Stuttgarter Beiträge zur Naturkunde

Serie A (Biologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-7000 Stuttgart 1

Stuttgarter Beitr. Naturk.	Ser. A	Nr. 434	10 S.	Stuttgart, 1. 9. 1989

New Observations on Burrowing in Strombid Gastropods

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With 5 figures

Summary

Strombus canarium and *S. gibberulus gibbosus* differ from each other and from other burrowing strombids in several aspects of the burrowing process, and in associated behavioral and morphologic characters. Thus, the burrowing habits of strombid gastropods are more varied than suggested by previous studies.

Zusammenfassung

Strombus canarium und *S. gibberulus gibbosus* unterscheiden sich voneinander und von anderen grabenden *Strombus*-Arten in den Grabgewohnheiten und den damit verbundenen ethologischen und morphologischen Merkmalen. Diese Unterschiede sind bei Strombidae-Arten wesentlich deutlicher, als bislang vorliegende Beobachtungen vermuten lassen.

Contents

1. Introduction

Strombid gastropods are represented in the Tertiary by several tens of species of amazing morphological diversity (see CLARK & PALMER 1923, WRIGLEY 1938, WENZ 1940, HARRIS & PALMER 1947, GLIBERT 1963, JUNG 1974, SAVAZZI 1979, in press b and c, and references therein). However, little or nothing about their life habits can at present be inferred from their morphology. Thus, observations on the life habits of Recent strombid gastropods are necessary, in order to discover the adaptive values of morphological characters. In a previous paper (SAVAZZI 1988), I described the burrowing habits of four species of *Strombus* and one species of *Lambis*. *Strombus (Euprotomus) bulla* and *S. (E.) aurisdianae* spend most of the time buried, while *S. (Lentigo) lentiginosus* and *S. (Conomurex) luhuanus* are prevalently epifaunal. In laboratory tanks, these strombids were observed to emerge from the sediment and to reburrow at intervals of a few hours. Immature *Lambis lambis*, on the other hand, burrow only occasionally, and cease to burrow once the adult shell lip is constructed. Burrowing or infaunal posture of other species of *Strombus* have been recorded in the literature (see review in SAVAZZI 1988). The burrowing process of these species, however, has not been studied. Thus, burrowing is widespread among Recent strombids. A few species of *Strombus*, on the other hand, appear to be exclusively epifaunal (SAVAZZI 1988).

The burrowing process of the strombids differs from that of other gastropods, in that the proboscis is used to displace sediment from beneath the shell, and the shell is not functional as a retraction anchor. Specialized burrowing sculptures are therefore unnecessary. *Strombus* (*Euprotomus*) is characterized by an elongated and upturned anterior canal, which has been interpreted as an adaptation to the infaunal habit (SAVAZZI 1988). The other studied species, instead, do not seem to possess morphological characters related to burrowing.

In spite of the behavioral and morphological differences summarized above, the dynamics of the burrowing mechanism is essentially the same in the five strombid species I have previously studied (SAVAZZI 1988). The present paper originates from the discovery that other species of *Strombus* possess significantly different behavioral and morphologic adaptations to burrowing.

2. Material and methods

Strombus (Laevistrombus) canarium (1 adult female, 1 slightly subadult male with rather thin outer lip) were collected on muddy sand with sparse algal cover in the intertidal zone at Tayud near Consolacion, Cebu, Philippines, in early February, 1988. *S. (Gibberulus) gibberulus gibbosus* (1 adult female, 2 slightly subadult males) were collected on clean coarse sand on intertidal sand bars near Cordoba, Mactan Isl., east of Cebu, in early March. This species was also collected at Ibo near Parola, Mactan Isl., but specimens from this locality were not observed in the laboratory. *S. (Canarium) urceus* (several tens of adults, 4 subadults without flared lip) were collected on muddy sand at Tayud, on clean sand at Ibo, and on both types of bottom in several localities in Bantayan Isl., NW of Cebu, in February and March. In all these localities, most adult individuals attain a significantly larger size than the single specimen available for my previous study (SAVAZZI 1988). This species is typical of the intertidal zone. *S. (Labiostrombus) epidromis* (about 10 adults of each sex) and *S. (Doxander) vittatus* (1 adult male) were collected by local skin divers in 2–4 m water on coarse sand with sparse algal cover at Binaobao, Bantayan Isl., in late February. An adult male of *S. (Dolomena) variabilis* was found among *S. urceus* sold in a market in Consolacion, Cebu, in early March, but it died soon after being placed in an aquarium. Shells of *S. variabilis* occur in large quantities at Santa Fe, Bantayan Isl., and are collected by the local population for sale to shellcraft factories, but living specimens are said to be rare. In fact, none could be found at this locality in late February.

In addition to the above material, several specimens of *Strombus* and *Lambis* belonging to the species I previously studied, with the exception of *S. bulla* (see SAVAZZI 1988), were obtained from the above localities and from fish markets, and their behavior was observed in aquaria.

S. epidromis and *S. vittatus* could be observed in a glass tank and in plastic buckets for only 12 hours, since no electricity was available for running an air pump. *S. canarium* was kept for 10 days in plastic cages submerged in the sea near the locality of capture, and observed at intervals of a few days. Algae growing on the plastic cages and on the shells of the molluscs apparently provided an adequate sorce of food, and, as previously observed in other strombids (SAVAZZI 1988), no detectable change in activity took place during this time. These specimens were eventually lost when a predator (probably a large crab) cut open the cages. The specimens used for the illustrations were captured in the same area at a later date, but their behavior could not be observed. *S. urceus* was kept for up to one week, and *S. gibberulus* for 10 days, in a glass aquarium equipped with air pump and filter. These specimens were observed at intervals of a few hours. All species were placed on their native sediment to observe their behavior. In addition, *S. canarium* and *S. gibberulus* were allowed to burrow in a variety of sediments ranging from clean and muddy coarse biogenic sand to fine clean sand.

The specimens illustrated in the present paper are in the possession of the Staatliches Museum für Naturkunde in Stuttgart (West Germany).

3. Observations

3.1. *Strombus canarium* (Fig. 1a–b)

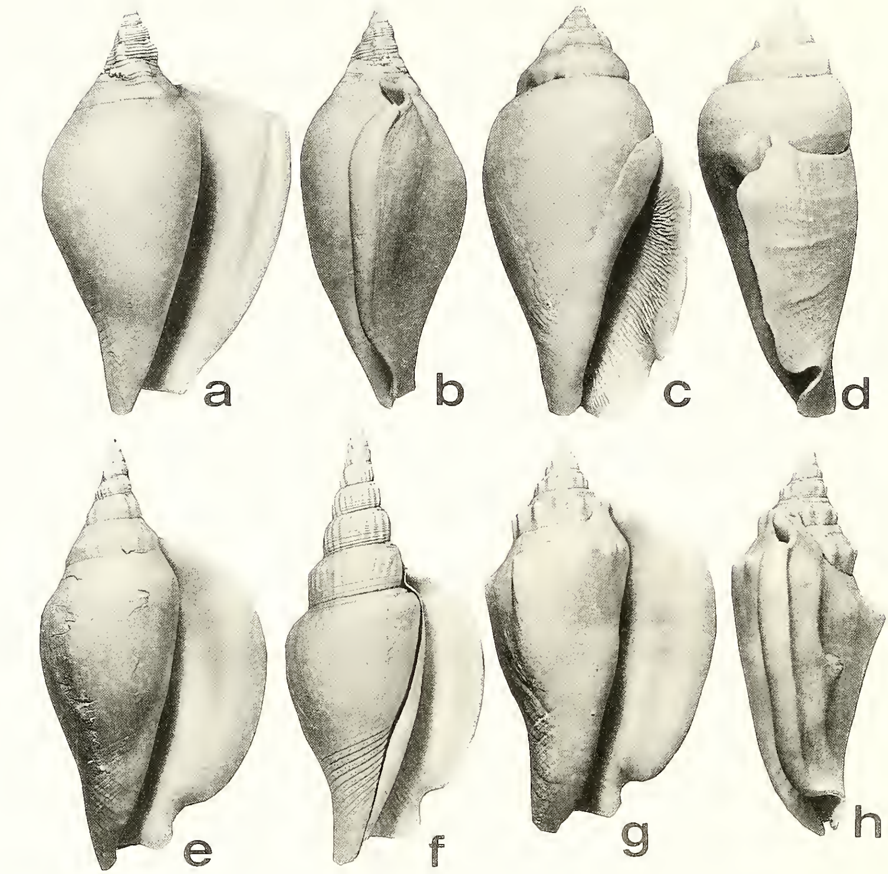
The two available specimens always burrowed as soon as they were placed on a sandy substrate, and thereafter remained immobile. The burrowing process begins with the repetition of 6 to 10 sequences, which possess both elements in common and substantial differences with those described in other strombids (see SAVAZZI 1988). Three phases are recognizable in each burrowing sequence:

1.) Probing phase, in which the propodus burrows in a downward and forward direction, and expands to gain a hold (Fig. 2a).

2.) Shoveling phase, in which the proboscis is used to push sediment from beneath the mollusc in a radial pattern (Fig. 2b–c). The series of movements shown in the illustration is occasionally repeated twice, before proceeding to the next phase.

3.) Retracting phase: the shell is moved forward, and the anterior canal is lifted high above the surface of the sediment (Fig. 2d, 4a). The shell is subsequently rammed backward and downward into the sediment, with a rolling movement (Fig. 2e, 4b). There is no rocking movement of the shell about its longitudinal axis.

While burrowing proceeds, the shell of *S. canarium* moves obliquely forward and downward, and its longitudinal axis becomes substantially inclined with the anterior region upwards. This results in the dorsal surface of the last whorl becoming parallel to and approximately level with the surface of the surrounding sediment (Fig. 3a). At the same time, the shell also rotates around its longitudinal axis, so that the mouth becomes inclined upward (Fig. 3a). At this point, a few forward and backward sliding movements of the shell in rapid succession settle the sediment around the shell. Typically, part of the dorsal surface of the shell remains visible. Subsequently, the proboscis emerges from the sediment, and is alternately extended along either side of

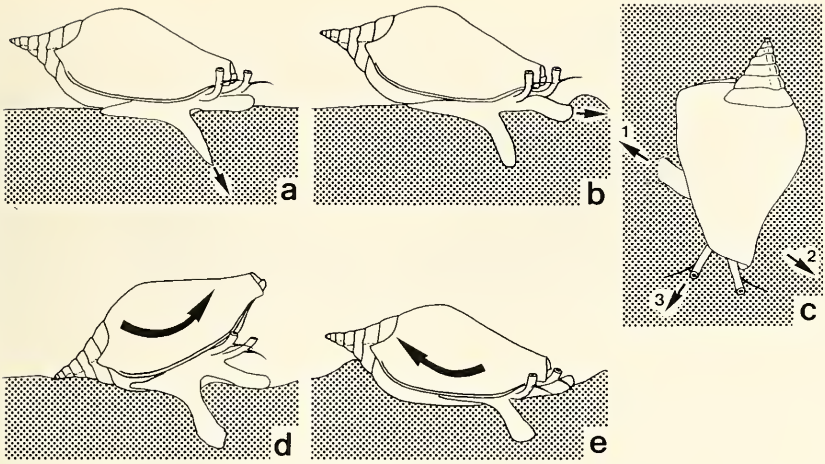


Figs. 1a–h. Shells of the Strombidae studied in the present paper. – a–b. *Strombus (Laevistrombus) canarium*, × 0,8 (adult, ventral and lateral views); – c–d. *Strombus (Gibberulus) gibberulus gibbosus*, × 1 (adult, ventral and lateral views); – e. *Strombus (Labiostrombus) epidromis*, × 0,6 (adult, ventral view); – f. *Strombus (Doxander) vittatus*, × 0,7 (adult, ventral view); – g–h. *Strombus (Dolomena) variablis*, × 1,3 (adult, ventral and lateral views). – See chapter 2. for the localities of origin.

the shell, to push sediment onto the exposed surfaces (Fig. 4c–f). The process is repeated a few times, alternating from one side to the other. In the native muddy sediment, this process completely covers the shell with sediment, but in clean coarse sand, the proboscis appears to have difficulty in moving large particles of sediment. The proboscis can be extended up to the suture of the last whorl.

3.2. *Strombus gibberulus gibbosus* (Fig. 1c–d)

Of the three available specimens, the female burrowed immediately after being placed in the aquarium. Subsequently, it was seen to emerge spontaneously from the sediment at intervals of 2 to 4 days, to reburrow shortly thereafter. For the first

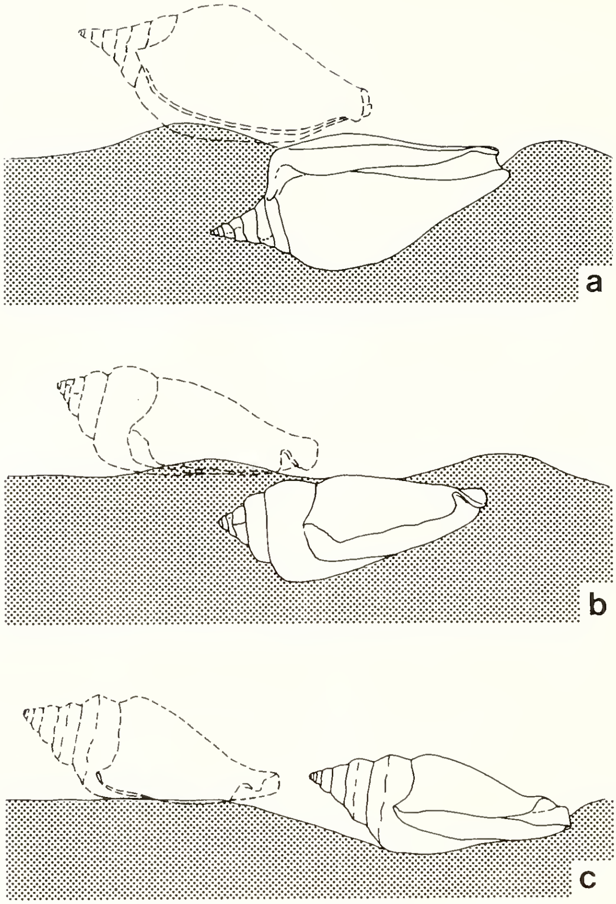


Figs. 2a–e. Burrowing sequence of *Strombus canarium*. – a. Probing phase (side view), – b–c. Shoveling phase (b: side view, c: top view); – d–e. Retracting phase (side views).

week, the two males remained at the surface, frequently moving about and feeding on algae growing on shells and on the glass walls of the aquarium. One of the two males subsequently switched to a prevalently infaunal habit, similar to that of the female specimen, while the other always remained epifaunal. This shows that different activity patterns may occur in the same species or in the same individuual. Therefore, caution should be used in interpreting the results of observations carried out on a single or a few strombid specimens, or for a short time span.

The burrowing sequence is essentially similar to that described for other strombids (Savazzi 1988), with the only exception of the sequence of movements of the proboscis in the shoveling phase, which is similar to that in *S. canarium* (Fig. 2c). This phase is usually repeated twice towards the end of the burrowing process. Burrowing is much faster than in all other studied strombids [1 to 1.5 minutes to burrow completely, compared with 5 to 30 minutes for the other species to burrow until the shell axis is level with the surface of the sediment; see Savazzi (1988), and the present paper]. Complete burrowing was accomplished in 5 to 7 sequences, which compares favourably with similarly sized gastropods possessing specialized burrowing sculptures (see Savazzi, in press a). Another important difference is that the eyes usually remains exposed at the surface during the burrowing process (Fig. 4g). When the mollusc is completely buried and immobile, both eyes are always kept at or above the surface of the sediment (Fig. 4h). Their small size and cryptic coloration makes them inconspicuous against a background of coarse sand. The eyes are quickly retreated out of sight when the mollusc detects a movement or is otherwise alarmed, but reappear after a short time.

Once burrowing is completed, the proboscis is not used to cover the shell with sediment in the way described for *S. canarium*. However, a few quick sliding movements of the shell forward and backward are usually sufficient to hide the dorsal surface of the shell beneath a thin layer of sediment (Fig. 3b).



Figs. 3a–c. Displacement of the shells during the burrowing process (side views). – a. *S. canarium*, – b. *S. gibberulus gibbosus*, – c. *S. urceus*. – The dotted outlines indicate the position of the shells at the beginning of the burrowing process, the solid outlines their position after the last burrowing sequence.

3.3. *Strombus urceus*

In a previous study (Savazzi 1988), observations on a single specimen led me to conclude that this species does not burrow (see illustration in Savazzi 1988, Fig. 1g). However, out of 24 specimens kept in an aquarium on different occasions, 2 adults burrowed in the way described for *S. gibberulus gibbosus* (see above). The burrowing process was very slow (up to 30 minutes), with frequent pauses, and always ceased when the shell axis was approximately level with the surrounding sediment. At this point, most or all of the shell still remained exposed (Fig. 3c). These two specimens were observed to burrow on several occasions, and two other adults were seen to use the proboscis to displace sediment from beneath the shell, without the other movements normally associated with burrowing. None of the subadults displayed any of the behavioral patterns associated with burrowing.

3.4. *Strombus epidromis* (Fig. 1e)

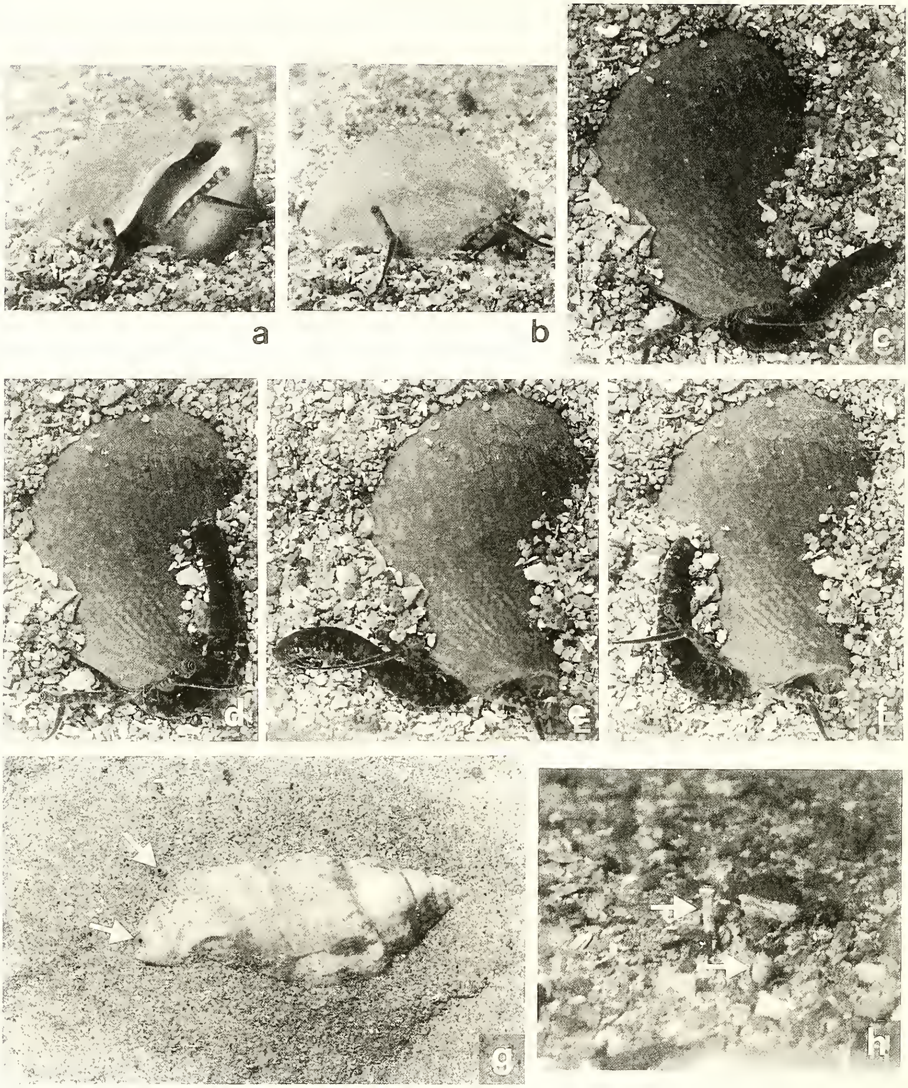
The animals of both sexes were almost constantly engaged in surface locomotion, but made no attempt to burrow. However, the local skin divers who captured them told me that this species is normally found partly buried in the sediment, with the dorsal region of the shell exposed. Information on the life habits of other marine invertebrates supplied by these divers proved to be accurate, and therefore, there is little reason to doubt of its reliability in the case of *S. epidromis*. The limited time during which I could observe the animals alive is likely responsible for the apparent discrepancy of this information with my personal observations. Two females had a coral overgrowth on the dorsal region (Fig. 5b), but all other specimens had remarkably clean shells. A similar coral overgrowth is occasionally seen also in *S. canarium*, which is a burrowing form (Fig. 5a). Therefore, its occurrence in *S. epidromis* is not inconsistent with burrowing habits.

3.5. *Strombus vittatus* (Fig. 1f)

The only available specimen moved constantly at the surface, but never burrowed. This species is the most active among the ones studied in this paper. Surface locomotion is remarkably fast, and the pace regular (about 30 leaps per minute, which is 2 to 5 times the pace I observed in other, similarly sized *Strombus*). Prior to each step, the proboscis probes the sediment in front of the animal in the exact spot where the propodus will be placed. This species is uncommon, and local skin divers were not able to provide any information about its life habits, except that it is found in the same environment as *S. epidromis*. The shell of *S. vittatus* was completely devoid of epibionts, except for a small patch of algal filaments on the dorsum of the last whorl.

3.6. *Strombus variabilis* (Fig. 1h)

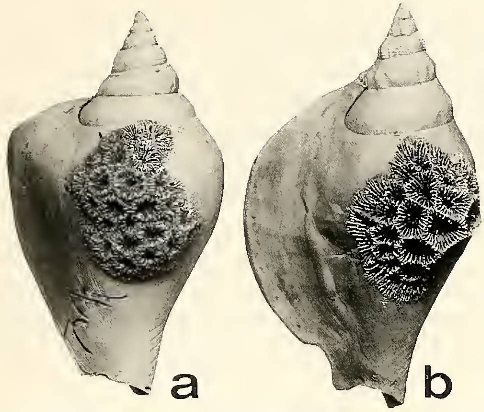
The behavior of this species could not be observed. Empty shells of *S. variabilis* are collected in very large quantities in the shallow subtidal zone of beaches (0 to 0.5 m below low water mark). Local collectors told me that living specimens, on the other hand, are rarely found, and that they invariably occur buried in fine clean sand. This suggests that the preferred habitat of this species may be at a slightly higher depth than that at which empty shells are collected. The ecologic communities of these beaches are characterized by the abundance of durophagous fishes and portunid and calappid crabs, and, except for these predators, by the almost total absence of epifauna (see Savazzi & Reyment, in preparation). Several invertebrates are present, but they either are infaunal (*Umbonium*, *Polinices*, leucosiid crabs), or stay buried most of the time, to emerge from the sand only when the bottom is exposed at low tide (*Nassarius*, *Neritina*, *Conus*, *Cypraea*, *Natica*, detritus-feeding crabs, polychaete worms). Therefore, it is reasonable to expect that *S. variabilis* does burrow, and that it spends a substantial amount of time buried. The shell of the only specimen collected alive has a glossy surface, completely devoid of epibionts.



Figs. 4a–b. Rocking movement of *Strombus canarium* (slightly oblique front view, × 1).
Figs. 4c–f. *S. canarium* using the proboscis to shovel sediment on top of the partly exposed shell (top views, × 1).
Fig. 4g. Burrowing *S. gibberulus gibbosus* (top view, × 0.7). – The *arrows* indicate the eyes.
Fig. 4h. Buried *S. gibberulus gibbosus*, with the eyestalks (indicated by *arrows*) projecting from the sediment (oblique view, × 2.5).

3.7. Other species

New observations confirm that adult and subadult *Strombus aurisdianae* are prevalently infaunal, and that adult, subadult and juvenile *S. luhuanus* and *S. lentiginosus* are facultatively infaunal (juveniles of this last species were not previously available; SAVAZZI 1988). Juvenile and subadult *Lambis lambis*, on the other hand, were never seen to burrow, contrary to what previously observed. Adult *Lambis lambis* and *L. millepeda* were likewise strictly epifaunal.



Figs. 5a–b. Coral overgrowth on the dorsal regions of living adults. – a. *S. canarium* (× 0.7), – b. *S. epidromis* (× 0.6).

4. Discussion

The burrowing process in *S. canarium* is significantly different from that of other strombids. In particular, the shell is used to displace sediment in the posterior direction. No morphological character in the shell of *S. canarium* appears to be directly related to this behavior. However, the orientation of the buried shell with the longitudinal axis strongly inclined backward is a direct result of the mechanics of the burrowing process. In this orientation, the dorsum of the last whorl lies parallel to the surface of the sediment (Fig. 3a). A comparable adaptation is observed in *S. gibberulus*, in which the dorsum of the last whorl is extremely compressed (Fig. 3b). In this species, the last and the penultimate whorls together form a roughly flat surface, close to the surface of the sediment. A closely comparable morphology is observed in much larger strombids from the Paleogene and Miocene (e. g., *S. tournoueri*, *S. pulcinella*, *Tibia (Semiterebellum) postalensis*, *Orthaulax* sp. pl.). It is proposed that these species, too, were burrowers lying within the sediment with the longitudinal shell axis inclined backward. The short, shouldered spire of *S. tournoueri*, in particular, suggests a burrowing process comparable to that of *S. canarium*.

The behavior of the eyes in *S. gibberulus* is unique among the strombids I have studied (see SAVAZZI 1988), but a partial similarity is found in *Terebellum*. This seraphsid (once placed in the Strombidae; see JUNG 1974) burrows horizontally beneath the surface of the sediment, keeping one eye at a time at the surface. Periodically, the exposed eye is retreated, and the other one emerges from the sand some distance forward along the path of the mollusc (ABBOTT 1962, JUNG & ABBOTT 1967). *S. gibberulus*, however, does not move through the sediment once buried. The unusually deep stromboid notch of this species (Fig. 1d, 3b) is likely adaptive to this behavior, by providing a suitable passage for the pedicle of the right eye. The anterior canal is not bent upward to a higher degree than observed in *S. urceus*, *S. mutabilis* and *S. variabilis* (which burrow only occasionally, or not at all), but it is more deeply notched in the dorsal direction, which may facilitate the passage of the left eye pedicle.

The burrowing behavior of several other strombids remains to be studied. It seems unlikely that the largest species of *Strombus* and *Lambis* (which can exceed 30 cm in length, and weight several kg) can burrow, except perhaps in their juvenile stages. A few small species of *Strombus* (*S. dentatus*, *S. terebellatus*) possess smooth, streamlined shells with wide anterior canals, that suggest prevalently infaunal habits of the type of *Terebellum*. Specimens of *Varicospira* in the collections of the Smithsonian Institution (Washington, DC) are accompanied by an annotation saying that they were collected in mud. Therefore, this genus may be infaunal as well. *Varicospira* is morphologically similar to Paleogene genera like *Rimella*, *Dientomochilus* and *Ectinochilus*, which might have had comparable life habits. The habits of Recent *Tibia* are poorly known. Collecting additional information on these Recent strombids will help to shed light on the life habits of the extremely varied fossil representatives of the family.

5. Acknowledgements

My wife EVA and several relatives and friends substantially helped my work by collecting information from, and bartering with local skin divers, fishermen and boat owners, arranging accommodations for the field and laboratory work, and participating in collecting trips in the field. The field work was financed by the Swedish Natural Science Research Council.

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