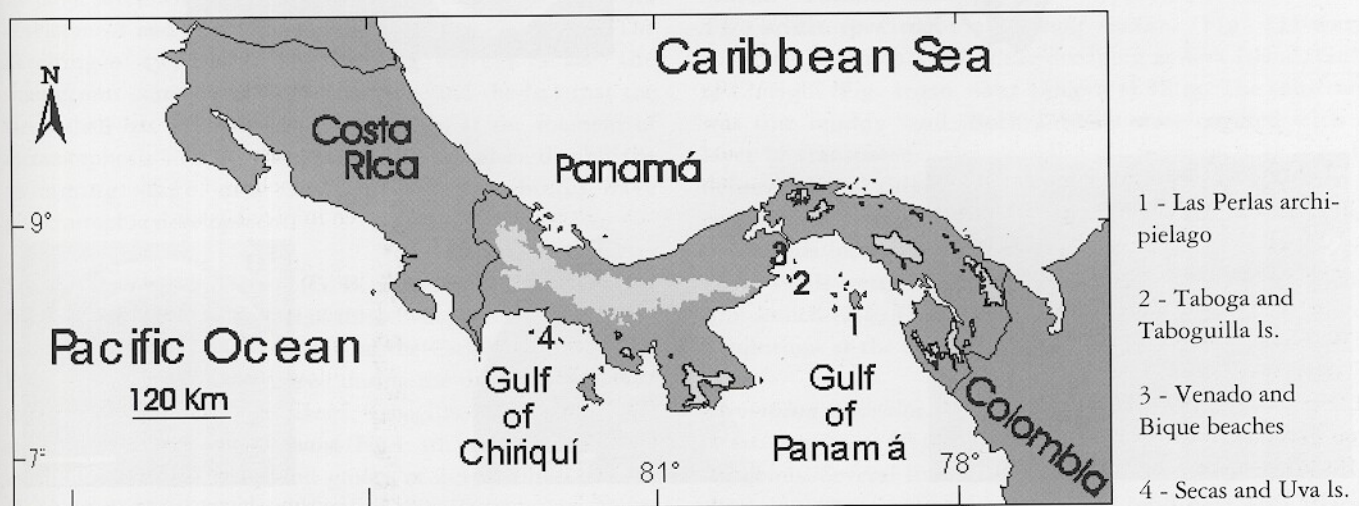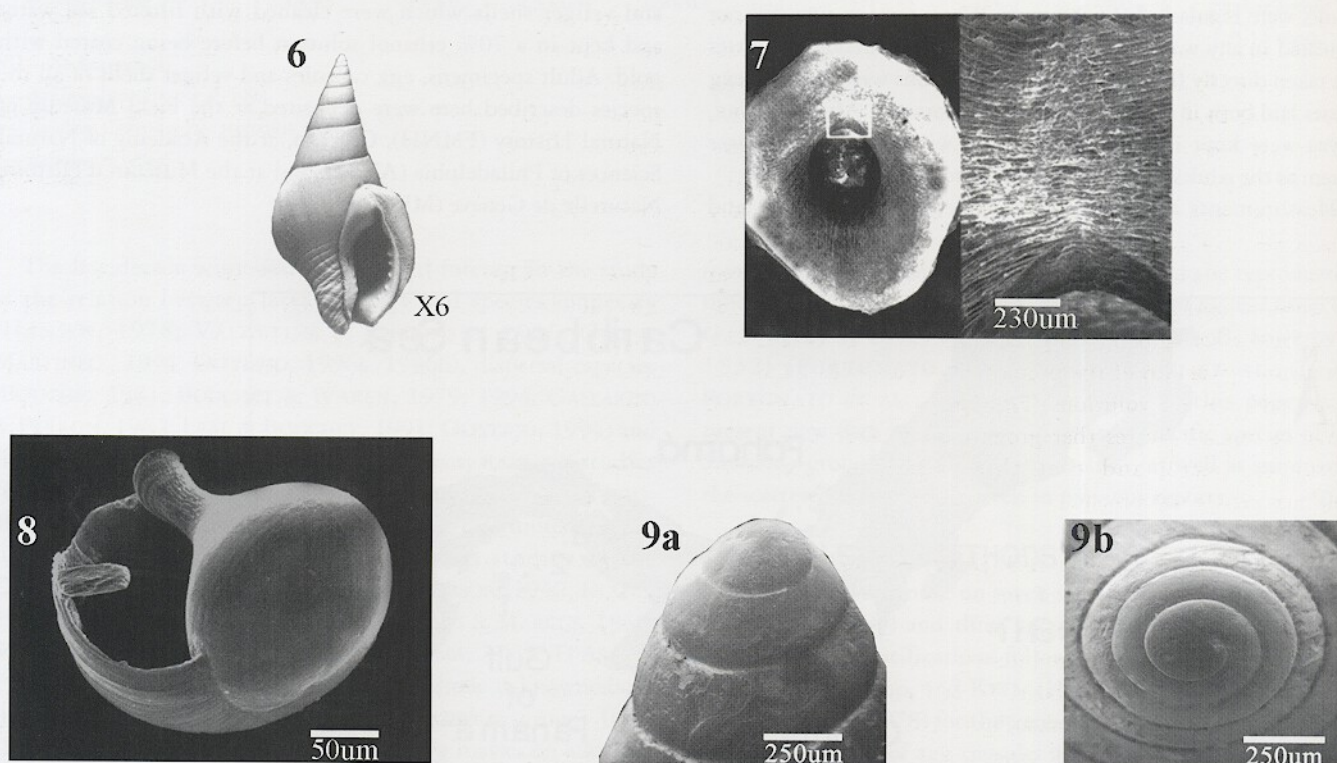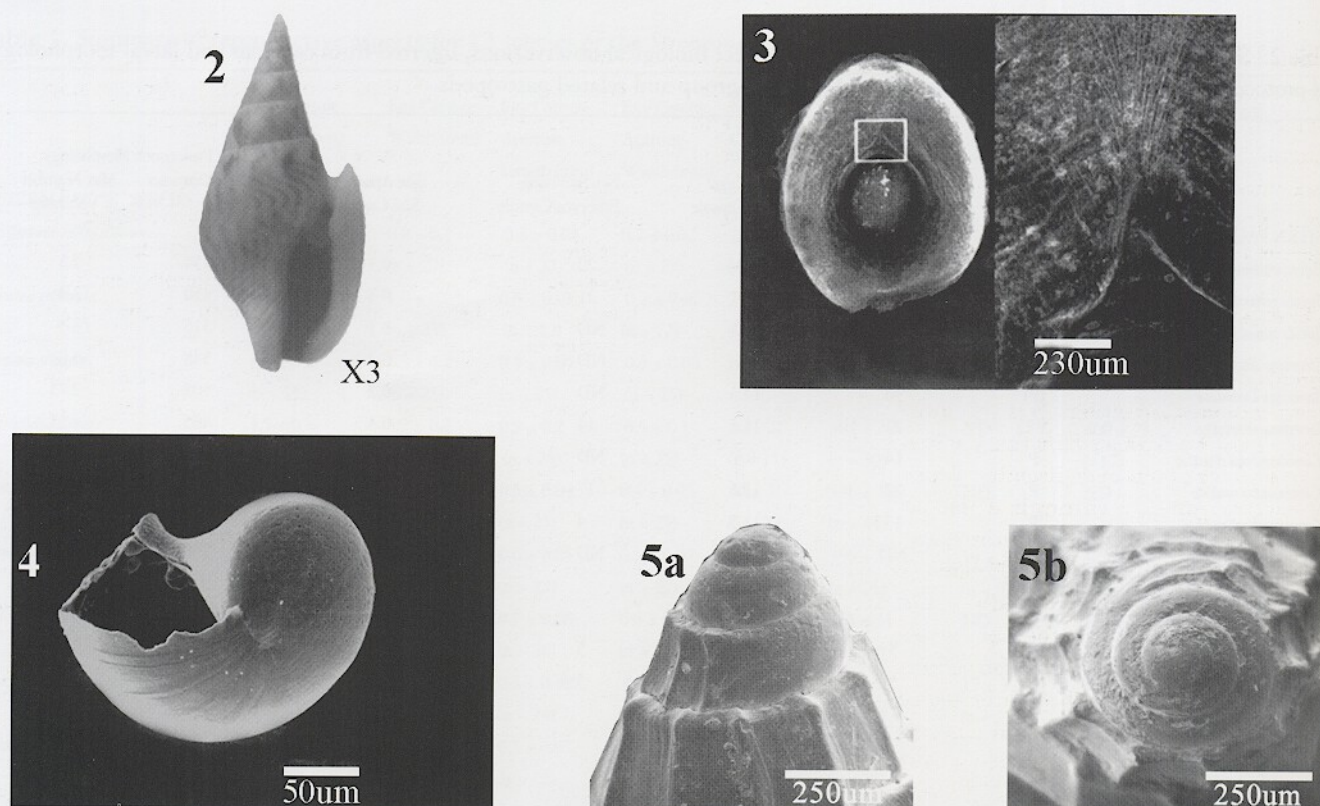

Figure 1. Map of Panama showing the localities where collections where made. Gulf of Panama: Bique, Venado, Farfan, Taboga Is., Taboguilla Is., Las Perlas archipelago. Gulf of Chiriqui: Pt. San Pedro, Uva Is., Secas Is.

Figure 2-5. *Bifurcium bicanaliferum* (B. G. Sowerby I, 1832) - Fig. 2: adult specimen (from JUNG, 1989 with permission); Fig. 3: SEM picture of the egg capsule (FMNH293337). The right side is a close up of the surface of the enclosed area in the left; Fig. 4: SEM picture of the veliger shell (FMNH293337); Fig. 5a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).

Figure 6-9. *Sincola (Dorsina) gibberula* (B. G. Sowerby I, 1832) - Fig. 6: adult specimen (from JUNG, 1989 with permission); Fig. 7: SEM picture of the egg capsule (FMNH293338). The right side is a close up of the surface of the enclosed area in the left; Fig 8: SEM picture of the veliger shell (FMNH293338); Fig. 9a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).

RESULTS

Measurements and counts for all 12 studied species are summarized in Table 1. The biological observations and protoconch morphological parameters used to infer modes of development are presented in Table 2. I first describe my own results from the eastern Pacific and then compare these to earlier results from the Caribbean.

I - EASTERN PACIFIC SPECIES

Bifurcium bicanaliferum (B. G. Sowerby I, 1832)

Bifurcium bicanaliferum (Fig. 2) is the only living species of this genus, which originated in the Caribbean Sea during the Miocene. Live adults and juveniles were collected during the dry season, January through April of 1994-1996, from extensive mud flats exposed during low tides at Bique and Venado beaches, in the Gulf of Panama (Fig. 1: stn. 3). They were also dredged from muddy sands near Taboga and Taboguilla islands, and in the Las Perlas archipelago (Fig. 1: stn. 1-2). Animals were usually found in aggregations of up to 30 specimens, gliding with their extremely long foot over the surface of the mud or buried in the top 2-3 cm. The only available hard substrate for oviposition was the shells of conspecifics. No oviposition was observed in the laboratory. Capsules are dome shaped with a basal membrane and an almost circular escape aperture in the center (Fig. 3). A suture runs through the center of the capsule, almost dividing it in two. This suture is most noticeable from the side where the escape aperture is deformed. Intracapsular development was completed 15 days after collection. Free swimming veligers at hatching have a well developed velum with black spots at the base of the cilia and a shell comprising 1.5 whorls (Fig. 4). Through the shell, the heart, the digestive gland, the stomach, and branchia are visible. Observations of the larvae showed the presence of greenish filamentous microalgae in the guts, possibly ingested as food. Veligers are very active and usually remain near the surface of the water. They survived for about 15 days, after which they all died. For this reason, further development and metamorphosis could not be observed. The hatching of swimming and feeding veliger larvae, the sinusigerous outer lip of the protoconch, and the fact that the larval shell has 2½ volutions (Fig. 5a, b) at the moment of metamorphosis indicates that growth takes place during the swimming stage, and that this species should have planktotrophic development.

Sincola (Dorsina) gibberula (G. B. Sowerby I, 1832)

Sincola gibberula (Fig. 6) is one of three living species of this once diverse genus in Neogene deposits of the Caribbean and eastern Pacific. Live adults were dredged during the dry season (January through March) of 1995 at Taboga, Tabogilla, and the Las Perlas archipelago in the Gulf of Panama (Fig.1: stn. 1-2). Animals were usually found alone or in small groups of 2-3 specimens in fine muddy sand. About 20 adult animals with compact masses of eggs attached to their shells were kept in the laboratory for observation. No oviposition was noticed in captivity.

Adults lay capsules in compact rows along the dorsal side of a congeneric shell, often covering the shell almost completely. Capsules were yellowish, translucent, and hemispheric, with a short and irregular basal membrane. The almost circular escape aperture, covered by a thin lid, is located in the upper side of the capsule (Fig. 7). A suture that nearly divides the capsule into two halves can be observed extending from the deformed escape aperture to the basal membrane. Successive layers of capsules commonly obstruct the escape aperture of capsules deposited below, causing mortality of the embryos within. Uncleaved zygotes, as well as embryos in different developmental stages were found in the same egg mass. Eggs were round and yellowish (Fig. 10A).

Intracapsular development takes place within about 15 days. The trochophore has two velar lobes (Fig. 10B, C). The veliger prior to hatching has a thin, fragile, transparent shell with no siphonal canal (Fig. 10D). Larvae increase their activity the day prior to hatching. The hatching veliger bears a shell and a large bilobate ciliated velum at the anterior end with black spots at the base of the cilia. The veliger shell has a short siphonal canal with a reddish edge (Fig. 8) and a small, round operculum. Through the shell, the heart, the digestive gland, the stomach, and branchia are visible. This free-swimming larval stage is very active and usually remains near the surface of the water. Veligers were alive for about 15-17 days. Although no extra food was provided, observations of the larvae showed the presence of greenish filamentous microalgae in the guts. The transition from the planktonic stage to the crawling juvenile was not observed because all the veligers died within 17 days after hatching. The hatching of swimming and feeding veliger larvae, and the sinusigerous shape of the protoconch outer lip are strong evidence for planktotrophic development. On the other hand, the larval shell has over 3 volutions (Fig. 9a, b) at the time of metamorphosis, which also indicates a period of growth during the planktonic stage.

Sincola (Sinuina) sinuata (G. B. Sowerby II, 1874)

Two adult specimens of *Sincola sinuata* (Fig. 11) were collected in March 1997 while dredging at Uva Island, Gulf of Chiriqui (Fig. 1: stn. 4) at a depth of 18 m. The substrate was fine muddy sand. Both animals were covered with a layer of transparent, almost spherical capsules with a well defined sutural ridge along the middle of the capsule and a comparatively wide basal flange (Fig. 12). A circular escape aperture is located in the center of the capsule. No eggs or larval shells were found in any of the collected material. The protoconch (Fig. 13a, b) has a weakly sigmoid outer lip and 3 volutions at the time of metamorphosis.

Strombina (Spiralta) elegans (G. B. Sowerby I, 1832)

Strombina elegans (Fig. 14) is one of two living species of this subgenus. Several live adults were collected in July 1995 by dredging on coarse to fine coralline sand near Uva Island (Fig. 1: stn. 4) at a depth of 20-40 m. One of the animals spawned on July 16. Ten egg capsules were laid on the walls
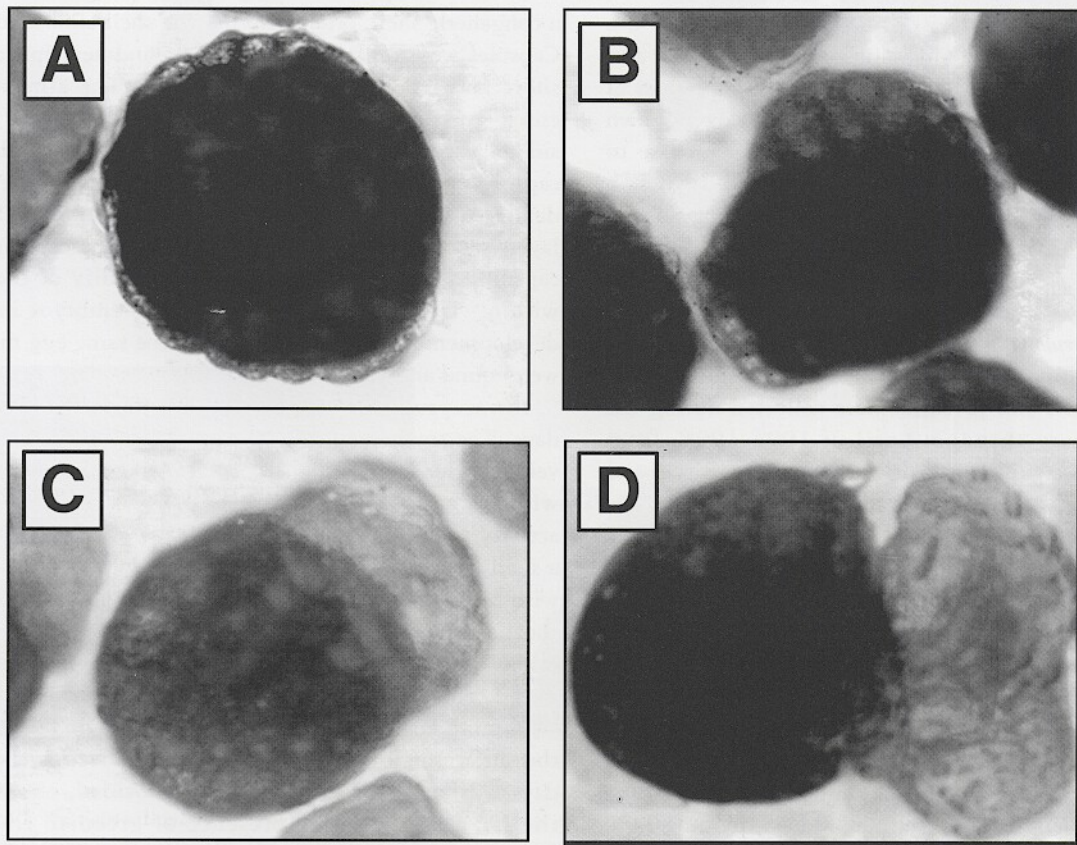
Figure 10a-d. Stages of the embryonic development of *Sincola gibberula* - A: eggs; B: embryo without torsion; C: embryo after torsion, velar lobes start to develop; D: pre-hatching veliger. Notice the thin shell and the velar lobes.
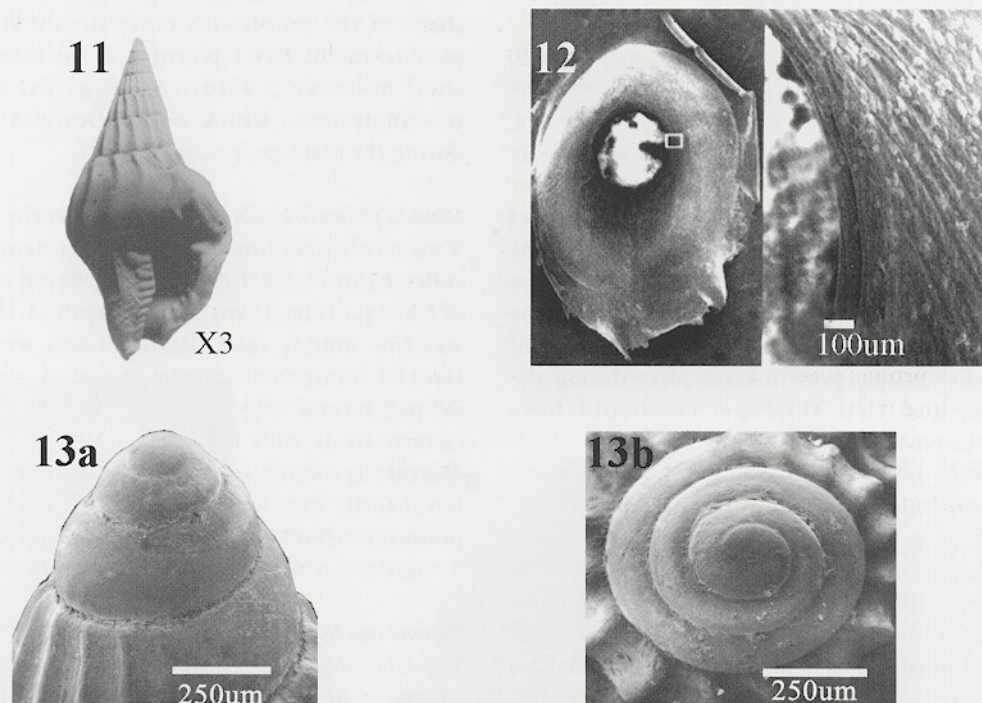

Figure 11-13. *Sincola (Sinuina) sinuata* (B. G. Sowerby II, 1874) - Fig. 11: adult specimen (from JUNG, 1989 with permission); Fig. 12: SEM picture of the egg capsule (FMNH293339). The right side is a close up of the surface of the enclosed area in the left; Fig. 13a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).

of the container where the animals had been placed just after collection. This was the first observation of spawning by a species of this group in captivity. On July 26, 20 egg capsules were observed on the walls of the aquaria where the animals were kept at the STRI Naos Marine Laboratory. Such behavior seems to be unusual among the species observed which otherwise seemed to prefer to lay their eggs upon conspecific shells. Capsules are semispherical, yellowish and have a thin but well delineated basal membrane just above the concave basal wall (Fig. 15). A suture runs longitudinally from one side of the egg capsule to the other. The capsules are the largest of all the species studied but the central, ellipsoidal escape aperture is comparatively very small (Table 1). Capsules were measured and removed to another aquarium for observation. Intracapsular development was very rapid. Embryos underwent torsion in four days. Intracapsular veligers with a very fragile shell were observed on the seventh day and oclusion occurred on the 9th. Free swimming veligers were very small at hatching, with a small velum and a shell comprising 1.25 whorls (Fig. 16). All the veligers died within 5 days of hatching. No signs of feeding were observed during the period that the larvae were alive. Nevertheless, the sinusigerous shape of the protoconch outer lip and the fact that the larval shell has 3 volutions (Fig. 17a, b) at the time of metamorphosis indicates that growth occurs during the veliger phase, i.e. it should be a planktotrophic larva.

Strombina (Strombina) lanceolata (G. B. Sowerby I, 1832)

Strombina lanceolata (Fig. 18a, b) is known only from the Galapagos Islands where it is relatively abundant (FINET 1985, 1991, 1994). It's habitat ranges from fine coral sand through hard coral mud, coralline rubble, fine sand, coarse sand, and mud. JUNG (1989, p. 60, fig. 82:19-21) found several egg capsules attached to a specimen in a sample from the San Diego Museum of Natural History collected by dredging on a sandy bottom in Tagus Cove, Albermarle island. I also had access to material collected by Dr. Yves Finet in 1993 in Gardner Bay, Española Is., and in Post Office Bay, Floreana Is. Capsules are roundish, with the basal membrane and the ellipsoid escape aperture characteristic of other studied members of the *Strombina*-group. A pronounced suture runs through the capsule almost dividing it in two halves (Fig. 19). Although some capsules had preserved eggs, no larval shells were found in any of them. The protoconch (Fig. 20a, b) has a weakly sigmoid outer lip and 2.75 volutions at the time of metamorphosis.

Strombina (Recurvina) recurva (G. B. Sowerby I, 1832)

Strombina recurva (Fig. 21a, b) is the oldest living species of the *Strombina*-group known in the eastern Pacific, occurring as fossils in Late Miocene deposits of Ecuador (Jama formation) (PILSBRY & OLSSON, 1941; JUNG, 1989). This species is found alive usually at depths from a few meters to about 40 m deep, although it ranges from the intertidal zone to 240 m. Several

shells with attached eggs were found in a lot of the Academy of Natural Sciences of Philadelphia that was dredged from a depth of 2-10 m on sand, east of Bahia Cocos, about 6 miles southwest of Puerto Culebra, Guanacaste, Costa Rica. The egg capsules were removed from the shell and fixed in 75% alcohol. Capsules are elliptical, with a basal membrane (Fig. 22). The capsules are smaller than those of *S. elegans*, but the eggs found in these capsules are the largest observed so far for any eastern Pacific species of the studied group (Table 1). Pre-hatching veliger shells with 1.75 whorls were found in several capsules (Fig. 23). The diameter of these intracapsular veliger shells is also the largest yet found in the group. The protoconch of *S. recurva* has 2.25 volutions (Fig. 24a, b), which indicates a period of further growth during the larval development.
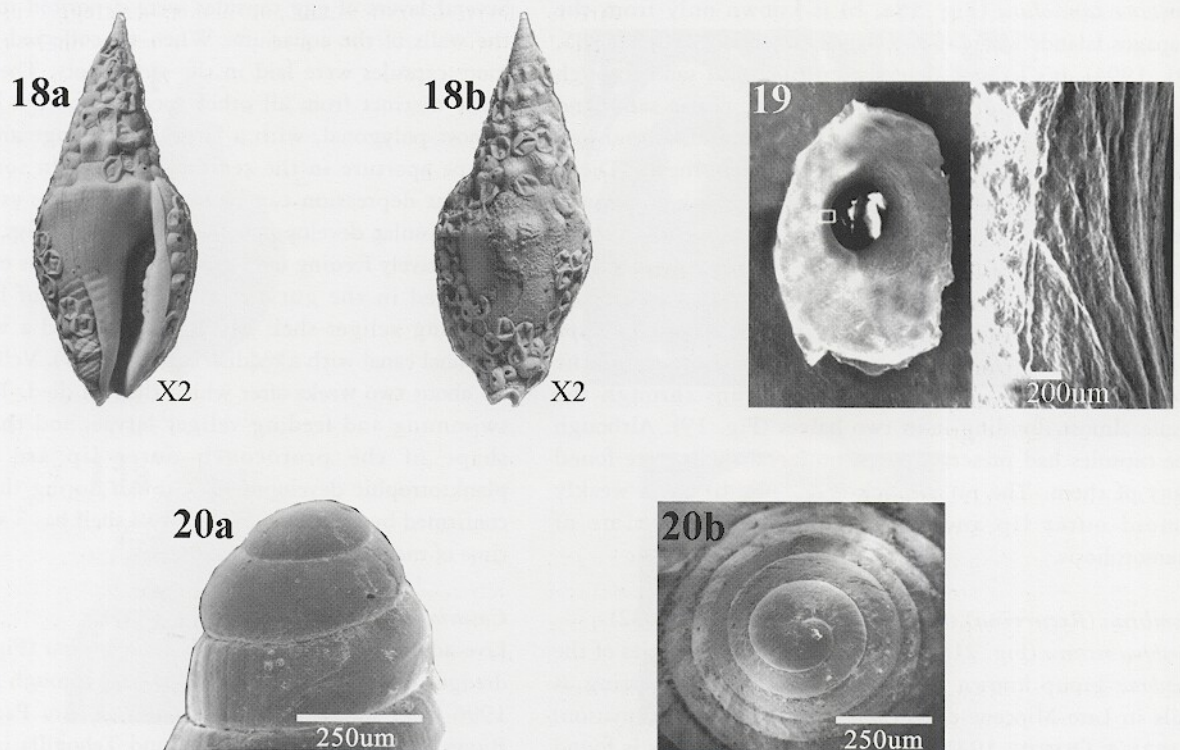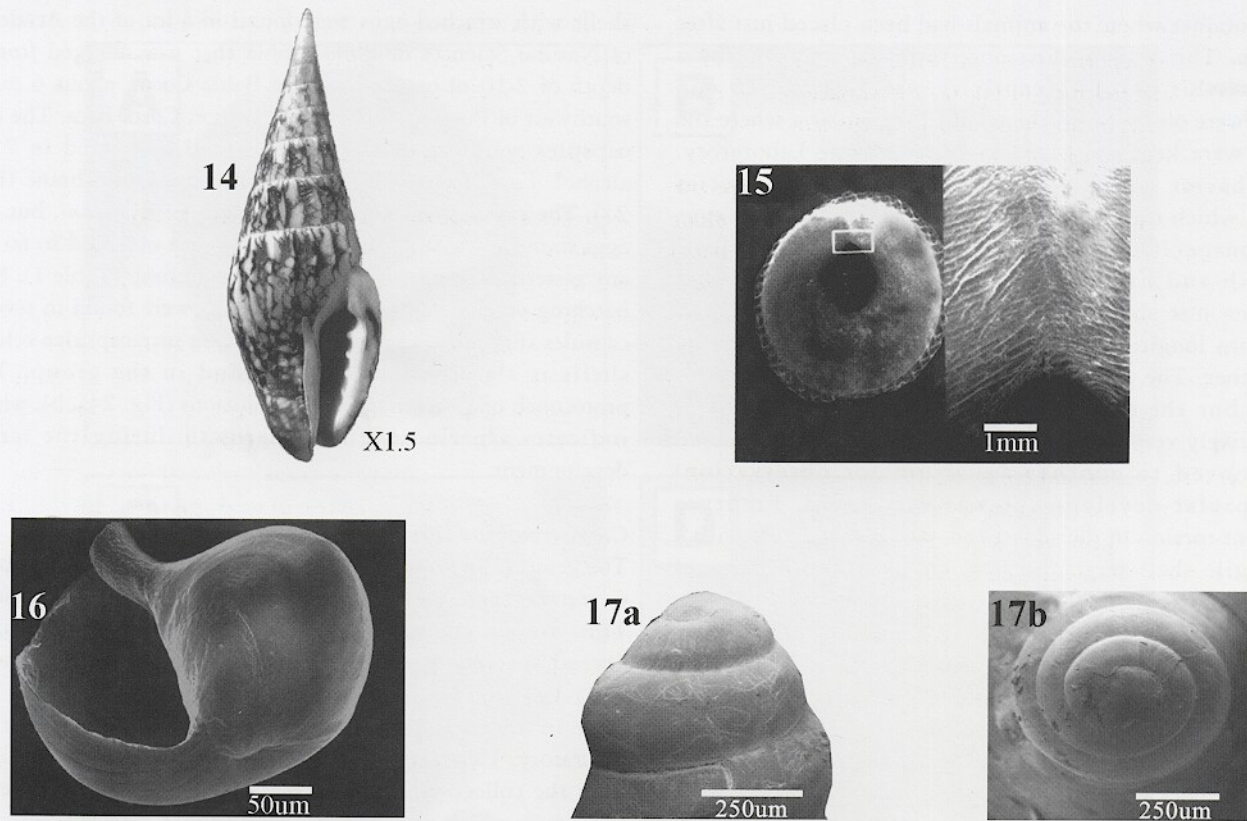
Clavistrombina clavulus (G. B. Sowerby I, 1834)

The genus *Clavistrombina* is an eastern Pacific monotypic taxon. *C. clavulus* (Fig. 25) is usually found under rocks at low tides. This is not a common species, and usually is found alone. Several specimens were collected during the dry seasons of 1995-1997 in Playa Bique, Gulf of Panama (Fig. 1: stn. 3), and kept in an aerated aquarium at the STRI Naos marine laboratory. Here, animals usually hide under rocks brought from the collecting site. Contrary to other studied species of this group which were active all the time, *C. clavulus* emerged from its hiding place only when feeding. The short foot and relatively short siphon of this species is unique among all the species collected alive by us. In May-June 1997 ovoposition was observed in one of the aquaria where two specimens were kept. Several layers of egg capsules were deposited in two places of the walls of the aquarium. When we collected these capsules, more capsules were laid in the same spots. These capsules are quite distinct from all other species reported here. They are almost polygonal, with a large basal flange and an ellipsoid escape aperture in the center (Fig. 26). In some capsules, a circular depression can be seen around the escape aperture. Intracapsular development takes about 15 days. Veligers were seen actively feeding (and greenish filamentous microalgae were observed in the guts) after the 6th day of hatching. The hatching veliger shell has 1.5 whorls and a well developed siphonal canal with a reddish edge (Fig. 27). Veligers were alive for about two weeks after which they all died. The hatching of swimming and feeding veliger larvae, and the sinusigerous shape of the protoconch outer lip are evidence for planktotrophic development. Growth during this stage is also confirmed by the fact that the larval shell has 3 volutions at the time of metamorphosis (Fig. 28a, b).

Cosmioconcha modesta (Powys, 1835)

Live adult and juvenile *Cosmioconcha modesta* (Fig. 29a, b) were dredged during the dry season (January through April) of 1994-1996 from several localities in the Gulf of Panama (Venado, Bique, Farfan beaches), Taboga and Tabogilla islands, and Las Perlas archipelago (Fig. 1: stn. 1-3). Several adults were also collected in July 1995 from several localities in the Gulf of

Figure 14-17. *Strombina (Spiralta) elegans* (B. G. Sowerby I, 1832) - Fig. 14: adult specimen (from JUNG, 1989 with permission); Fig. 15: SEM picture of the egg capsule (FMNH293340). The right side is a close up of the surface of the enclosed area in the left; Fig. 16: SEM picture of the veliger shell (FMNH293340); Fig. 17a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).

Figure 18-20. *Strombina (Strombina) lanceolata* (B. G. Sowerby I, 1832) - Fig. 18a-b: adult specimen (MHNG23078). Notice egg capsules attached to the shell. Fig. 19: SEM picture of the egg capsule. The right side is a close up of the surface of the enclosed area in the left; Fig. 20a-b: lateral and apical view of protoconch.

Chiriqui (Secas Is., Uva Is.) (Fig. 1: stn. 4) in muddy sands. As with other species reported here, the extremely long foot of *C. modesta* is well adapted for gliding on the surface of the mud. Egg masses collected in the field and laid in the laboratory were studied. Adults lay egg capsules on conspecific shells (Fig. 29b). An egg mass is usually composed of several layers of transparent, semispherical capsules with a well defined sutural ridge along the middle of the capsule and a basal flange (Fig. 30). A circular escape aperture is located in the center. Different embryonic stages were found in the same egg mass. Laboratory observations of oviposition show that a single egg mass is the result of several consecutive spawnings. Intracapsular development is similar to the other species reported here and occurs within 20 days. *Cosmioconcha modesta* hatches as a veliger with 1.75 whorls (Fig. 31) that actively swims and feeds (no special food was offered, but greenish filamentous microalgae were observed in the guts of the veligers). Veligers were kept alive for about two weeks after which they all died. The hatching of swimming and feeding veliger larvae, and the sinusigerous outer lip of the protoconch, are signs of planktotrophic development. At the time of metamorphosis, the larval shell has 2.5 whorls (Fig. 32a, b), which indicates that growth occurs during this free-swimming stage.

Cosmioconcha parvula (Dall, 1913)
Live adults of *Cosmioconcha parvula* (Fig. 33) were dredged during July 1995 from a fine muddy bottom off Uva island in the Gulf of Chiriqui (Fig. 1: stn. 4), at a depth of 70 m. One of the animals had an egg mass on its shell composed of several dozen capsules. Capsules are small, roundish, with a median suture (Fig. 34). The elliptical escape aperture is located in the top center of the capsule and has a small basal membrane near the concave basal wall. Several capsules had small, yellowish eggs and others had embryos in different stages of development (Table 1). Intracapsular development was followed through hatching of the free-swimming planktonic veliger with 1.25 whorls. Further development was not followed because all the veligers died after 5 days. Although no signs of feeding were noticed during this period, the hatching of a competent swimming veliger larvae, the sinusigerous lip of the protoconch, and the fact that the larval shell has 2.5 volutions at metamorphosis (Fig. 35a, b) are evidences of planktotrophic development during which the larvae should feed and grow.

Cosmioconcha redheri (Hertlein & Strong, 1951)
Several live specimens of *Cosmioconcha redheri* (Fig. 36) were dredged from 22-26 m near Uva island in the Gulf of Chiriqui in July 1995 (Fig. 1: stn. 4) in coarse sand with broken coral rubble. Thirteen egg capsules were found on the shell of a single individual. Capsules were in the pattern characteristic reported for the previous species. Capsules were round, with a wide flange near the concave basal wall (Table 1) and a unique pattern of circular lines (Fig. 37). The escape aperture is round and large relative to the size of the capsule (Table 1). There is no noticeable sutural ridge in the capsule. No larval shells were found in any of the collected material. The protoconch (Fig. 38a, b) has a weakly sigmoid outer lip and 3 volutions at the time of metamorphosis.

II - Caribbean Species

Strombina (Strombina) pumilio (Reeve, 1859)
Strombina pumilio (Fig. 39) occurs commonly along the central and western coast of Venezuela in depths of 2-6 m, where it is usually buried in the top layer of coarse sand or among turtle and eel grass beds (CIPRIANI & PENCHASZADEH, 1993). Animals can be located by their long and extremely mobile siphons that stick out of the sediment. Such behavior and mobility seems to be characteristic of most species of the *Strombina*-group observed so far. Adults lay translucent, domed-shaped egg capsules (Fig. 40) in masses placed on the dorsal side of conspecific shells. This species was shown to have direct development with fully developed juveniles crawling out of the capsule (Fig. 41) (CIPRIANI & PENCHASZADEH, 1993). Protoconchs have 1.5 volutions (Fig. 42a, b) and a weakly sigmoid outer lip, which agrees with direct larval development.

Strombina (Lirastrombina) francesae J. Gibson-Smith, 1974
Strombina francesae (Fig. 43) is apparently rare and restricted to Los Roques archipelago and surrounding areas along the central coast of Venezuela (JUNG, 1989). This species is usually found in coarse sand where patches of algae drift are abundant (CIPRIANI & PENCHASZADEH, 1993). Adult animals were found buried in the top 2 cm of sediment. Their shells were covered with several layers of transparent and hemispheric egg capsules (Fig. 44). Spawns, capsules and juvenile protoconchs (Fig. 45) were described by CIPRIANI & PENCHASZADEH (1993). Observations on late embryos removed from egg capsules showed a well developed foot and cephalic tentacles, but no signs of a velum. The authors concluded that the species has direct development. This conclusion is supported by the weakly sigmoid shape of the protoconch outer lip and its maximum number of volutions (1.5) (Fig. 46a, b).

DISCUSSION AND CONCLUSIONS
Reproduction and development of the species of the *Strombina*-group reported here closely resembles that reported for most other columbellids, especially in the dome-shaped morphology of the egg capsule and the planktotrophic larval stage (BANDEL, 1974, 1976; D'ASARO, 1970; MARCUS & MARCUS, 1962, 1964). The main difference is that most of the species reported here lay their eggs on the shells of conspecifics, even when other substrates are available. This maybe interpreted either as some kind of 'brood protection' or as an adaptation to a muddy habitat, or both.

Figure 47 shows characteristics of the protoconch for 54 species of the *Strombina*-group, both fossil and living which have been used to infer modes of development (modified from JACKSON ET AL., 1996). The larger, filled symbols indicate the eight species discussed in this paper whose larval development
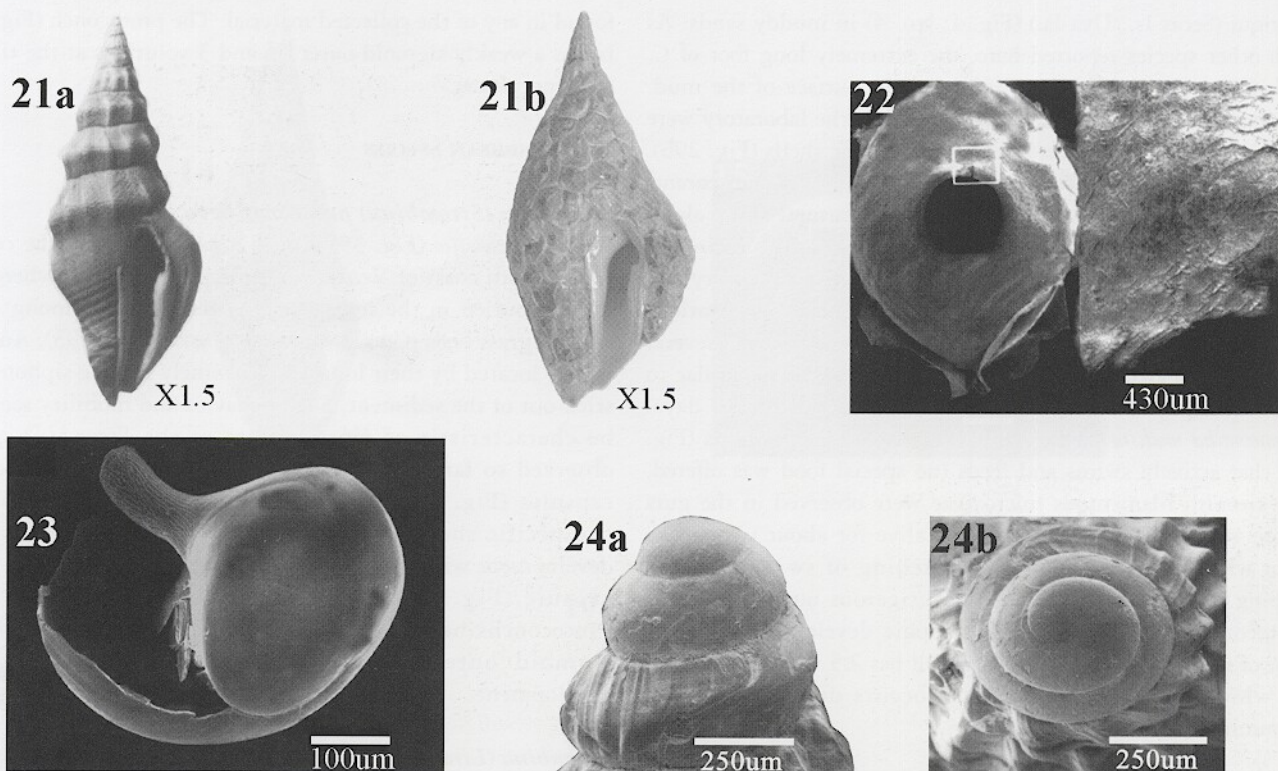
Figure 21-24. *Strombina (Recurvina) recurva* (B. G. Sowerby I, 1832) - Fig. 21a-b: adult specimen (ANSP307933). Notice egg capsules attached to the shell; Fig. 22: SEM picture of the egg capsule. The right side is a close up of the surface of the enclosed area in the left: Fig. 23: SEM picture of the pre-hatching veliger shell; Fig. 24a-b: lateral and apical view of protoconch.
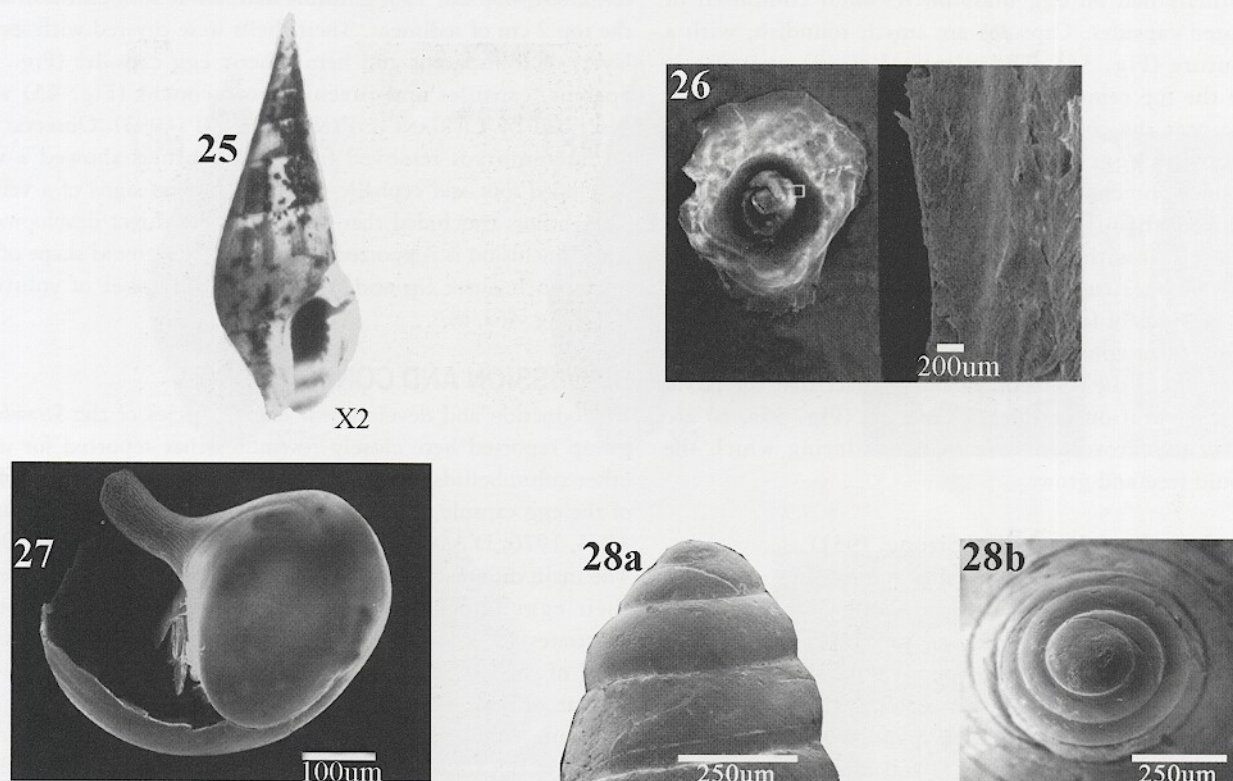

Figure 25-28. *Clavistrombina clavulus* (B. G. Sowerby I, 1834) - Fig. 25: adult specimen (from JUNG, 1989 with permission); Fig. 26: SEM picture of the egg capsule (FMNH293341). The right side is a close up of the surface of the enclosed area in the left; Fig. 27: SEM picture of the veliger shell (FMNH293341); Fig. 28a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).
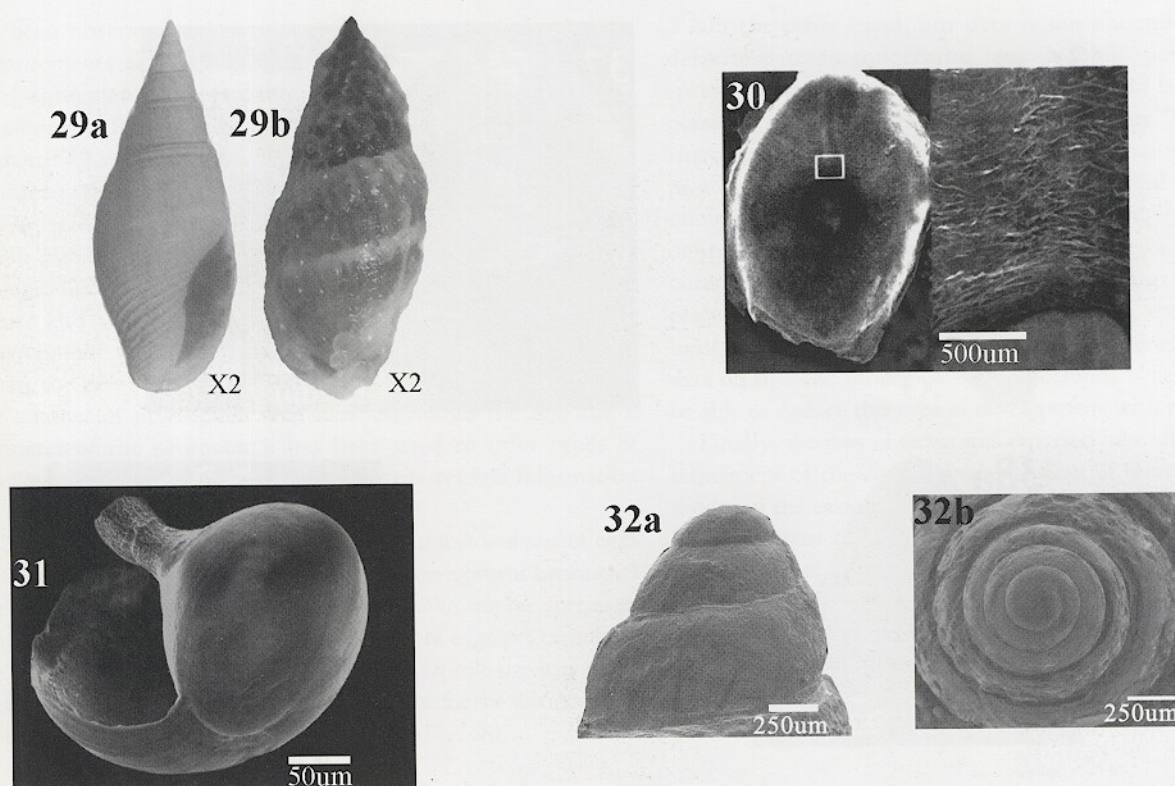
Figure 29-32. *Cosmioconcha modesta* (Powys, 1835) - Fig. 29a-b: adult specimen (FMNH293342). Notice egg capsules attached to the shell; Fig. 30: SEM picture of the egg capsule. The right side is a close up of the surface of the enclosed area in the left; Fig. 31: SEM picture of the veliger shell; Fig. 32a-b: lateral and apical view of protoconch.
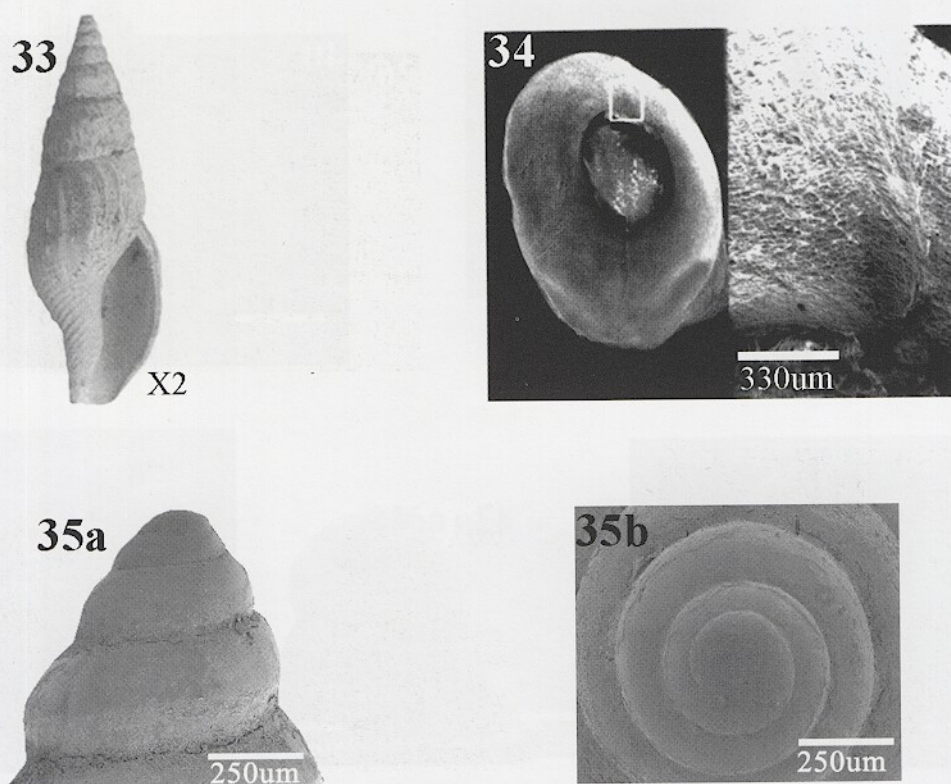

Figure 33-35. *Cosmioconcha parvula* (Dall, 1913) - Fig. 33: adult specimen (FMNH280885); Fig. 34: SEM picture of the egg capsule. The right side is a close up of the surface of the enclosed area in the left; Fig. 35a-b: lateral and apical view of protoconch.
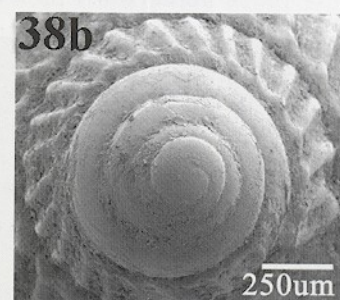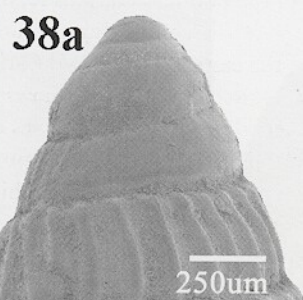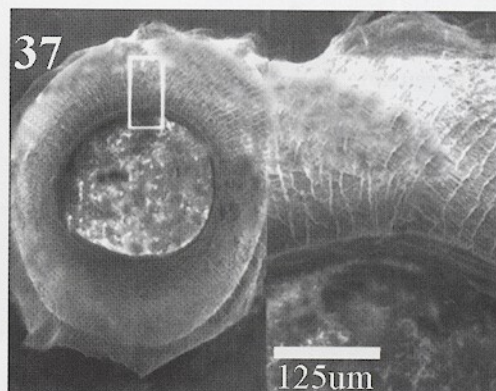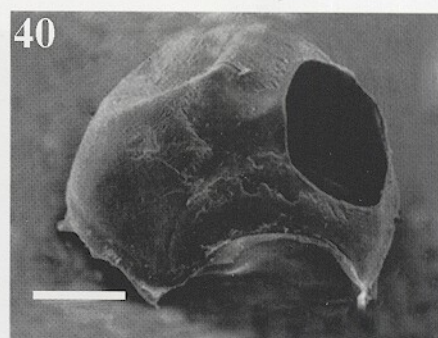
Figure 36-38. *Cosmioconcha redheri* (Hertlein&Strong, 1951) - Fig 36: adult specimen (FMNH280886); Fig. 37: SEM picture of the egg capsule. The right side is a close up of the surface of the enclosed area in the left; Fig. 38a-b: lateral and apical view of protoconch.
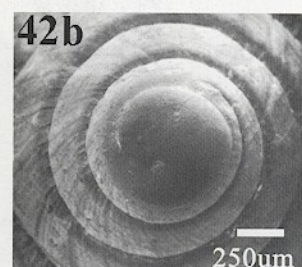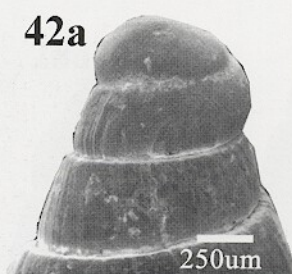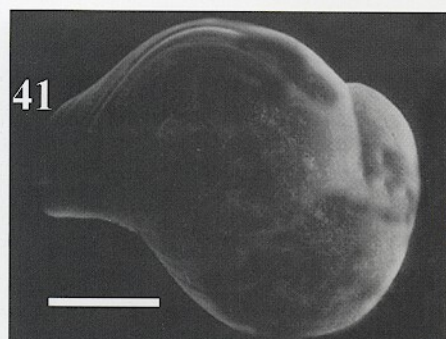
Figure 39-42. *Strombina (Strombina) pumilio* (Reeve, 1859) - Fig. 39: adult specimen (from JUNG, 1989 with permission); Fig. 40: SEM picture of the egg capsule, scale bar 5mm (fom CIPRIANI & PENCHASZADEH, 1993 with permission); Fig. 41: SEM picture of the veliger shell, scale bar 0.25mm (from CIPRIANI & PENCHASZADEH, 1993 with permission); Fig. 42a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).

has been observed independently, rather than derived from measurements and observations of the larval shell. There is a good agreement between inferred and observed patterns of development for planktotrophic and direct developers, which lends strong support to the continued use of morphological data to infer patterns of development for fossil taxa (SCHELTEMA, 1977, 1978; JABLONSKI & LUTZ, 1979, 1980, 1983; HANSEN, 1980, 1982; JABLONSKI, 1982, 1986). However, more direct biological observations of life histories are necessary to refine the limits and the criteria to be used to infer types of larval development for different taxa. In the case of the *Strombina*-group, the best criteria to evaluate development types seem to be the number of protoconch volutions. Although the maximum diameter of the protoconch has been used to infer types of development of other gastropods, it contributes less information for species of the studied group.

There was no clear relation between the number and size of eggs or capsules and the observed mode of larval development because all these parameters vary enormously among planktotrophic species as can be seen in Table 2. Possibly, the number of eggs per capsule or the number of eggs per capsule normalized to capsule size may prove useful with observations of more species, at least for the distinction of species with direct development from the rest (Fig. 48).

On the other hand, our data is not enough to deduce any definite pattern concerning lecitotrophic species. Of all the species reported here, *Strombina recurva* could be classified as a possible candidate for this type of development. The fact that the intracapsular veligers found had 1.75 volutions and the protoconch has 2.25 indicates a further period of growth. The question is where does this growth takes place, inside the capsule or in the plankton. The sinusigerous shape of the protoconch outer lip leads us to think that some of this growth could take place during a planktotrophic stage. Besides, the protoconchs of most of the known direct developers have fewer whorls. More data on this and other possible lecitotrophs is needed in order to be able to deduce this type of development with more confidence.

Finally, the new observations reported here allow considerable refinement of the contrasting evolution of larval developmental modes in the eastern Pacific and Caribbean. Figure 49 (modified from JACKSON ET AL., 1996) shows the frequency of the three developmental modes for 73 species of the *Strombina*-group since the Early Miocene and the possible relation between developmental mode and geographic range. The proportion of species with direct development increased progressively in the Caribbean even before the mass extinction at the end of the Pliocene as reported previously (JACKSON ET AL., 1996).
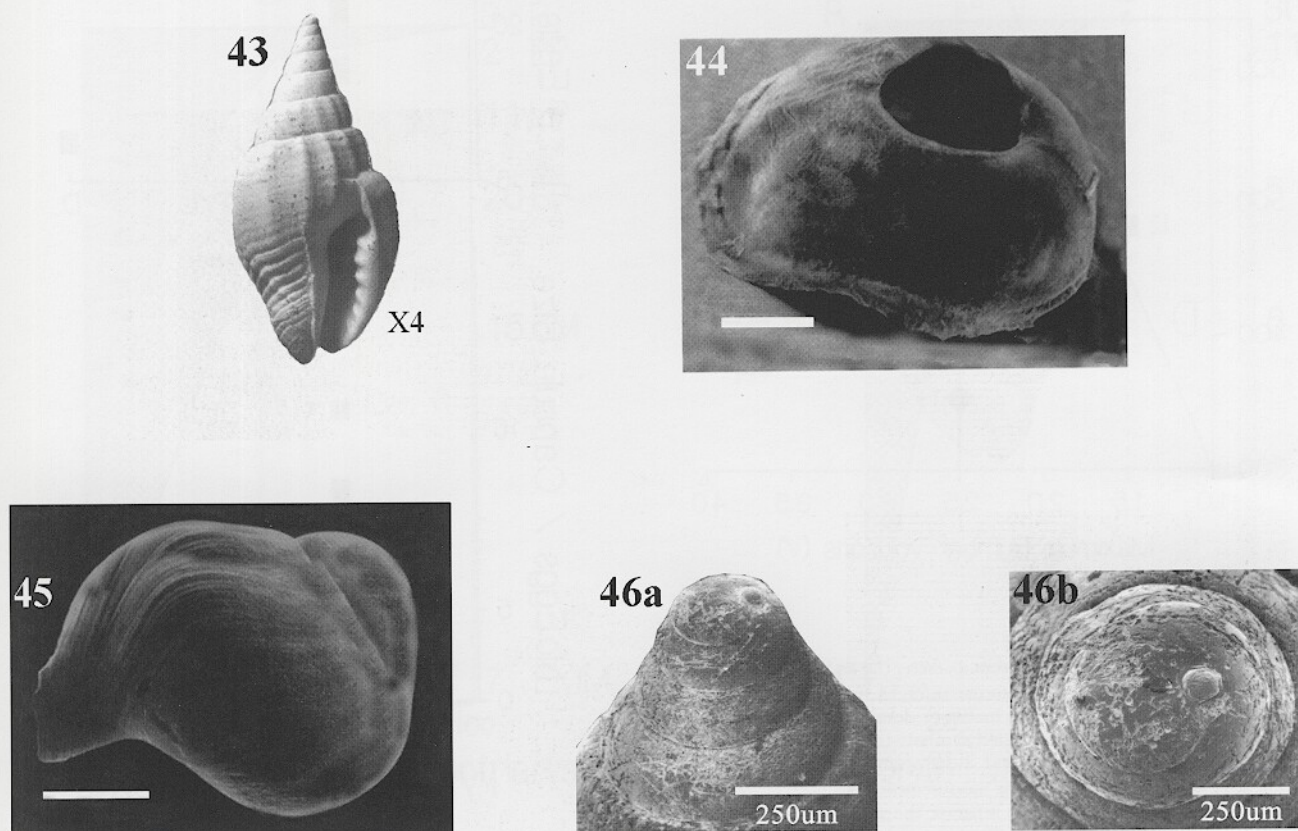
Figure 43-46. *Strombina (Lirastrombina) francesae* J. Gibson-Smith, 1974 - Fig. 43: adult specimen (from JUNG, 1989 with permission); Fig 44: SEM picture of the egg capsule, scale bar 0.25mm (from CIPRIANI & PENCHASZADEH, 1993 with permission); Fig. 45: SEM picture of the veliger shell, scale bar 0.25mm (from CIPRIANI & PENCHASZADEH, 1993 with permission); Fig. 46a-b: lateral and apical view of protoconch (from JUNG, 1989 with permission).

However, lecithotrophic development was less important in the eastern Pacific than surmised previously, an observation that is in better agreement with data from echinoderms (LESSIOS, 1990) and corals (RICHMOND & HUNTER, 1990).

ACKNOWLEDGEMENTS

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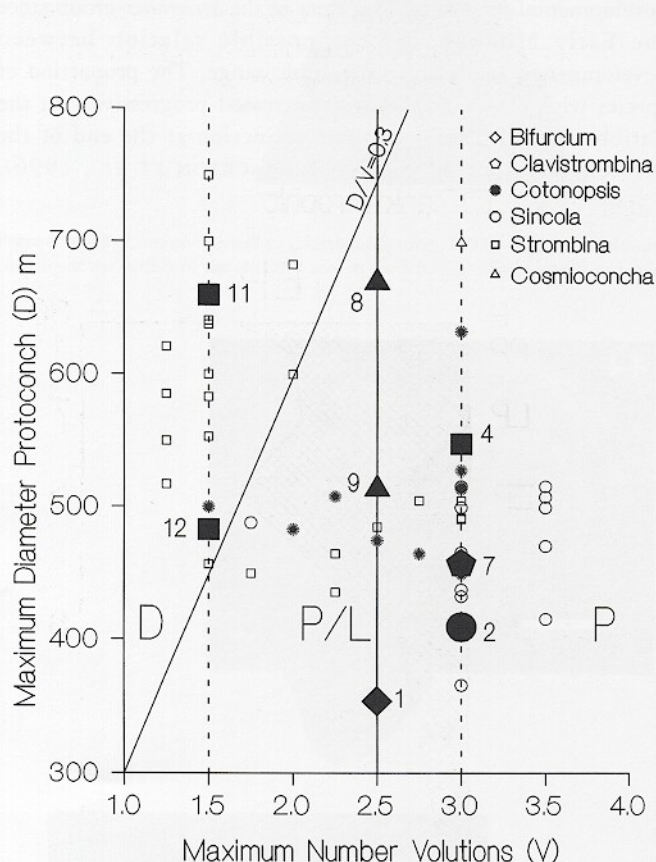

Figure 47. Relation between the maximum diameter (D) and maximum number of volutions (V) of the larval shell (protoconch) for 54 species of the *Strombina*-group, fossil and living, used to infer modes of development (modified from JACKSON ET AL. 1996). The larger, filled symbols indicate the eight species discussed in this paper whose larval development has been observed independently, rather than derived from measurements and observations of the larval shell. The vertical dashed lines separate the graph into three areas of inferred development based on the maximum number of protoconch volutions: D - direct development (V < 1.5); P/L - planktotrophic or lecithotrophic development (1.5 < V < 3.0); P - planktotrophic development (V >= 3.0). The values of D and V for D/V = 0.30 are designated by the solid oblique line. The vertical solid line constrains the values of V for lecithotrophic species.
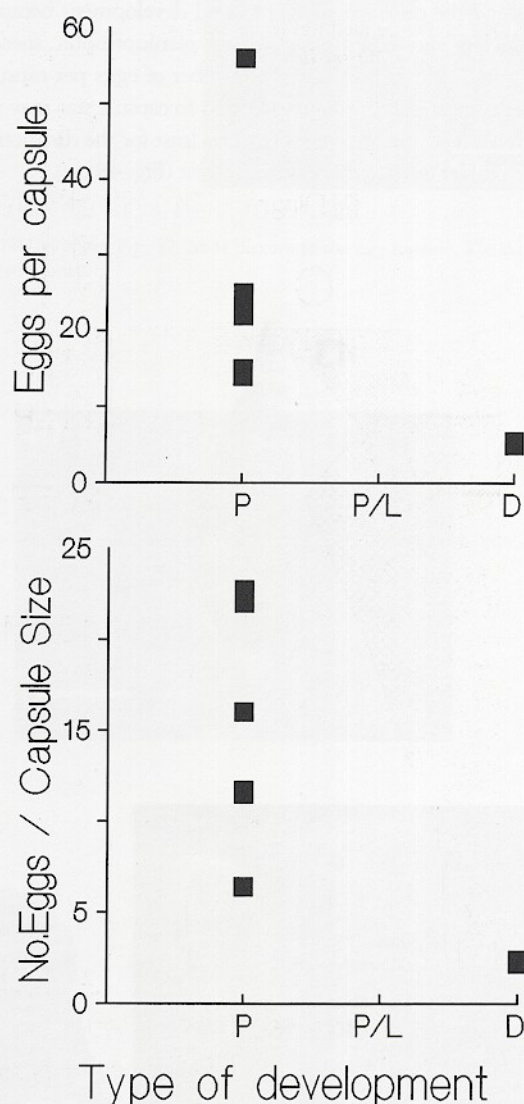

Figure 48. Relation between the number of eggs per capsule and the number of eggs per capsule normalized to capsule size and the type of development for eight species of the *Strombina*-group. These are the same species represented by filled large symbols in figure 47.

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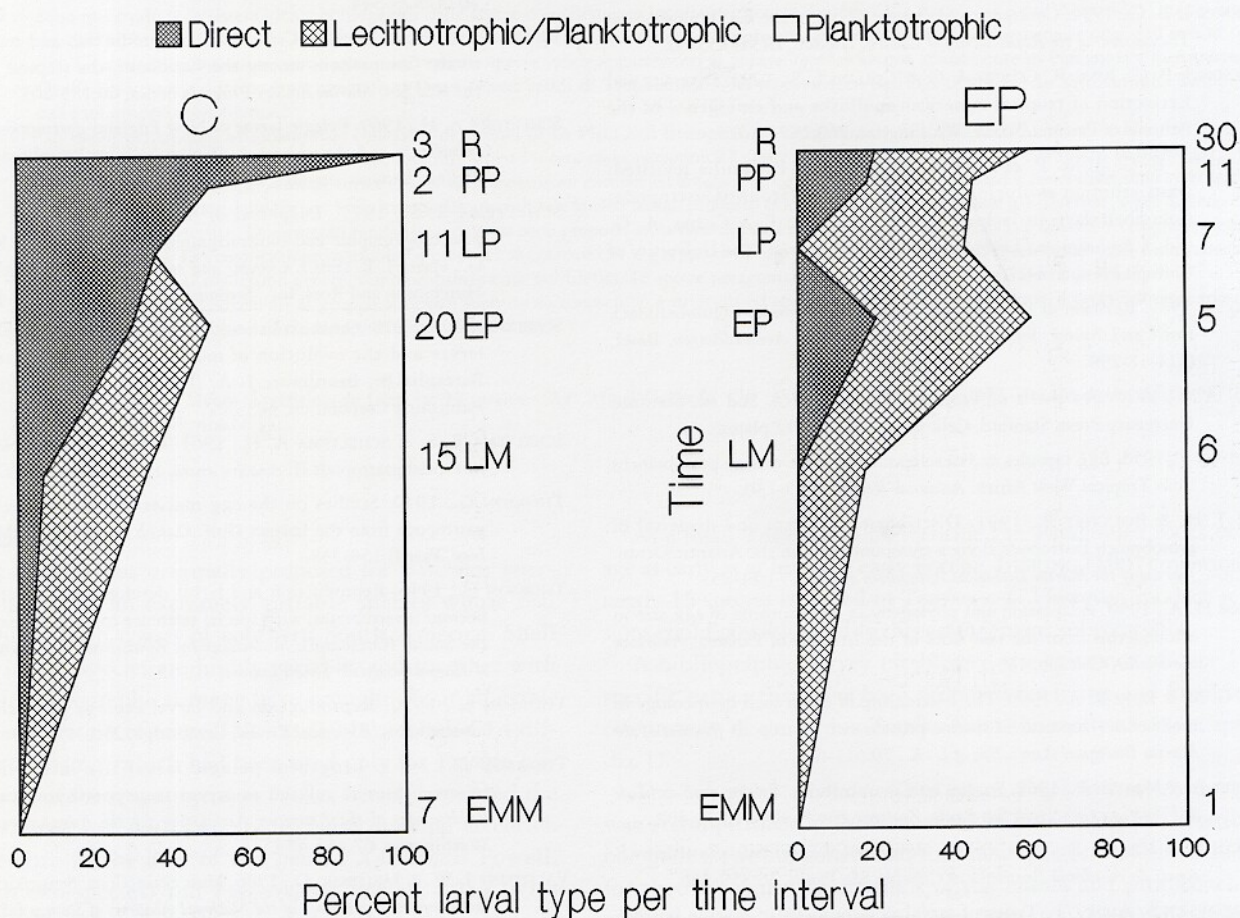
Figure 49. Temporal changes in the relative numbers of species of the *Strombina*-group inferred to have planktotrophic (P), either planktotrophic or lecithotrophic (P/L), and direct (D) development. A total of 73 species (fossil and Recent), from the eastern Pacific (EP) and the Caribbean (C) for which values for the maximum number of volutions and the maximum diameter of the protoconch could be evaluated, were analyzed. Numbers to the right of the boxes represent the number of species per time interval evaluated for each ocean. Time intervals considered are: Recent (R), Plio-Pleistocene (PP), Late Pliocene (LP), Early Pliocene (EP), Late Miocene (LM), Early-Middle Miocene (EMM).

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