

About abnormalities on the number of eyes and the evolution of the possible eye-sight related shell aspects in Strombidae; introducing new shell terms in Strombidae morphology (Gastropoda: Stromboidea, Strombidae)

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ABSTRACT Aberrations on the number of eyes and strombid notches, the evolution of the eye-sight, the use of the anterior canal and other morphological adaptations to the shells of the family are discussed. Animals with 3 and 4 eyes instead of 2 eyes are reported just as shells with 2 strombid notches instead of one strombid notch. The use of the term ‘siphonal canal’ is discouraged and replaced by ‘anterior canal’. A new term is introduced: the strombid lobe for the broadly rounded projection on the outer lip posterior to the strombid notch.

KEY WORDS Strombidae, *Strombus*, eyes, eye sight, anterior canal, strombid notch, strombid lobe

INTRODUCTION

Strombidae Rafinesque, 1815 is the largest extant family in the superfamily Stromboidea Rafinesque, 1815, a family of well-known marine snails with many colourful and diversely shaped shells including beautiful shell morphologies. Although the number of species is quite limited (over 100 species at present), the shells are very popular with shell collectors. The family is important as a food source for the human race and is abundantly collected almost everywhere they live, but especially in the Philippines. Recent Strombidae occur exclusively in tropical and subtropical seas, mostly in shallow and very shallow water (Clench & Abbott 1941; Abbott 1960, 1961) while for instance, extant members of the family Aporrhaidae Gray, 1859, also belonging to the Stromboidea, mainly occur in deeper water in subtropical to cold water seas (differences in depth and water temperature).

Most members of the family Strombidae can be recognized by the presence of a so-called ‘strombid notch’, a sinus of the labrum of the shell through which the second (right) of its two

long eyestalks extends out from the shell (Savazzi, 1991). The first (left) eye-stalk extends out from the sinus at the anterior end of the shell, often wrongly called ‘siphonal’ canal, which I will explain in this paper. The strombid notch is almost exclusively a Strombidae evolutionary adaptation lacking in the other families in the superfamily Stromboidea; the only exception being members of the Rimellidae Stewart, 1927. For example, *Varicospira decussata* (Basterot, 1825) from the Miocene of Dax, Landes Department, France, has a perfect strombid notch (Plate 2A, C). Also living members such as *Varicospira cancellata* (Lamarck, 1816), a well-known species from the Philippines, and *Varicospira crispata* (Sowerby, 1842) have a clear strombid notch (Plate 2B, D). The other members of the family Rostellariidae Gabb, 1868 (and the Seraphidae Gray, 1853) did not develop a true strombid notch but have long eye stalks. A photo of the live *Terebellum terebellum* (Linnaeus, 1758) from Guam (Courtesy of Bob Abela) is shown (Plate 3D), along with an empty shell from the Philippines showing the lack of a strombid notch (Plate 3A).

Eyes are located at the end of the long eye stalks of the strombid species. The eyes themselves are almost human at first sight: a central dark coloured spot with one or more differently colored circles including white around this central spot. When the eyes are focused on the viewer, it almost feels like you are being spied on (just look at photos of live animals). What the affected animal is likely to see is not yet known. It can be black and white, just shades, but colors can also be the case. This can be a subject of further (scientific) study, and the London museum is working on this aspect (personal communication).

Members of all other families included in Stromboidea have not developed a strombid notch in the evolutionary path, though evolutionary trends towards this phenomenon can be observed. For example, the recent members of Aporrhaidae have the head between the first and the second digitation like *Aporrhais pespelecani* (Linnaeus, 1758) and *Tibia* species such as *Tibia insulaechorab* Röding, 1798 (Rostellariidae) have protective spines on the apertural rim (Plate 1B and A respectively).

The majority of Strombidae snails are found in fairly shallow waters, often in combination with seagrass species. A lot of them are burrowers in clean sand, coarse sand or muddy sand. Strombids are known to be herbivores or detritivores (Abbott 1960, 1961). It is therefore somewhat surprising that strombids are thought to have excellent vision (due to the peculiar development of eyes on eye stalks). Unlike most mobile “higher Caenogastropoda” (like tonnoideans and Neogastropoda (Simone 2005: 247)), Strombidae do not hunt or prey on other animals. These other Caenogastropoda probably don't use the eyes as a primary agent, but other sensory organs such as smell or vibrations. Why strombids developed eyes on stalks is therefore problematical but is likely not necessary for the

feeding process, but possibly to escape predators.

The shell morphology and the diversity of stromboid gastropods was the subject of the research of Savazzi (1991). Especially the evolution of the shell shape and the snails' way of life was his main interest.

The extreme diversity in shell form of strombid gastropods is interpreted by Savazzi (1991: 311) as the result of three independent factors:

- (1) The terminal growth pattern of the Strombidae allows the circumvention of geometric constraints on shell morphology found in gastropods with continuous or periodic growth patterns;
- (2) Shell morphology in the Strombidae is adaptive to epifaunal locomotion, burrowing, infaunal or semi-infaunal habits and passive protection from predators. Specialization for one of these functions often conflicted with the others, thus bringing about a forced choice among mutually exclusive morphological characters;
- (3) Conservatism in life habits and anatomy of the soft parts has allowed the multiple evolution of extreme shell morphologies, as well as the secondary return to relatively unspecialized morphologies.

Especially factor (2) seems the important driver of the development of eye sight in the evolution of Strombidae.

One of the very remarkable facts on Stromboidea is that the soft parts between the recognised families in the superfamily do not vary much (Jung 1974). Perhaps this is due to the simple diet of the snails, which originates the successful basis scheme of organs of the snails, fit for a long period of time involved in the evolution that led to the diversification into families of which only a few are still extant.

Instead of altering the basis scheme of organs, the snails are highly adaptive to the environment or habitat, which resulted in a multitude of shell forms.

METHODS

The discovery of strombid shells with double strombid notches (coll. AMD) and photos of live animals with more than 2 eyes were the trigger for this study. Shell aspects of Strombid shells are discussed based on personal observations and related to literature directly or indirectly involved with 'Eyes on Stalks' unique development within Gastropoda within the superfamily. Evolutionary paths of these aspects are discussed where possible within the scope and the general knowledge.

ABBREVIATIONS

AMD = Collection of Aarl M. Dekkers, Purmeiend, the Netherlands.

MNHN = Musée National d' Histoire Naturelle, Paris, France.

TERMINAL GROWTH

Almost all Strombidae – and the species in the other families in the superfamily – are characterized by terminal (or determinate) growth. After the shell attains the adult size the aperture undertakes a change in shape. The adult conch lip is often flared or wing-shaped. Shell secretion is subsequently restricted to selective thickening of the interior of the shell and thickening of the wing and apertural rim. Projecting teeth or digitations are formed in certain clades and species at the edge of the shell lip. Shell secretion stops completely or continues very slowly with the deposition of semi-transparent callus on some parts of the ventral surfaces. In older snails the thick parietal callus and the callus on the outer lip sometimes

gets a silvery or purple-blackish hue. This is especially seen in species without projections on the outer lip, like members of *Laevistrombus* Abbott, 1960. The digitations on the outer lip are an interesting and attractive aspects of Strombidae. In the process of terminal growth, the formation of the labrum (the wing), the strombid notch is also formed. Before this final stage, the shell has a more or less conoidal form with a thin lip, almost mimicking a *Conus* shell.

DIGITATIONS

Spines are initially built as folded digitations of the outer lip in species of *Lambis* Röding, 1798. Extensions of the mantle occupy the interior of the spines, and progressively fill them with shell material. Once the spines are completely filled, the mantle retracts within the shell aperture, leaving a slit-shaped scar along the ventral surface of the spines. This is especially well visible with the members of the genus *Lambis* and related genera like *Ophioglossolambis* Dekkers, 2012 and *Harpago* Mörch, 1852 with large digitations.

In many species in other genera, outer lip thickening occurs in adulthood without large spines developing. In the shells of these species, bumps are often visible where the strong ribs of the body whorl end at the outer lip. This was also noted by Vermeij (2014: 329) but not exclusively for Strombidae members. “Ventrally directed serrations, lobes or spines occur in many Indo-West Pacific stromboidians. In *Tibia*, blunt spines associated with obsolete spiral cords are oriented ventrally at the edge of the adult outer lip”. These ‘obsolete spiral cords’ can be seen in the shell of *Tibia* species by the lighter coloured spiral banding. More directly it is seen in the related *Rostellariella delicatula* (Nevill, 1881), which is shown on Plate 1C. These obsolete spiral cords occur also in the stromboidian genera *Tridentarius*

Kronenberg & Vermeij, 2002 and *Terestrombus* Kronenberg & Vermeij, 2002, which are also remarkable by the very minimal strombid notch (on Plate 3B). The strombid notch is thought to be the hallmark of Strombidae, but in these two genera the evolutionary path made it disappear (secondary loss) which may be a consequence of their lifestyle as speedy sand burrowers.

In *Terestrombus terebellatus* (Linnaeus, 1758), 5 white beams can be seen towards the apertural rim, 2 of them besides the shallow strombid notch, resulting in very small rounded dents (Plate 3B). This is also the case in *Tridentarius dentatus* (Linnaeus, 1758) (Plate 3C).

Vermeij noted that in *Tridentarius dentatus* (Linnaeus, 1758) “there are three ventrally directed spines, one anterior to and two behind the strombid notch” hence the chosen name *Tridentarius*. But on closer inspection, there are two more obsolete spirals situated more posteriorly resulting in knobs on the outer lip that did not fully develop into little spines. Most likely all the spiral ribs and obsolete spirals both ending in either spines or bumps are reinforcements of the shells as a protection from predators (new observation). The spines themselves can be important as protection and / or for stabilizing the shell on the surface on which the animal crawls. With Vermeij (2014: 329) I also conclude that these configurations arose independently in several lineages, but with hesitation. Vermeij is limiting it to Strombidae, but it also counts for *Tibia* (Rostellariidae Gabb, 1868). The coding in the DNA of the reinforcements and the spines in Stromboidea is perhaps very old and on/off in the lineages as evolution found it of benefit or due to life habits and perhaps as old as the Harpagodinae Pchelintsev, 1963 (Aporrhaidae). The Harpagodinae members (upper Jurassic - lower Cretaceous) possess angulations, which strengthen the broadly expanded labrum.

Perhaps it is better to state that the configurations originated early in Stromboidea (instead of Strombidae) and switched on or off in the evolution of the clades. Is this an example of Atavism? In biology, an atavism is a modification of a biological structure whereby an ancestral genetic trait reappears after having been lost through evolutionary change in previous generations (definition from Wikipedia). In short, an 'atavism' is an evolutionary throwback to more primitive times. As said, the DNA contains, genomes which serve as archives of the evolutionary past in whatever lineage. It only has to be turned “on” again, for whatever reason, in the evolution.

We have found no evidence of a link between the evolutionary development of digitization and the evolution of vision and long eye stalks in Strombidae in literature.

The development of strong cords resulting in digitations is not limited to Stromboidea. A remarkable radiation of gigantic early Cypraeidae in the Eocene of western Europe (Dominici *et al.* 2020) also show this almost unique feature. These gigantic Eocene fossil cypraeid species showing strong dorsal ridges and spines as prolongation of ridges. No dents along the aperture as commonly seen in present day cypraeids. Shells resembling a *Lambis* species. Shown here (Plate 4A-D) are the newly described species *Vicetia bizzottoi* Dominici, Fornasiero & Giusberti, 2020. There are several other species from the European Eocene (England, France, Spain and Italy) in the genera *Vicetia* and *Gisortia*. *Gisortia coombii* (Sowerby in Dixon, 1850) is also such rare dream fossil shell, with flower-like spines, but no ridges to reinforce the shell (Pacaud, 2008). Another species is *Vicetia hantkeni* (Lefevre, 1878) also on Plate 4E. The development in these gigantic cowries and the later evolved strombid species are analogous. The ridges,

reinforcements and spines in strombids are not modified versions of a structure present in a common ancestor with cowries but probably have developed independently as adaptations to a likewise shared habitat, probably off shore and rather soft substrate, not seen in any other group of gastropods.

Examples of all kind of strombid notches are on the Plates 5 and 6. The shallow strombid notches in the big American strombs are exemplary for the huge species crawling on the sandy surface soil (Plate 5). *Macrostrombus costatus* (Gmelin, 1791) and *Titanostrombus goliath* (Schröter, 1805) are illustrated: not more than 9 mm on a shell of 310 mm large! The smaller (but still medium size to large) species on Plate 6 show us deeper incised strombid notches: smaller and deeper. These species are all in the same subfamily of the Strombidae: the Strombinae Rafinesque, 1815. Exception is *Mirabilistrombus listeri* (Gray, 1852), which has a very wide and deep strombid notch. This species is in the other subfamily Carininae Dekkers, 2008. Dekkers (2008) named these groupings as tribes in this work, but the definitions given there are herein supported as subfamilies. Carininae - definition: includes all smaller forms of the family Strombidae. Shells are small to medium sized, often decorated with small knobs on the shoulder and mostly decorated on the body whorl with axial ribbing, strombid notch shallow to clearly visible; lip thickened sometimes on the inside and sometimes on the outside, sometimes flaring and sometimes not so flaring, columella and inside of lip often decorated with lizae or teeth. Type genus: *Canarium* Schumacher, 1817. In the tree in Latiolais *et al.* 2006, the 2-split in the branches are seen and supported by molecular comparison.

A real eye-opener is the size and form of the strombid notch compared to the size and form of the sinus (=opening) of the anal canal. A good observer can detect the logical build of these two structures in a strombid shell: look at the shell at the anterior end and level the labrum horizontally. Then you will notice that the strombid notch is in line with the anal canal in height and in form. This has not been posted previously, to my awareness.

STROMBID LOBE

In the stage of adulthood an indentation, called strombid notch, is often found along the lateral margin of the adult wing, rather anteriorly. Also, in most of the larger extant Strombidae, there is a kind of curtain or flap between the strombid notch and the anterior canal. I have not found a name in the literature for this special strombid shell function and suggest calling it '**strombid lobe**'. Basically, I found that there are two types of strombid lobes: fairly large lobes that are vertically oriented and a second group with lobes that are quite small and follow the outline of the labrum. Genera that have shells with a large, down pointed strombid lobe are: *Harpago* Mörch, 1852; *Lambis* Röding, 1798; *Lentigo* Jousseau, 1886; *Ophioglossolambis* Dekkers, 2012; *Solidistrombus* Dekkers, 2008 (not available 'synonym' *Sinuistrombus* Bandel, 2007) and *Tricornis* Jousseau, 1886. These are the larger shelled Indo-Pacific species and genera. Examples of these strombid lobes are shown on Plate 6C, D, and F with *Tricornis tricornis* ([Lightfoot], 1796), *Lambis lambis* (Linnaeus, 1758), *Lentigo lentiginosus* (Linnaeus, 1758) and *Solidistrombus sinuatus*) showing the strombid lobe with the down pointed fingers (=ribbing). The smaller shelled Indo-Pacific genera mostly have the smaller type of strombid lobe. Curiously, the huge species in the American radiations have the smaller kind of strombid lobe or even lacking

just as the strombid notches are hardly present; see *Titanostrombus goliath* (Schröter, 1805) (Plate 5A-C). Perhaps these differences can be linked to be evolutionary aspects of the animals. I have noticed that many of the smaller types are sand burrows and it is likely that a small strombid lobe aligned with the outer lip is an advantage when digging into the sediment. The larger shelled Indo-Pacific genera with shells with a large, downward facing strombid lobe are usually crawlers on the sediment instead of burrowers and then a larger lobe is an advantage as it provides better protection for the weak parts of the animal and especially the vulnerable eyestalks. The smaller type of strombid lobe also offers protection to the animal but in a lesser degree, which is not a real disadvantage when buried in the sediment. The conclusion is that the strombid lobe offers protection to the weak parts of the animals and especially the eyestalks. It is related to the living habits of the species.

Note that the strombid lobe is only formed in adult shells; the juvenile shells have a straight thin ending of the aperture. Shells of Strombidae remain thin walled throughout the late juvenile, immature and subadult stages. The adult wing is initially built as a very thin and fragile membrane that gradually becomes thickened on its internal, ventral, surfaces. Secondary thickening may also take place on parts of the internal and external (ventral) surfaces. This results in a remarkable increase in shell weight: the shell can be more than doubled or tripled in weight (Savazzi 1991: 314) from the almost adult to fully adult stage. Only in this adult stage the labrum is fully formed with a strombid notch (not in all species), strombid lobe and digitations in some species.

THE SNOOT

The head of the gastropods can have one of 3 major varieties for consuming the desired food. The simplest one is just a plain head without any elongated parts. One of the more successful varieties, the proboscis, is a feature developed in the higher evolutionary lineages in Gastropods. The highly developed proboscis is (partly) retractable. This kind developed in the higher Caenogastropoda starting with Calyptraeidea and including all following superfamilies including Naticoidea, Cypraeoidea, Tonnoidea and Neogastropoda (Simone 2019: 28). In Strombidae a proboscis has not yet developed, but instead the elongated snout has already a retractor muscle (Simone 2019). The Strombidae seems to be a first step in the development of the proboscis in Gastropods. It makes it easier for the animals to get the food while buried in the sand for the burying species or in the crawling mode of the larger species. The development of the retractable snout is seemingly not related to the evolution of the eye-sight. I place this development in the context of the mobility and lifestyle of the animals.

THE DEVELOPMENT OF THE ANTERIOR CANAL

Gastropods in which the siphonate condition arose were mobile, bottom-dwelling, microphagous animals (Vermeij, 2007: 469). According to Vermeij, conservative estimates indicate that the siphonate condition arose the incredible number of 23 times (and were secondarily lost again 17 times). Active predatory habits became associated with the siphonate condition in for instance many members of the Neogastropoda.

Many infaunal predatory gastropods have a short (though often very deeply notched)

siphonal canal through which a very long proboscis emerges. Wide, deep siphonal notches and dorsally deflected canals offer great flexibility to the siphon and proboscis, and may enable the gastropod to detect dangers and opportunities of importance above as well as ahead of the snail (Vermeij, 2007: 474). The siphonal canal in most living siphonate gastropods is associated with organs that produce a narrow anterior inhalant current of water. Associated sensory organs detect both the concentration and direction of chemical cues released by distant food, enemies, or mates (Vermeij; 2007: 473, Lindberg and Ponder 2001). Inhalant streams in non-siphonate gastropods are more diffuse, meaning that ventilation of the mantle cavity is controlled passively or actively by other structures than a siphon. Among the extant siphonate snails are the 'higher Caenogastropoda': cerithioideans, campanuloideans, and stromboideans. These are however either herbivorous or microphagous and not predatory snails. Simone (2001) has shown that the siphonal canal of cerithioideans is not associated with a fully differentiated siphon (Vermeij, 2007:474). Also, a developed siphon is lacking in Strombidae (Plate 8C, *Macrostrombus costatus* (Gmelin, 1791) aquarium photo); only a simple mantle flap is present.

The anterior channel in strombid species is commonly referred to as the 'siphonal canal' which is an obvious misunderstanding as the shell structure is not used by the animal for a siphon, but is instead used to protrude the left eye stalk. This is a remarkable invention in the gastropod lineages and truly unique. There is not one other gastropod family that uses the 'siphonal canal' for one of the eye stalks. Here we see the evolution of two sinuses used for the eyes: the anterior channel (or canal) and the strombid notch. Members of the closely related family Seraphidae have not developed a

strombid notch, but recent members of this family use the broad anterior end of the shell to accommodate both eye-stalks. Here the shell is adjusted in a different way, likely facilitating the protection of the head of the animals with a broad roof and a broad 'window' for the eye-stalks, retaining a very smooth torpedo like form for fast moving in the sand. Same intention, different solution. This 'hooded' protection is also found in some genera of the family Ovulidae (personal observation) where the animals use the extension of the shell as a kind of hood. This observation is in line with that of Vermeij: "a long siphonal canal extends the shell's passive defence by shielding the vulnerable anterior organs from above and below while the gastropod is active" (Vermeij, 2007: 474).

According to Vermeij (2007: table 1) the siphonate character arose already in the Early Jurassic (Toarcian) in Stromboidea. The family of the aporrhoids, a basal family in the Stromboidea, have been siphonate since their first appearance in the Early Jurassic, though it is not very easy to see: it is just the broad sinus between the 2 front spines.

All early representatives of siphonate gastropod groups appear to have been microphagous (Stanley 1977), as are living cerithioideans and stromboideans, which also have high-spired siphonate shells. Predatory habits of tonnoideans and neogastropods have been possibly the triggers for the evolution of the proboscis and associated organs of the digestive system (Kantor 1990, 1996; Riedel 2000) and the further use and development of the siphonal canal in these lineages. The 'bauplan' was already invented in the early roots of gastropod evolution. But the question is why the early siphonate condition arose.

The (early) siphonal condition (cerithioideans, campanuloideans, and stromboideans) seems to be linked with active crawling animals on a sand/mud bottom, which have a shell form that enables the animals to crawl easily and thus fast. It probably evolved as the front end of the shell in conjunction with the strong spiral (coiling) and elongated shell shape. Active predatory animals evolved later and started using the existing 'bauplan' of the anterior canal with the development of a siphon which was well protected by the existing anterior (now truly siphonal) canal. More sessile snails (an older 'bauplan') as patellids and trochids are non-siphonate and have a big flat base of the shell or a more or less rounded aperture, for better fixture on the hard underground where they crawl slowly. Conclusion: the (early) anterior ('siphonal') bearing shelled snails are either herbivorous or microphagous and not predatory, thus the development of an anterior canal is not (directly) linked with the feeding habits. The remaining logic beneficiary lies in the assumption that it is the result of the development of fast locomotion and the assumption of Vermeij that it has evolved for the benefit of protection. For the head and the organs there placed, including the eyes. I herewith like to discourage such an ingrained term as "siphonal canal" and replace it by the term "anterior canal" for Strombidae and Cerithidae. I hope subsequent authors will do the same.

DEVELOPMENT OF THE STROMBID NOTCH

The strombid notch is, as said, a development uniquely in Stromboidea (Strombidae and Rimellidae) and all other known gastropods lack this feature on the anterior part of the edge of the labrum. The strombid notch can be rather shallow or deeply incised into the labrum, differentiated on the species or genus, as

discussed before and shown on Plates 5 and 6. Kollmann (2005) allocated the subfamily Harpagodinae to the family Strombidae on the basis of the basal notch. Due to the presence of an identical small basal notch in the Aporrhaidae, he later (Kollmann 2009) placed the Harpagodinae in the family Aporrhaidae. Perhaps the origin of the strombid notch is already as early as the Mesozoic era.

As the location of the strombid notch is on the labrum at the anterior part, the right side of the animal, one eye is pointing sideways to the right, leaving the left side of the animal unwatched. However, watching movements of strombid species (personal observations), the animal moves in a straight line using both eyes in forward direction, thus the head is not in line with the apex of the shell, but instead the shell is oblique compared to the head. It seems that 2 eyes through the anterior canal is more logical to us (as in *Terebellum*, Seraphsidae) but apparently there are better evolutionary arguments for the evolution of the strombid notch. One argument could be that the smaller anterior canal is a better protection against predators like crabs and the shell can be smaller constructed as part of the head is protected by the labrum. In the adult stage the mantle just has to skip a part of the reinforcing of the labrum to create the strombid notch. This seems to be an easy adaptation, which renders a safe condition and the possibility to peep out under the roof of the labrum. Thus, also an evolutionary trend for the benefit of safety in combination with the development of the eyes and the unique development of long eyestalks. The Seraphidae have developed a torpedo like shell which enables them to move with high speed through the clean sand. They lost the broad shell form as in Strombidae in favour of speed and thus did not develop a strombid notch for the long eyestalks.

The Rimellidae arose in early Eocene and already demonstrated strombid notches (in *Ectinochilus* Cossmann, 1889; *Dientomochilus* Cossmann, 1904; *Dasyostoma* Stewart, 1927; *Varicospira* Eames, 1952) in the Eocene period and onwards. In genera of the Strombidae, strombid notches are absent or very obscure in the Eocene (*Oostrombus* Sacco, *Orthaulax* Gabb, 1873). The evolutionary relation between the Rimellidae and the Strombidae is not yet clear.

Early (large) strombids like the very large *Dilatilabrum roegli* (Harzhauser, 2001) from the Chattian (Late Oligocene) of Greece and *Dilatilabrum fortisii* (Brongiart, 1823) from the middle Eocene of Italy lack a strombid notch or have a very shallow indentation but do have the general *bauplan* of the larger extant strombid species. Also, *Dilatilabrum trigonus* (Grateloup, 1834) from the lower Miocene of France still lacks a strombid notch. Even *Tricornis tricornis* (Lightfoot, 1786) from the Pleistocene (Ras Doumeira, Djibouti, Gulf of Aden) of the Arabian Sea has a very shallow strombid notch (personal observation). Only extant *T. Tricornis* of the Egyptian Red Sea have well developed strombid notches. This is also seen in American gigantic strombid species like *Lobatus dominator* (Pilsbry & Johnson, 1917) from the Oligocene up to the upper Miocene of the Caribbean which lacks a strombid notch, even the extant *Titanostrombus goliath* (Schröter, 1805) has only a very shallow strombid notch (Plate 5A-C). These large to gigantic strombid species are likely not burrowers but remain surfaced on the sand and therefore did not develop a strombid notch. The conclusion could be arrived that strombid notches developed primarily in the branches of burrowing strombids and that the very shallow or almost obsolete strombid notches in the large not burrowing species could be secondary loss or the basic situation.

Bandel (2007) also notes that *Dilatilabrum* (for which he erected the new family Dilatilabridae) resemble *Strombus* in shell shape with an expended outer lip but do not have a strombid notch. As they lived in the Paleogene, he concludes that they may represent the stem group to the Strombidae. Strangely, he places the younger genera *Oostrombus* and *Orthaulax* (Eocene, Oligocene and Miocene), which have smoothed shells with callus covering the spire as seen in *Calyptrophorus* in the family Thersiteidae Savornin, 1915. Perhaps these *Oostrombus* and *Orthaulax* species were the early burrowing representatives of the Strombidae (with smooth shells), but still lacking a strombid notch. *Orthaulax* can be a enlarged version of *Calyptrophorus*. Further study is needed on the relations between those genera.

Whatever the origin of the Strombidae, the stem group consists of shells without strombid notch. And even up to present times the large strombid species that live epifaunal (living on and not in the substrate) lack strombid notches or have very shallow ones and strong and rapid small burrowers as *Tridentarius* Kronenberg & Vermeij, 2002 and *Terestrombus* Kronenberg & Vermeij, 2002 have secondary lost the strombid notch. Just as members of *Terebellum* Röding, 1798 (Seraphidae) with similar life habits do not have a strombid notch (Plate 3A & D).

In the collection of the author, several strombid shells are housed with 2 instead of 1 strombid notch, at least a structure that looks like it, an anomaly not often seen and not previously reported to my knowledge. The question that arises is: (1) is this an occasional anomaly caused by damage to the mantel, the soft tissue that builds the shell, or (2) is the second strombid notch an anomaly to house a third eye-stalk?

On Plate 9 several examples of this abnormality from the authors' collection are shown. It concerns three from the genus *Euprotomus* Gill, 1870 and one from the genus *Lentigo* Jousseume, 1886, which are likely genetically closely related when molecular tested. Is this a coincidence?

In the case of *Lentigo lentiginosus* STR2728 (Figure 9D), no damage to the shell is visible, thus eliminating the possibility of early damage to the soft tissue due to *e.g.* crab attacks. This is also the case of *E. aurisdiana* STR3079 (Figure 9C) though this example bears extraordinary double shoulder knobs. Both *E.*

bulla (STR1428 and STR2227) (Figure 9B) have a dorsal situation that might point at tissue damage, especially STR2227, with raised dorsal rim which points at an early tissue damage. But ending in the apertural rim as an almost perfect second strombid notch. STR1248 (Figure 9A) has a sharp additional shoulder lacking knobs, ending in the apertural rim with a narrow indentation looking a bit like a second strombid notch, but probably is not.

Whether all those abnormal condition of double strombid notch must be the cause of abnormal eye-stem number or tissue damage is hard to tell from only the empty shells.

Character	Strombidae	Rimellidae	Seraphsidae	Rostellariidae	Aporrhaidae	Struthiolariidae
Long eye-stalks	present	present	present	present	-	-
Open anterior canal	present	present	present	-	-	-
Strombid notch	Present or absent	present	-	-	-	-
Short eye-stalks	-	-	-	-	present	present
First labral digits used to protect the head	-	-	-	present	present	-
Average living depth	shallow	shallow	shallow	Shallow to deep water	Shallow to deep water	shallow

Table 1. Comparison of characters of recent Stromboidian families (Xenophoridae excluded)

DEVELOPMENT OF EYE-STALKS AND DEVELOPMENT OF STROMBID NOTCHES

Except Strombidae, the living species of the stromboidean families Rostellariidae (see *e.g.* figures in Man in 't Veld & Visser, 1998), Seraphidae (see *e.g.* Jung & Abbott, 1967: pl. 319, pl. 321 bottom figure) and Rimellidae (observation Kronenberg, 2013) also have their eyes at the tip of long eye-stalks. Thus, this is a synapomorphy of these families within the Stromboidea, distinguishing them from evolutionary older families as the Aporrhaidae and Struthiolariidae, and suggesting a common ancestor where the longer eye-stalks and apparent same usage of the eyes developed (Maxwell *et al.* 2019, the construction of Epifamilies herein). The occurrence of long

eye-stalks is in relation to the development of a strombid-notch is given in Table 1.

Eye-stalks development is a dominant condition or trigger of strombid notch development in both Strombidae and Rimellidae. Most likely the long eye-stalk is a development that arose as result of animals' burrowing modes, a chance to stay safely under the sand / mud while scanning the area for danger. Strombidae and Rimellidae probably have shared ancestors, and the genus *Calyptrophorus* (at present in the Rostellariidae) can be the one (Kollmann 2009: 59). Kollmann (2009: 60) "The Calyptrophorinae Bandel possess a basal notch. They may have given rise to the Rimellinae and perhaps other Stromboidea with a basal notch, while the Rostellariidae, which generally lack a notch,

have evolved from Hippochrenes Montfort". These animals (Calyptraphorinae) were burrowers with a smooth shell with a callus layer over the shell that lived in the Cretaceous, Palaeogene and Eocene after which they became extinct. Shells of this group have a broad sinus next to the small open anterior canal, which can be the basic *bauplan* of the later strombid notch and anterior canal used for the long eye-stalks in Strombidae.

ABNORMALITIES IN THE NUMBER OF EYES

In the normal situation, the number of eyes is always 2, each eye on a separate eye-stalk. It is the normal condition; however, deviations are reported in this document. A Caribbean strombid species with a doubled (twin) eye on a stalk (Kronenberg, 2013) has already been reported. In that case, the eyes stayed together like Siamese twins. On the accompanying photo of "*Strombus lobatus* Linnaeus, 1758" in that report, it is clear that the twin-eyes at the tip of the right eye stalk are smaller than the other normal left eye and that it almost looks a split of one normal eye into 2 'Siamese' eyes.

Anomalies in living creatures are perhaps not even rare, but reports about them are. In the past, all kinds of anomalies were collected and put on alcohol in special collections or even displayed as an attraction (especially when it came to people) at traveling exhibitions. In this paper two species with anomalous number of eyes are reported from Turtle Crossing for both, a sandy plateau with scattered coral heads from 12-14 m on the south of the island of Roatan, Bay Islands, opposite of Honduras mainland. This is a clear and unspoilt area with no pollution or other suspect circumstances (observation of Mickey Charteris, the discoverer). It is therefore unlikely that environmental influences are the cause of the deviations. The two species are

Queen Conch, *Aliger gigas* (Linnaeus, 1758) (Plate 7A) with 4 eyes and the Milk Conch *Macrostrombus costatus* (Gmelin, 1791) (Plate 7B) with 3 eyes.

Special attention is also required for the 4-eyed *Conomurex luhuanus* (Linnaeus, 1758) photographed by Shawn Miller (Plate 8A-B). This snail has a normal left eye-stalk with a normal eye protruding through the anterior canal, and the right eyestalk with three eyes of one has a cleaved stem and two eyes are connected just in the form of Y. The eyes look natural and the size is not much different from normal eyes. Also seen in the photo is the proboscis, which appears to be normal. The strombid notch is wider than normal and also the anterior canal is wider than normal, almost twice the normal size (compared to collection material AMD). Thus, there is a relation between shell aspects and the multiple eyes in this aberrant example.

Also, Stephen Maxwell, Cairns, Queensland, Australia once caught a *C. luhuanus* with an additional eye but that was years ago and the animal was discarded, even without taking photos (personal communication, May 2017). The author discussed the abnormal multiple eyes with Maxwell, but he could not recall if the shell had additional features related to the multiple eyes; the shell is no longer in his collection/possession.

In the authors collection, several strombid shells are housed with 2 strombid notches per shell, as discussed before (Plate 8). This is an anomaly that can be caused by damage to the shell secreting mantle or possibly related to multiple eye-stalks. With empty shells it is not possible to determine the cause of the double strombid notch.

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We express our great thanks to Mickey Charteris, Roatan, Bay Islands, Honduras for making the great photos of the live 3-eyed and 4-eyed *Strombus* examples from Roatan, his home town. The same for excellent photos by Shawn Miller of the live *C. luhuanus*. Without these photos it would be impossible for us to demonstrate the deviations in the number of eyes in Strombidae. Thanks also to Tammy Myers, Ormond Beach, Florida, USA, for the aquarium photo of the Milk Conch. All involved are thanked for permission to use these excellent photos. David Berschauer is thanked for editing, and Stephen Maxwell, Cairns, Australia, is thanked for mounting the photographic plates.

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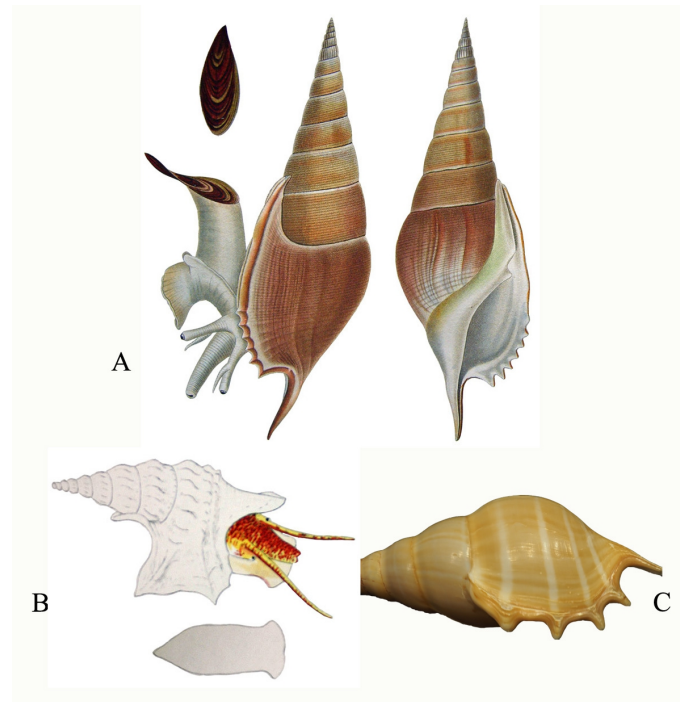


Plate 1. Rostellariidae and Aporrhaidae

A = *Tibia insulaechorab* Röding, 1798 (as *Rostellaria curvirostris*) in Kiener, 1843, Vol. 4, Rostellaria pl. 1, fig. 1. Drawing showing the live animal with the eyes on stalks. Large sinus near the anterior spine for the snout and lacking a strombid notch.

B = *Aporrhais pespelecani* (Linnaeus, 1758) in Forbes & Hanley, 1853, pl. II, fig. 3, 3a (as *Aporrhais pes-pelecani*). Animal showing eyes close to the body mass, no stalks. A large sinus for the snout and lacking a strombid notch.

C = *Rostellariella delicatula* (Nevill, 1881); AMD STR0996, Andaman Sea, southern Thailand, trawled by Thai boats, deep water, 1977. Part of the shell showing the 'internal' white bands reinforcement structures resulting in the labral spines.

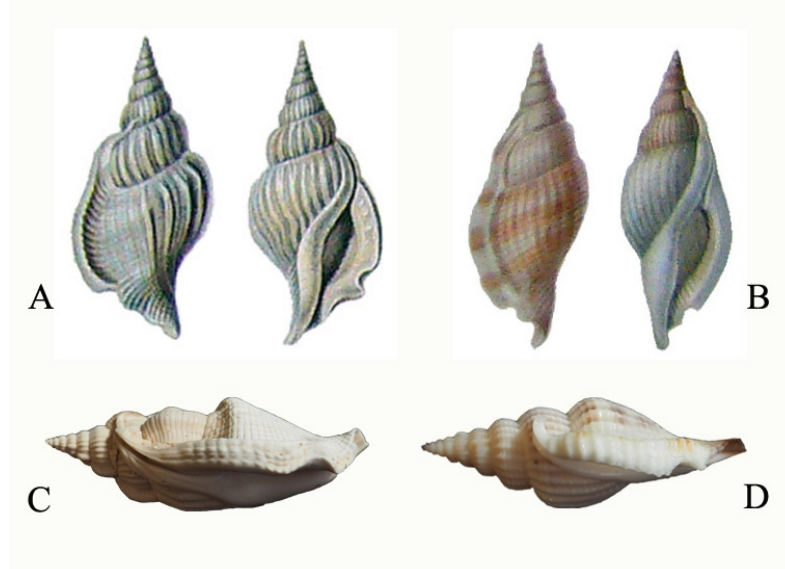


Plate 2. Rimellidae

A = *Varicospira decussata* (Basterot, 1825) in Duclos in Chenu, 1844, pl. ?, fig. 5, 6 (as *Strombus decussatus*). Drawing showing a clear strombid notch.

B = *Varicospira crispata* (Sowerby, 1842) in Duclos, 1844, pl. 16, fig. 9, 10 (as *Strombus crispatus*). Drawing showing the small but well visible strombid notch.

C = *Varicospira decussata* (Basterot, 1825), AMDSTR927. H 26 mm. St. Martin d'Oney, France. Self-collected. Miocene – Aquitanien. Clear strombid notch.

D = *Varicospira crispata* (Sowerby, 1842), AMD1329. H 22.2 mm. Bohol, Philippines, showing the strombid notch.



Plate 3. Seraphidae and smooth Strombidae

A = *Terebellum terebellum* (Linnaeus, 1758); AMD STR3532, H37.5 mm. Olango Island, Philippines, night dive 20-25 meter. Shell side view showing the lack of strombid notch.

B = *Terestrombus terebellatus* (Linnaeus, 1758); AMD STR3867, H47.4 mm. Calituban Island, Philippines, from fisherman. November 2006. Side view of the shell. Towards the apertural rim 5 white beams can be seen, 2 of them besides the shallow strombid notch, resulting in very small rounded dents.

C = *Tridentarius dentatus* (Linnaeus, 1758); H51.2 mm. Quezon Baraguy, Puring, Palawan, Philippines. Taken in coral sand at 1-3 meters. 09-2006. Clearly seen are the 3 dents and another 3 bumps on the apertural rim connected with 5 white banding. Also the indentation between the first 2 dents serve as shallow strombid notch. Also, the anterior canal is open towards the first 2 dents, both ready for the eye-stalks.

D = *Terebellum terebellum* (Linnaeus, 1758); ~80 ft, Agat Bay, Guam; ~2003-2004; aquarium photo Bob Abela, Guam. Eyes on stalks looking backwards.

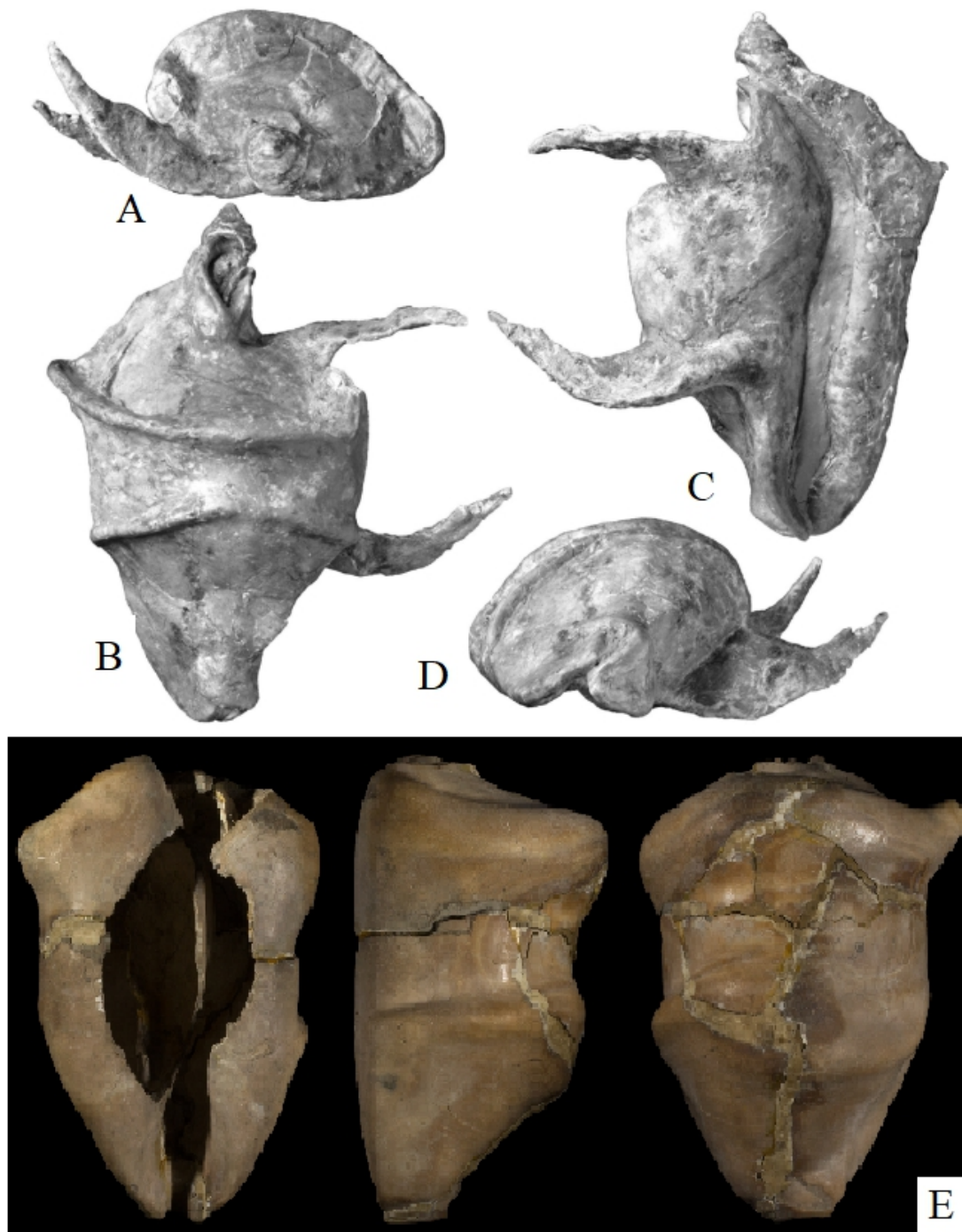


Plate 4. Eocene gigantic Cypraeidae

A to D = *Vicetia bizzottoi* Dominici, Fornasiero & Giusberti, 2020. (Holotype MGP-PD 32314, measuring 335 mm in length). (a) Posterior view, (b) ventral view, (c) dorsal view, (d) anterior view. Gigantic Eocene fossil cypraeid species showing strong dorsal ridges and spines as prolongation of ridges. No dents along the aperture as commonly seen in present day cypraeids. Shell resembling a *Lambis* species.

E = *Vicetia hantkeni* (Lefevre, 1878). MNHN.F.R11785. Specimen with dorsal ridges, measuring approximately 120 mm in length. Gan, La Tuilerie, France. Collected by Didier Merle. Photo Credit: RECOLNAT (ANR-11-INBS-0004), Jocelyn Falconnet, 2017.



Plate 5. Big Strombidae with shallow strombid notch

A-C = *Titanostrombus goliath* (Schröter, 1805); AMD STR3409. H 235 mm. Recife, Brasil, 2000. Depth of the strombid notch ca. 5 mm of this almost fully adult (not yet thickened lip).

D = *Macrostrombus costatus* (Gmelin, 1791); AMD STR0379. H 187 mm. Photos showing the very shallow strombid notch.

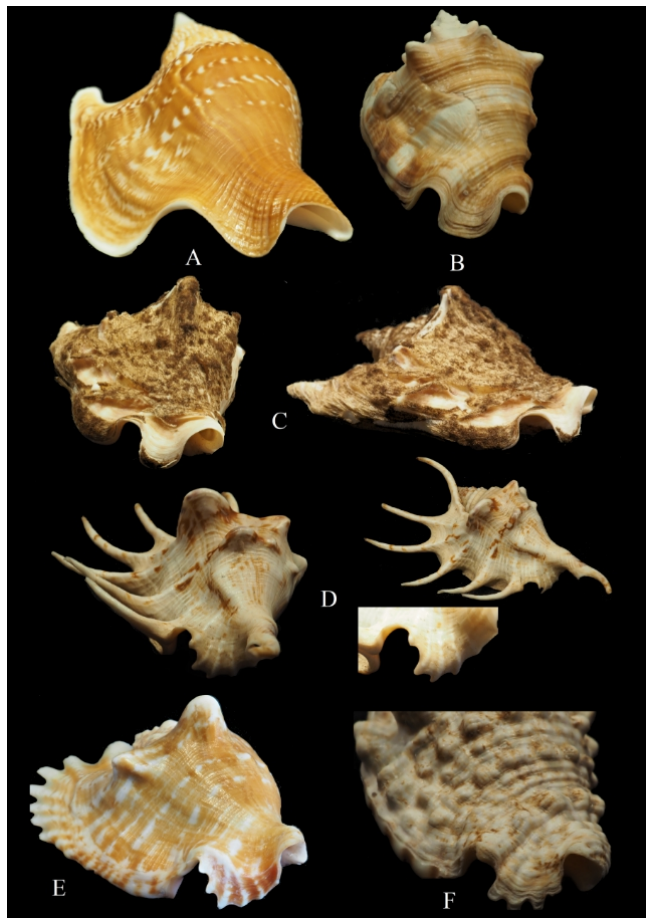


Plate 6. Strombidae with deep strombid notch or large strombid lobe

A = *Mirabilistrombus listeri* (Gray, 1852); AMD STR0573. H 144 mm. Ranong, SW Thailand. Enormous broad and deep strombid notch.

B = *Persististrombus granulatus* (Swainson, 1822); AMD STR1275. H 61.1 mm. La Mira, Las Perlas Islands, Panama, on hard sand flats. Big and deep strombid notch.

C = *Tricornis tricornis* ([Lightfoot], 1786); AMD STR3498. H 68.9 mm. Coll. by B. Gras, Mah Kabi, Yemen, Red Sea. With periostracm. Very big and deep strombid notch.

D = *Lambis lambis* (Linnaeus, 1758); AMD STR2242. H 152 mm. Pandanan Island, Philippines. Large strombid lobe with 5 fingers of which one is in the large and deep strombid notch.

E = *Solidistrombus sinuatus* ([Lightfoot], 1786); AMD STR1860. H 86.1 mm. Caubyan Island, Philippines. Strombus lobe with at least 5 downward fingers. Strombus notch also with dents, very deep.

F = *Lentigo lentiginosus* (Linnaeus, 1758); AMD STR3555. H 80 mm. South of Mombassa, Kenya, at 2 meter on sand in algae field. Strombid lobe with 4 downward fingers.



Plate 7. Certain Strombids displaying bifurcated eye stalks

A = *Aliger gigas* (Linnaeus, 1758) with 4 eyes. Turtle Crossing, which is a sandy plateau with scattered coral heads from 12-14-meter-deep on the south of the island of Roatán, Bay Islands, opposite of Honduras mainland, Honduras. Photo courtesy of Mickey Charteris (Caribbean Reef Life), Roatán, Islas de La Bahia, Honduras.

B = *Macrostrombus costatus* (Gmelin, 1791) with 3 eyes. Turtle Crossing, which is a sandy plateau with scattered coral heads from 12-14-meter-deep on the south of the island of Roatán, Bay Islands, opposite of Honduras mainland, Honduras. Photo courtesy of Mickey Charteris (Caribbean Reef Life), Roatán, Islas de La Bahia, Honduras.



Plate 8. Certain Strombids displaying bifurcated eye stalks

A, B = *Conomurex luhuanus* (Linnaeus, 1758) with 3 eyes, Okinawa, Japan. Photo courtesy of Shawn Miller (Okinawa Nature Photography), Okinawa, Japan.

C = *Macrostrombus costatus* (Gmelin, 1791). Aquarium photo, courtesy of Tammy Myers, Ormond Beach, Florida, USA.



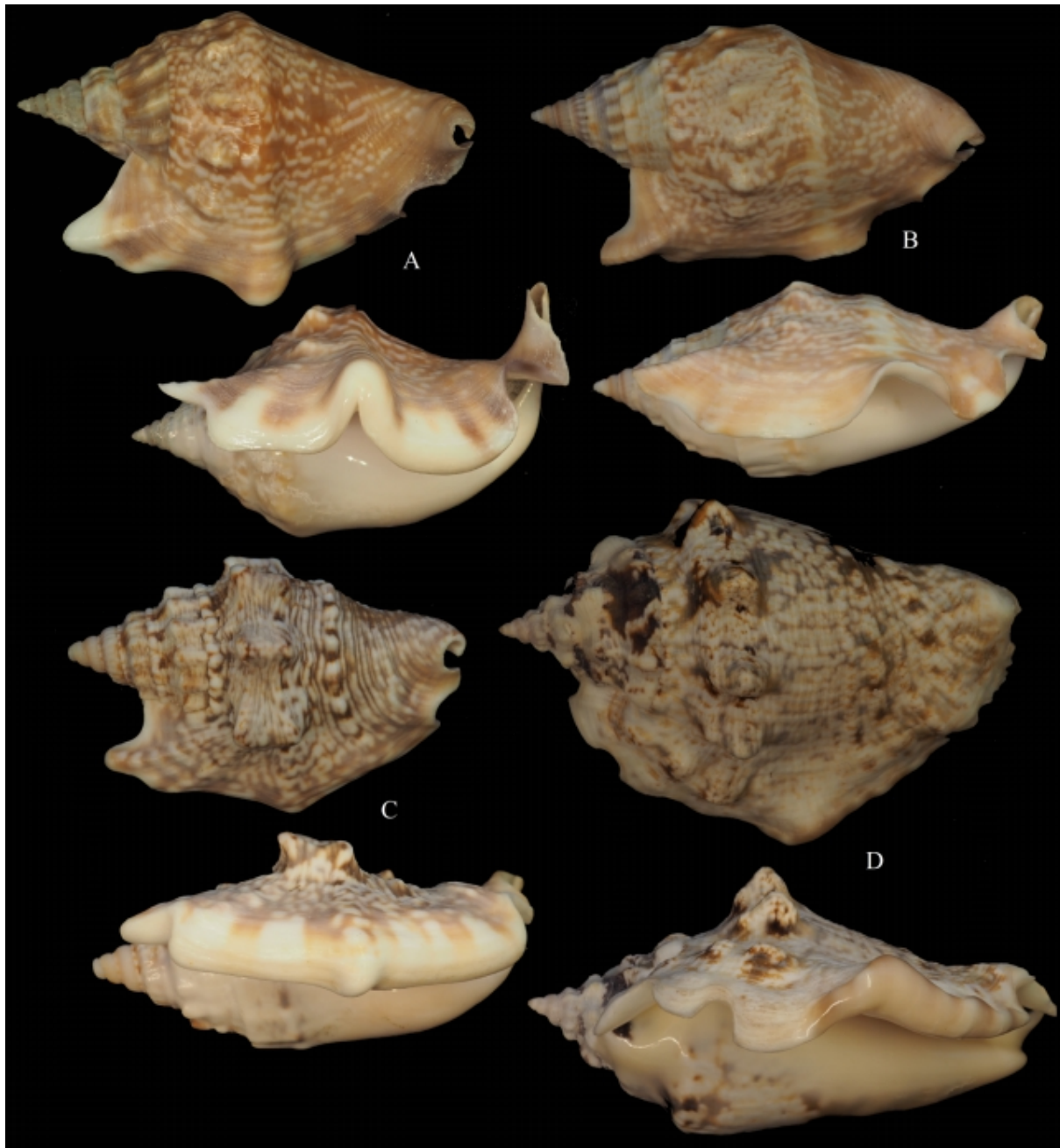


Plate 9. Various Strombid shells displaying growth structures

A = *Euprotomus bulla* (Röding, 1798). Bohol, Philippines. H. 59 mm AMD STR1428. Sharp additional shoulder lacking knobs, ending in the apertural rim with a narrow indentation.

B = *Euprotomus bulla* (Röding, 1798). Beni Island, Philippines. H. 58 mm AMD STR2227. With raised dorsal rim which points at an early tissue damage. But ending in the apertural rim as almost perfect second strombid notch.

C = *Euprotomus aurisdiana* (Linnaeus, 1758). Beni Island, Philippines. H. 51.7 mm AMD STR3079. Looks like a undamaged shell, but with elongated or double shoulder knobs.

D = *Lentigo lentiginosus* (Linnaeus, 1758). Olango Island, Philippines. H 71.5 mm STR2728. Perfect shell, no damage.