The Clockwork Olive: Perspectives from the "American Shoulder"

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Abstract

The structure and the biological significance of the Olivinae fasciculate ornamentation known as "American Shoulder" after its exclusive presence in the (sub)genus *Americoliva* are investigated for around 20 Western Atlantic / Gulf of Mexico / Caribbean species. The applicability of the "Chevron Paradigm" by Tursch & Greifeneder (2001) to the subchannel area is questioned and contrary evidence is proposed. A robust correlation between lip thinning phases and the generation of the typical American Shoulder features is observed: their coincidence with rapid growth stages as reported by Strano (2017) is plausible but wasn't established decisively in absence of destructive investigations. The issues of intraspecific and interspecific variability are addressed thanks to an extensive photographic coverage, and a new general description of the American Shoulder emerges from the investigations. The initial identification of some specimens included in this study is questioned on the basis of their subchannel pattern, hinting at its possible use as an accessory character in species determination, and suggesting to include its exhaustive description in new nomenclatural acts involving the (sub)genus *Americoliva*.
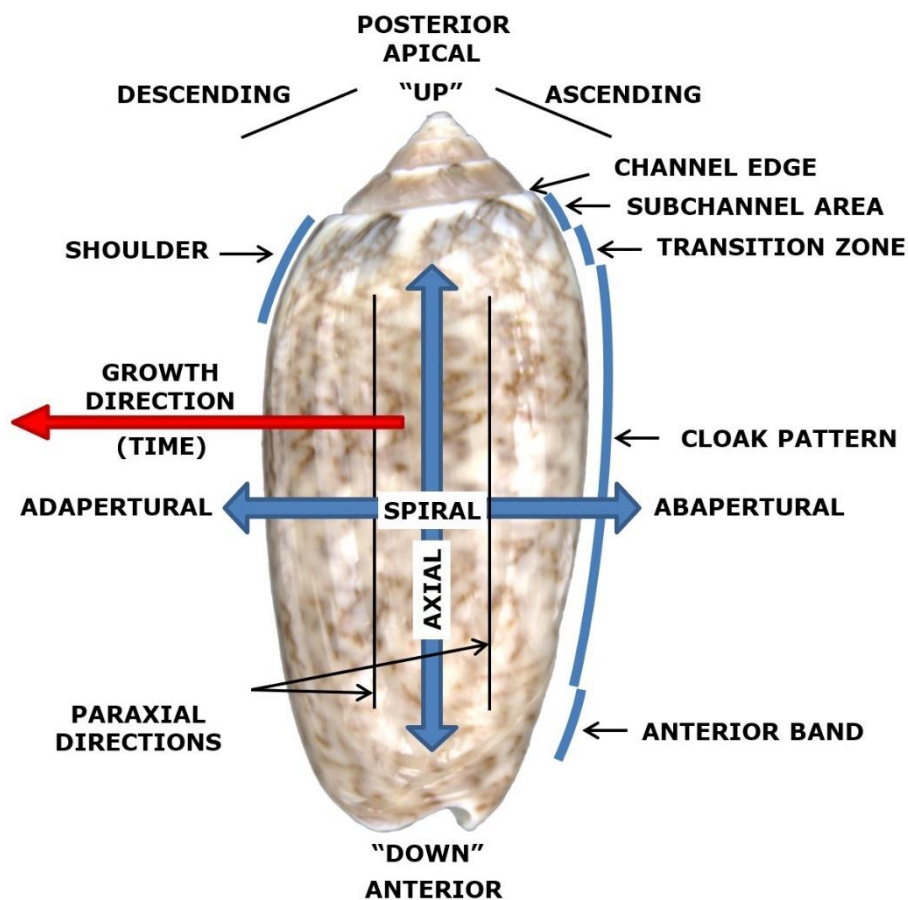

Figure 1. Olivinae shell topology as adopted in this paper. See also the Glossary.

1 Introduction

1.1 Terminology

The readers not versed in olivology may help themselves with the glossary proposed in Figure 1 and under Appendix 1. Terminology is mainly form Tursch & Greifeneder (2001), with modifications and integrations. The nomenclature of shell layers by Sterba (2006) is adopted as used by Strano (2017), based on a simplified four-layer + protein glaze model that disregards the "internal lining" observed by Tursch & Greifeneder (2001) (uninteresting for the purposes of this study). Except in the case of *Vuilletoliva splendidula* (Sowerby, 1825), that is endowed with one more outer layer, and starting from the innermost, Olivinae shell layers include:

- internal, aragonite in spire-wise lamellae;
- medium, aragonite with paraxial lamellae;
- activation zone corresponding to the "transition zone" by Tursch & Greifeneder (2001) – according to Strano (2017), this white calcite layer is the forefront of shell growth;
- external, with composition and structure similar to the internal layer, and with pigments that determine the observable shell pattern;
- protein glaze, the "external pellicle" by Tursch & Greifeneder (2001).

1.2 Genomics and Morphometrics: Two Sides of the Same Coin?

Genomics (for a compelling overview, see Lesk, 2017) has been available since a few decades, in the forms of computer-based sequencing and of the many applications and scopes of biosequences alignment programs. Even before its affirmation in systematics, books like Patterson (Ed.) (1987) preconized the potentially lacerating gap between phenetics and the new *in silico* cladistics, and proposed conflict mitigation strategies based on the search of a common ground where the two disciplines would emerge as two sides of the same coin. Among the authors that commendably agree about the need of an integrated morphometric – genomic approach, one may cite Steiner et al. (2009) and – in olivology – Kantor et al. (2017). Yet, bridging the gap between morphometrics and genomics remains a demanding task, and many researchers, sometimes with an unquestioning attitude (suffice to cite Dominguez and Wheeler, 1997 or Donoghue, 1985), still prefer taking a stand on either side and disregard the approach that they deem less reliable, or that they are less competent about.

Actually, the purely digital nature of automated phylogenetical analyses makes them strictly dependent on software parameters, on methodological choices, on the availability of uncontaminated biological samples, on strict lab policies, and on other seldom-discussed factors including the reliability of molecular clocks and of the strategies adopted for their calibration. Furthermore, both the generation of phylogenies and the definition of species by genomic means are based on an algorithmic representation of the concepts of parsimony and consensus which, in turn, are ultimately the expression of user-defined numerical thresholds. All the factors mentioned require an in-depth knowledge about the ways in which data are collected, arranged and processed, and a very thorough statistical competence: in fact, more or less inadvertently, assumptions may be injected in any dataset in form of "cherry picking", in other words, of more or less subtle imbalances in the set of specimens considered and of more or less conscious over- or underrepresentation of subgroups in the diversity range considered. True to the old information technology adage, "garbage in, garbage out", any such choice will result in inconsistent resolution of the nodes in any phylogenetic tree generated, as plainly shown by Figure 2 in Kantor et al. (2017), whose dataset included 15 specimens of *Oliva caroliniana* Duclos, 1840, 7 referrable to *Oliva lacanientai* Greifeneder & Blocher, 1985, 5 referrable to *Oliva dubia* Schepman, 1904 while some (sub)genera of Olivinae were covered by no more than one or two specimens.
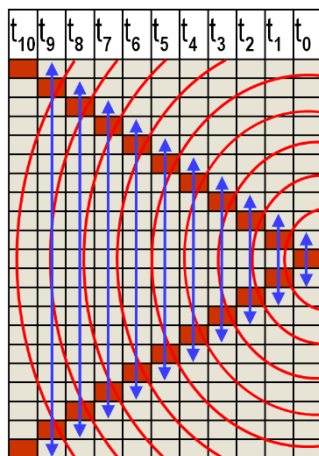
Figure 2. The chevron paradigm exemplified: at t_0 an initial active point in the Shell Growing Edge (SGE) discharges pigment and enters quiescent recharge state. From that point, a chemical signal is propagated in both directions. The cascade of activations in subsequent tempuscules generates a basic chevron pattern, in a process that can be described as a wavelike propagation (red waves). In the orthogonal reference grid, isochrones are vertical columns. For mutual elision and non-retrogradation of wavefronts see the glossary and Tursch & Greifeneder (2001). Redrawn and modified after Tursch & Greifeneder (2001).

1.3 Olivinae Ornamentation: the Chevron Paradigm

The complexity of the powerful and often decisive genomic methods, and of statistical genomics in particular (see Fridley and Wang, 2023), their dependance on competent, well-informed choices and their vulnerability to bad practices are both a cause of inconsistent results and a possible reason why genomics did not entirely supersede classic, morphological methods in taxonomy and systematics. Among the morphological characters of Olivinae shells, their distinctive ornamentation has attracted the attention of many authors: not for chance specific epithets such as *amethystina*, *caerulea*, *flammulata*, *fulgurator*, *lepida*, *nivosa*, *rubrolabiata*, *rufofulgurata*, *picta* etc. abound. While the ornamental patterns in their entirety are often species-specific, some recurrent aspects can be generalized at supraspecific level. With particular reference to the last body whorl, recurrent features include a distinctive subchannel pattern (see the glossary: the posterior mantle filament and its channel are treated e.g., in Burch, 1988 and in Van Osselaer & Tursch, 1994), restricted to the posterior part of the whorl (Fig. 1: shoulder) adjacent to the spiral filament channel, a transition zone, and a "cloak pattern" engaging the greatest part of the whorl. Discussion about the ornamentation of the anterior part of the shell is outside the scope of this paper.

The physiological mechanism that underlies the generation of the color patterns observed on the surface of the cloak of an Olivinae shell was elucidated in the outstanding monograph by Tursch & Greifeneder (2001). Dubbed "chevron paradigm" (CHP – see also the Glossary and Fig. 2), as any similar paradigm it describes the evolution in time of a pattern being generated in a system of orthogonal coordinates. The CHP was also algorithmically implemented in computer programs, evolved from those by Meinhardt (1998) that, in turn, are rooted in the seminal works by Raup & Michelson (1965) and Waddington & Cowe (1969): those programs are in fact capable of generating more or less realistic images of the olivine cloak ornamentation.

1.4 Spatial Coordinates Distortion at the Cloak's Edge

The shoulder is an area of increased adapical shell curvature that marks a change in shape, coincident with the posterior tract of the Shell Growing Edge (SGE): it can be expected that space-related phenomena such as pigment deposition are affected by the different spatial constraints at the cloak's periphery (at the opposite end of the shell, the anterior band is similarly affected by its own spatial constraints). Tursch & Greifeneder (2001) in their subchapter "Special cases. shoulder patterns" demonstrate how the last whorl can be compared to the central section of an ellipsoid, where the shoulder marks an increasingly important Mercator-like adaxial distortion of the otherwise orthogonal reference grid of pattern deposition. They hypothesize that the

movement of the SGE in such a distorted reference grid is the only, purely geometrical, reason of pattern differentiation in the subchannel area. At sub-points 9.7.1 and 9.7.2 (their copyright-protected, detailed images are not reproduced here because for their full understanding the entire accompanying text would also need to be reproduced), Tursch & Greifeneder show how the surfacing of medium layer patterns behind a thinner external layer, and the degeneration of chevrons into quasi-vertical or abaperturally-arched lines, concur to the formation of any subchannel pattern, including paraxial, vertical or subvertical elements. Such a conviction is the expression an unquestioning faith in the CHP, and will be scrutinized more under.

1.5 The Oliva Growth Model by Giorgio Strano

Besides being constrained by geometry, the evolution of ornamental pattern is an epiphenomenon that follows, and is constrained by, growth. The conclusive investigations by Strano (2017) shed light on the cyclical nature of the Olivinae growth strategy, based on growth / rest phases (respectively associated with thinning and thickening of the shell's lip) that periodically impact both the ornamentation and the structure of the shell, marking relatively rapid phases of shell restructuring interspersed among longer rest phases. Rather than a juvenile character, a sharp lip is demonstrably a recurring if infrequent condition: Strano suggested caution when applying to other Olives the growth curve proposed for *O. mustelina* Lamarck, 1811 where, as a general rule, the spiral full-girth section of adult specimens shows four or more rest-structures (the curve grows asymptotically), and the last teleoconch whorl can encompass up to the last 10-12 years of life (Strano, 2017), even though the tightening of rest-structures in the lip of gerontic specimens may impede their counting. The Olivinae lifespan and the recursion of pattern elements will be discussed more under.

Strano worked with mid-axial full-girth sections, at the SGE center, without any special attention to the subchannel area. Yet, the relevance of his work for the aims of this study stems from the obligatory association between lip thinning and rapid growth: he reported no evidence of lip thinning without shell rapid growth, nor of shell rapid growth without lip thinning. Transitively, other phenomena coincident with lip thinning may parsimoniously be related with rapid growth phases in the *Oliva* growth cycles. Furthermore, the accurate description of the aptly named "rest structures", and the provision by Strano (2017) of five diagnostic clues of relented or interrupted growth offers another opportunity to correlate ornamentations and rest phases.

1.6 The Utopia of Impartial Morphology: introducing *Americoliva*

As much as we may like it, as much as it may require just a vernier caliper and two keen eyes, and although since a few centuries we cannot do without it, we must anyway admit that morphology itself can be contentious, deceiving and, in line of principle, no less prone to subjective decisions than genomics. It suffices to think to the genus *Oliva* Bruguière, 1789: according to the monographs emerged in the last five decades, and excluding later new taxa, estimates about the number of valid specific or subspecific entities in the genus *Oliva* range from the 176 by Petuch & Sargent (1986) to the 79 species by Tursch & Greifeneder (2001), with a prudent 87 by Sterba (2003) and a more optimistic 101 by Hunon et al. (2009) in between. Whichever its actual granularity, since the inception of the genus by Bruguiére (1789-1792) that diversity originated in time no less than five hundred species or form names (most of which are covered by the huge bibliographic work by Voskuil, 2018): clearly, morphology-based systematics of Olivinae has always been debatable, to say the least, even at supraspecific level.

Even more so for one of the most interesting Olivinae supraspecific entities, *Americoliva*, that includes species from the Western Atlantic / Gulf of Mexico / Caribbean Area, from the Pacific Central American provinces, and from Eastern Atlantic. Formally instituted at page 209 of Petuch (2013), since then *Americoliva* has most frequently be used as a full genus, but the World Register of Marine Species database lists the entry as unaccepted, considering it as a synonym of *Oliva* Bruguière, 1789 - the same fate of its antecessor subgenus *Oliva (Strephona)* Gray, 1847 and its junior homonym *Strephona* Mörch, 1852. The genus is accepted by The Olividae and Olivellidae Scratchpad website (see the References) as including both all the species formerly included in *Strephona* Mörch and the newer species created after the formal institution by Petuch (2013). Type

species is *Oliva sayana* Ravenel, 1834. Epitomizing a combination of high intraspecific variability and low interspecific variability, the hallmark of Olivinae (not by chance, Abbot, 1991 warned that «When you purchase an *Oliva* from a dealer these days, you are spinning the wheel of identification chance.»), *Americoliva* puzzled and mystified also very authoritative researchers: by looking at one tell-tale mistake, we will introduce the reason why high-resolution morphological details are so sorely needed to separate correctly the *Americoliva* species.

1.7 *Americoliva* and the Not-so-objective Morphospecies Approach

When, in Chapter 13 of their monograph, Tursch & Greifeneder (2001) explained their "objective morphospecies approach" for species identification, they misapplied multivariate cluster analysis to "reduced extensive measurements" (shape factors of the shell, such as height/width). Their conception of clustering is undermined by some very bold stances that, particularly for *Americoliva*, deprive of any resolving power their analyses:

- The distribution of points within each cluster is insignificant: their figure 13.09, that cannot be reproduced for copyright reasons, exemplifies some totally unnatural patterns of distribution, when in fact the clusters of shape factors are density-based (Kriegel et al., 2011) and, as such, show areas of higher density than the remainder of the data set, where objects in sparse areas are usually considered to be noise and border points. Examples abound, e.g. Figure 5 in Marzouk et al. (2016) or, for Olividae, Figure 6 in Strano (2017).
- The area of a cluster is delimited by all its perimetral (most sparse) objects.
- Whenever the areas of two clusters overlap, even if it were only for a small area, they are part of the same "morphological continuum".
- Any morphological continuum corresponds to a single species.

Those assertions, especially if made squarely and at the same time, are untenable, for statistical and methodological reasons whose illustration goes well beyond the scope of this study.

But, interestingly, even though ill-formed, the "objective morphospecies approach" works excellently when improper cluster overlap does not occur, e.g., when separating obviously different or just vaguely similar species: that success is the cause of a false sense of security. It's exactly in *Americoliva* that the approach fails miserably. For any combination of shape factors considered in two or more *Americoliva* species,

- high intraspecific variability results in wider, blurred clusters;
- low interspecific variability results in a reduced distance among cluster barycenters, and consequently in a high probability of overlap among clusters.

Not by chance, Tursch and Greifeneder end up lumping most *Americoliva* species – with a few exceptions, that include the Pacific and the East Atlantic species – in a single, misleading and useless pseudo-taxon, the "*Oliva fulgurator* group".
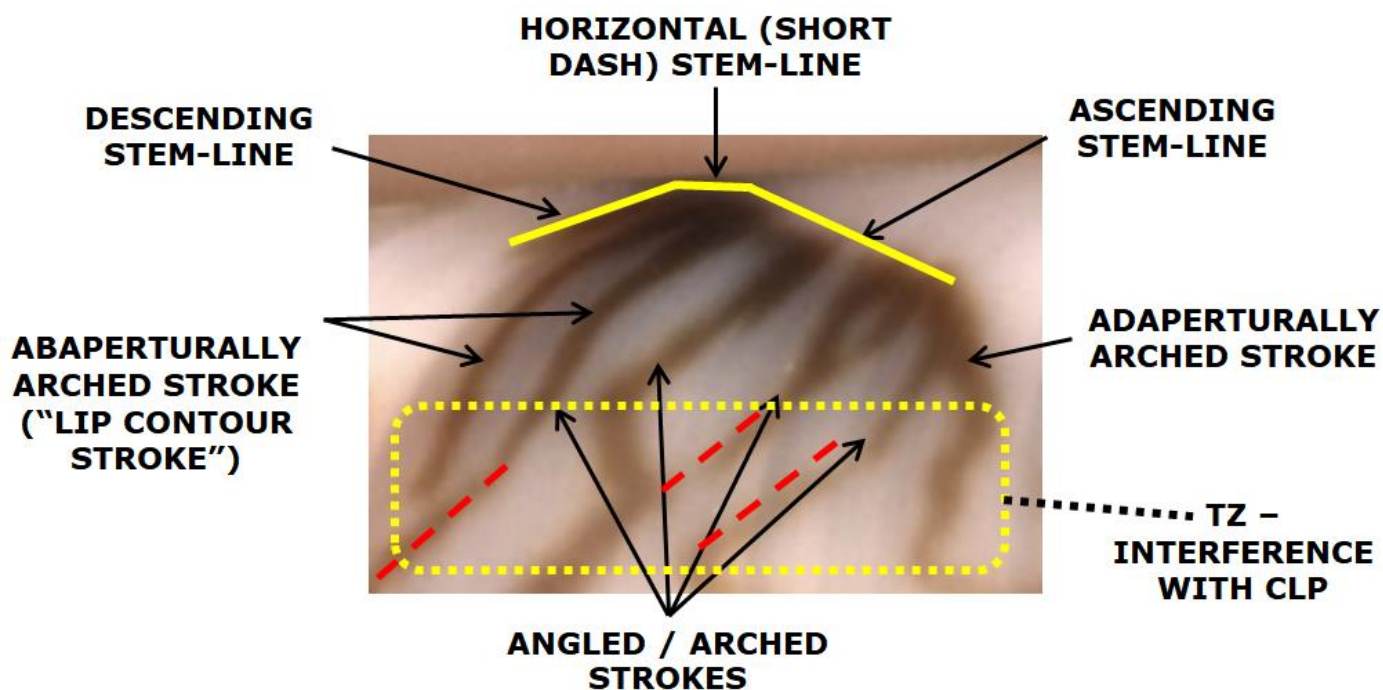
Figure 3. A typical American Shoulder (AS) Feature – observe how the strokes' lower (posterior) tip may trigger the propagation in the transition zone of "children-lines" compliant with the Chevron Paradigm (CHP) (red dashed lines). #1205 is an undetermined specimen from the *A. reticularis* group, from Martinique

1.8 Need for Details in Olivinae Morphology: Introducing the American Shoulder

Summarizing, we can safely state that, while a detailed morphological analysis is always needed to discern any Oliva species, to disentangle the *Americoliva* species such an analysis should be even more accurate. To ensure nomenclatural stability, morphology-based species descriptions should exhaustively and unambiguously describe any small, potentially species-specific detail, including those previously unexplored, such as the one this study concentrates on: an apomorphic and not fully understood set of patterns in the *Americoliva* ornamentation, positioned at the shell's shoulder (see Fig. 1) and dubbed "American Shoulder" (AS) by Tursch and Greifeneder (2001). In general terms, the American Shoulder is the combination of features made by usually coalescent / fasciculate lines, that include more or less paraxial linear or arcuate elements, and that appear in the subchannel area of the *Americoliva* species. The presence of subvertical elements connected with a visible, or following an ideal, "stem-line" will be more extensively illustrated in the Results section.

Study aims include:

- providing a novel and exhaustive description of the American Shoulder;
- ascertaining its coincidence with particular lip conditions;
- investigating its possible relation with growth stages;
- assessing its intraspecific variability;
- assessing its degree of variability at interspecific level.

Specimen			Species of *Americoliva*		Locality	Lip Condition		
Count	#	Size mm	Count	Name		Thin	Interm.	Thick
1	840	46.5	1	*barbadensis* Petuch & Sargent, 1986	St.James Parish, Barbados	☐	☑	☐
2	841	33.1				☑	☐	☐
3	843	37.3	2	*bewleyi* Marrat, 1870	Santa Marta, Colombia	☐	☑	☐
4	62	40.2	3	*bifasciata* Küster in Weinkauff, 1878	Haiti (unconfirmed)	☐	☑	☐
5	769	46.0			Florida	☐	☐	☑
6	176	43.2	4	*circinata* Marrat,1870	Espiritu Santo, Brazil	☑	☐	☐
7	775	49.7			Unavailable	☑	☐	☐
8	232	52.0	5	*fulgurator* Lamarck, 1811	Colombia (unconfirmed)	☐	☐	☑
9	235	40.0			West Point, Aruba	☑	☐	☐
10	240	47.9	6	*goajira* Petuch & Sargent, 1986	Colombia	☐	☑	☐
11	875	47.0			Guyana, Berbice County	☐	☐	☑
12	726	20.2	7	*jamaicensis zombia* Petuch & Sargent, 1986	Haiti	☐	☑	☐
13	727	24.3				☐	☑	☐
14	1193	31.4	8	*lilacea* Paulmier, 2013	Martinique	☐	☑	☐
15	1194	30.6				☐	☑	☐
16	64	46.3	9	*nivosa bollingi* Clench, 1938	Florida (unconfirmed)	☐	☑	☐
17	757	47.6			Tampa Bay, Florida	☐	☑	☐
18	59	31.6	10	*nivosa clenchi* Petuch & Berschauer, 2019	Cape Canaveral, Florida	☑	☐	☐
19	60	46.0				☐	☑	☐
20	825	59.2	11	*nivosa maya* Petuch & Sargent, 1986	Cabo Catoche, Yucatan, East Mexico	☐	☑	☐
21	886	54.1			Yucatan Peninsula, East Mexico	☑	☐	☐
22	439	31.3	12	*olivacea* Marrat, 1870	Rapid Point, Union Isl., St. Vincent	☐	☑	☐
23	440	29.2				☑	☐	☐
24	580	46.2	13	*porcea* Marrat, 1870	Isla Coche, Venezuela	☐	☑	☐
25	746	42.3			Venezuela	☑	☐	☐
26	234	47.1	14	*reclusa* Marrat, 1870	West Point, Aruba	☐	☐	☑
27	918	35.2			Palm Beach, Aruba	☑	☐	☐
28	493	33.1	15	*reticularis* Lamarck, 1811	Lesser Antilles (unconfirmed)	☑	☐	☐
29	698	53.2			Cuba, Cayo Blanco	☐	☐	☑
30	497	35.7	16	*reticularis ernesti* Petuch, 1990	Azuero, Panama	☐	☑	☐
31	729	30.0			Honduras	☐	☑	☐
32	748	72.4	17	*Sayana* Ravenel, 1834	Florida	☐	☐	☑
33	776	50.3			Florida	☑	☐	☐
34	1204	36.3	18	sp. A	Martinique	☐	☐	☑
35	1205	36.2	19	*sp.* B		☐	☑	☐
36	660	30.7	20	*sp.* C *cfr. jamaicensis* Marrat, 1867	Puerto Rico	☑	☐	☐
37	271	26.3	21	*sp.* D *cfr. jamaicensis* Marrat, 1867	Las Salinas, Dominican Republic	☐	☑	☐
38	56	37.0	22	*sp.* E *cfr. bewleyi* Marrat, 1870	Isla Conejo, Los Testigos, Venezuela	☐	☐	☑

Table 1. List of specimens included in this study. Lip condition refers to the apical lip extremity. See text for the specimen selection criteria.

2   Materials and Methods

While Strano (2017) sectioned spirally and polished a relevant number of *Oliva* specimens, this study offers a purely photographic survey, to preserve the integrity of the author's collection, and to allow anybody to replicate similar investigations without sacrificing any specimen shell.

Species nomenclature is the fruit of some reflection: *A. porcea* Marrat, 1870 is used in place of the *nomen*

dubium A. tisiphona, and *A. sargenti* Petuch, 1987 is replaced by its senior synonym *A. reclusa* Marrat, 1870. Two specimens from Martinique, initially identified as *Americoliva lilacea* Paulmier, 2013 are listed as *Americoliva sp.* considering important differences in protoconch and ornamentation. Also, two specimens akin to *Oliva jamaicensis* Marrat, 1867 and one probable *Oliva bewleyi* Marrat, 1870 proved impossible to identify conclusively, and are separately listed. The author is the sole responsible of any misidentification of the specimens, some of which were unaccompanied by reliable locality data, a minor shortcoming for the purpose of this study.

To explore the correlation between growth cycles and the creation of AS features, a set of 38 Western Atlantic (including Gulf of Mexico and Caribbean) *Americoliva* leiotropic (Cook, 1914) shells from the author's collection, for a total of around 20 species, was selected as per Table 1, to include both sharp-lipped, thick-lipped and intermediate specimens. Lip sharpness was subjectively defined by sight and touch, and can be verified in the lip pictures provided more under. A full-shell ventral and dorsal view of all the specimens cited in this study is available on the author's website cited in the References. The species were chosen on the basis of specimen availability and quality, with no particular concern about systematics. For practical reasons, among those with mostly intact lip edge in the subchannel zone, no more than two specimens per species were selected, where possible with different lip thickness. For a few species, only one specimen with intact lip was available, and another damaged one was included to investigate pattern consistency.

Separate pictures of the inside and the outside of the apical lip extremity were taken, with a horizontal field of view of around 16mm. For the apical photography of the specimens, a video camera mounted on a fixed stand and connected to a photo camera objective was used. The stand table was equipped with a manual, mechanical X/Y/Z micrometric stage, suitably moved in small equal increments between manual frame captures, capturing a few tens of perfectly coaxial frames, subsequently focus-stacked. For an orderly presentation, all the apical photos were resized to the same number of pixels, and equally oriented.

To improve the coverage of the subchannel area, an approach based on peripheral photography was adopted for three specimens (Figures 15, 17 and 18) thanks to a contraption allowing the horizontal clockwise rotation of *Americoliva* specimens in equal discrete steps. Thirteen frames centered on the shoulder area were digitally captured, manually cropped to ensure consistent framing and digitally stitched in ring-like projections. This time-consuming method was abandoned because the improvements over the apical focus-stacking were marginal. All the details about the photographic equipment and optical setup are available upon request.

3   Discussion

3.1 The Paradox of the AS and the Crisis of the Chevron Paradigm

Due to its the complexity, the subject of the AS was gracefully avoided even by keen investigators with huge collections and decades of experience: rather than providing an exhaustive description of the AS, they get by with just a few drawings and some general examples. When addressing this recalcitrant problem from the heights of the 38 specimens considered in this study, the author is so reckless to start by questioning the conclusions drawn by Tursch & Greifeneder (2001) who had thousands of *Oliva* specimens close at hand.

In fact, one of the reasons why the AS looks indescribable is that it includes elements that cannot be explained under the CHP + grid distortion + surfacing medium layer scenario. A first paradox stems from the obvious observation that the lip edge marks an isochronous line: it's all there, and all at once. Consequently, any pattern element that follows the lip contour (such as the lip contour strokes in Figure 2) is also following an isochrone: *ergo*, it must be laid down all-in-one-shot in the shorter or longer tempuscule marked by that isochrone. It's unimportant whether the lip remains stationary in that position for one hour or one week: what matters is that such an element is not generated in the typical diachronic, one-dot-at-a-time fashion as the cloak pattern elements.

A second paradox is created by lines that appear to converge to, or diverge from, the same point at the channel edge, or that simply coalesce at the channel edge, a situation that remains unsatisfactorily explained regardless of which layer is involved and regardless of reference grid distortion (the latter may account for curvature, not for occasional convergence). In Figure 4A-D, a simplified version of four typical AS features (respectively, one symmetrical "tooth" in a cogwheel pattern, an "open hand", a "fence" and a series of elements following the lip contour) is proposed in dot-by-dot style, with the different lines composing each feature marked in different colors. Figure 4E shows the standard application of the CHP in translational sweeping mode (right to left) with successive generation of three chevrons (as exemplified in Figure 3) while Figure 4F represents 180° of rotational clockwise sweep of a SGE where three points (red, green, blue) undergo two cycles of activation. The rotation may represent the peripheral grid distortion advocated by Tursch & Greifeneder (2001), or a SGE whose posterior tip is temporarily anchored at a fixed point at the channel edge. To render the full shape of the rotating chevrons, Figure 4F covers all the 180° arc, but it should be remembered that - under the CHP - inactivation on collision would occur any time two lines overlap at the same grid cell.
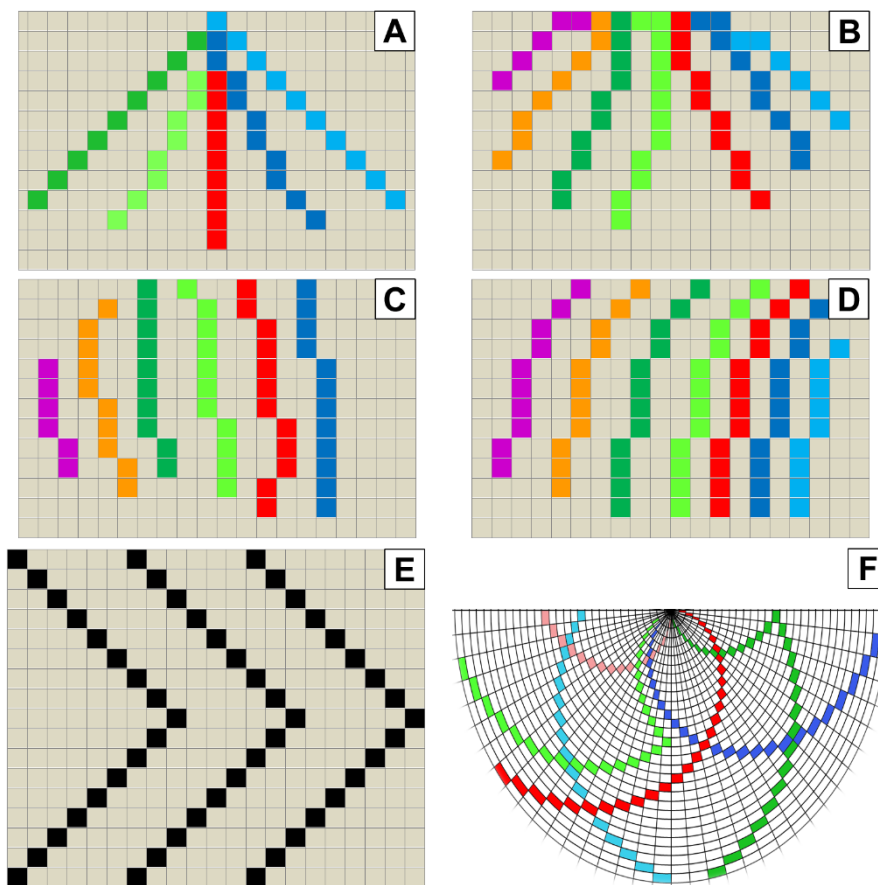

Figure 4. Incongruence between the Chevron Paradigm and the shape of AS features. A: "Cog tooth" (Pacific *Americoliva*, but also partly visible in e.g. #726); B: "Open Hand" (e.g. #1205); C: "Fence" (e.g. #825); D: "lip contour straight-strokes" (e.g. #757); E: translational CHP; F: Rotational CHP.

It can be easily understood that there is no way to reconcile the two flavors of the CHP, 4E and 4F, with the lines composing the four reference features 4A – 4D. Moreover, even hypothesizing that the CHP had some secret way to circumvent its own rules, and were capable to retrograde or to follow isochrones, the application of the CHP to fasciculate features such as Figure 4A and 4B would be teleological: all the chevron angles should miraculously vary in a coordinate way to grant the converging / coalescing effect.
But there is another more obvious reason to exclude a CHP control over the AS features: the intermediate stages of dot-by-dot fasciculate pattern generation do not correspond to the intermediate stages of development actually observed for those features.

If the AS features aren't made by CHP lines, a special name is needed to identify their components. To that

purpose, Figure 3 disclosed the term "stroke" (also, some anterior band features, observed in Americoliva as well as other genera of Olivinae outside the scope of this paper, could be defined as strokes), a concept flexible enough to accommodate both the author's many uncertainties and his few certainties. The latter boil down to:

- strokes appear only in the subchannel area;
- most strokes are visually distinct (thickness, color...) from the adjacent cloak pattern lines;
- most strokes negate the CHP;
- some strokes – including lip contour strokes – look like they were laid down all-in-one-shot (but not necessarily instantly): they will be dubbed "straight-strokes", and coincide with (part of) an isochrone line. At any given moment, the SGE itself marks an isochrone line: as a consequence, any stroke parallel to the SGE is better explained as a straight-stroke;
- depending on the nature and the size of the transition zone, strokes have the capability to generate CHP lines in the transition zone, that merge with the adjacent cloak pattern;
- strokes can converge and coalesce escaping the "inhibition on collision" rule of the CHP;
- some strokes may be the fruit of the unveiling of lower layers;
- strokes normally coalesce in a well-developed AS feature, but may also appear between two consecutive features, in irregular groups or even individually.

On such an uncertain ground, caution is obligatory: one may concede that some form of one-dot-at-a-time diachronic progradation may involve the strokes, in which case they could be grouped in two "families": the subchannel version of chevrons, subject to more flexible rules and the all-in-one-shot straight-strokes.

Summarizing, the multipurpose concept of non-CHP-compliant strokes is consistent with observations and is required to provide an appropriate description of the AS features. The existence of a transition zone provides additional evidence of the distinct nature, coexistence and interference of strokes and CHP lines. In fact, as e.g. shown in Figure 3 and 10, by examining the lower (anteriormost) part of an AS feature it's frequent to observe diachronic "cloak-style" lines ("children-lines") obviously triggered by the lower tip of a stroke. The reverse wasn't observed, maybe because reverse stroke generation triggered by the upper (posteriormost) cloak pattern elements would very often require retrogradation. Not by chance, whenever the transition zone is adequately developed, most strokes have no children lines. As a general rule, it may be stated that strokes may overlap but do not branch: any form of branching of lines from a stroke may occur only in the transition zone, where the CHP is effective.

A problematic transition zone was observed in *A. bifasciata* (see Figures 14, 15, 20), where the thin antler-like projections connected with the cloak pattern may be coalescent strokes, aborted children-lines, proper cloak pattern elements or a mix of all three elements. Any further investigation concerning the possible peculiarity of *A. bifasciata* is incompatible with both the declared scope of this study, and the insignificant number of specimens considered. A generalized mode of pattern generation for the subchannel area, not limited to Americoliva but applicable to all Olivinae, is exemplified in Figure 5.

Position	Acronym	Name	Kind of pattern element	Mode of generation	Chevron Paradigm applies?
	SA	Subchannel Area	Stroke	Quick / instantaneous	NO
	TZ	Transition Zone	Anterior (lower) tip of strokes Occasionally, Lines	Occasionally, strokes may trigger lines Occasionally, line generation may occur	Partly
	CLP	Cloak Pattern	Line	Diachronic (dot by dot)	YES

Figure 5. Pattern Generation Modes in the Subchannel area.

3.2 AS Features and Lip Conditions

Specimens referable to three different lip conditions were separately observed to ascertain the correlation, if any, between the AS pattern features and the possible lip states. The following general conclusions were drawn:

- **Thick lip** is typically not coincident with portions of a feature, and instead may coincide with other isolated pattern elements (typically, no pattern at all);
- **Sharp lip** is typically coincident with the central part of a feature, marked by strokes connected with a dark horizontal dash-like or punctiform stem-line placed at the channel edge;
- **Thinning / thickening lip** – the remaining transitional specimens can be easily referred to the initial or conclusive phase of the AS feature generation.

Figure 6 shows both sides of the lip adapical extremity of 8 thick-lipped specimens. No trace of AS features can be observed at the lip edge. The deplorable state of #875 provides a peek into lip stratification, confirming the presence of a thin internal layer with darker blotches like those exposed in the sharp lip pictures of Figure 7.

Figure 7 shows both sides of the lip adapical extremity of 12 sharp-lipped specimens. At the lip edge, the central part of an AS features is being generated, coincident with the horizontal, channel edge-bound part of the stem-line, including lip-contour straight-strokes in #59, #235, #440, #660 (partly), #746, #775, #841. Apical views provided in Figures 20 and 21 show that the sharp-lipped condition is reflected also by a darkened area visible inside the outer wall of the filament channel. The black features at the channel edge may be regarded as remnants of the protrusion of a darker internal layer, overlaid by the external layer elsewhere but uncovered at the channel edge.

Figure 8 shows both sides of the lip adapical extremity of 18 intermediate stage specimens. At the lip edge, the phase of inception (ascending stem-line) or completion (descending stem-line) of an AS feature can be observed. Incipient lip contour straight-strokes are evident in #62, #497, #727, #825.

3.3 AS Features and Growth Cycles

The obligatory association between lip sharpening and rapid growth established by Strano (2017) allows to hypothesize that also the AS features may mark rapid growth phases. Both are the expression of those rhythms whose understanding would require an integrated physiological and mathematical approach (Glass & Mackey, 1998). With just a few shells at hand, we cannot either investigate Olivinae physiology for an adequate amount of time, nor obtain an amount of data suitable for an exhaustive mathematical modeling of each species (several tens of specimen for each taxon studied would be needed), that moreover would lead us into the intricacies of an accurate translation in numbers of the still elusive AS patterns. Let's face it: as Vinarski (2014) reminds us, we must bow our heads to Blainville (1825) and Rafinesque (1814), the founding fathers of malacology: conchology alone can't efficiently describe transitory moments in the mollusk lifecycle, that are much better dealt with by malacology proper.

This notwithstanding, we are free to work deductively: the detail of the lip shown in Figures 6-8 is too small to observe overall color discontinuities or color bands inside the aperture, but can be used to ascertain the presence of the remaining three clues by Strano (2017) for locating rest-structures and previous positions of the shell's lip. In fact, the adapertural termination of an AS feature coincides with:

- Protein foil's dark lines:
    - Figure 6 (#875)
    - Figure 7 (#176, #746, #776)

    o Figure 8 (#64, #757, #825)
- Cloak pattern disruption (see also "Minor events" more under):
    o Figure 6 (#56, #234, #769, #1204)
    o Figure 7 (#176, #235, #746, #775, #776)
    o Figure 8 (#62, #64, #240, #271, #497, #726, #727, #757, #825, #843, #1194)
- Bulging lip:
    o Figure 6 (#234, #698, #748, #1204)
    o Figure 7 (#493)
    o Figure 8 (#497, #757, #840, #1194)

The case for AS features as rapid growth markers in *Americoliva* looks promising but, without multiple polished spiral sections of each specimen at different latitudes including the subchannel area, the number and the regularity of the AS features leave some open questions about the temporal coincidence of growth bouts and AS feature appearance.
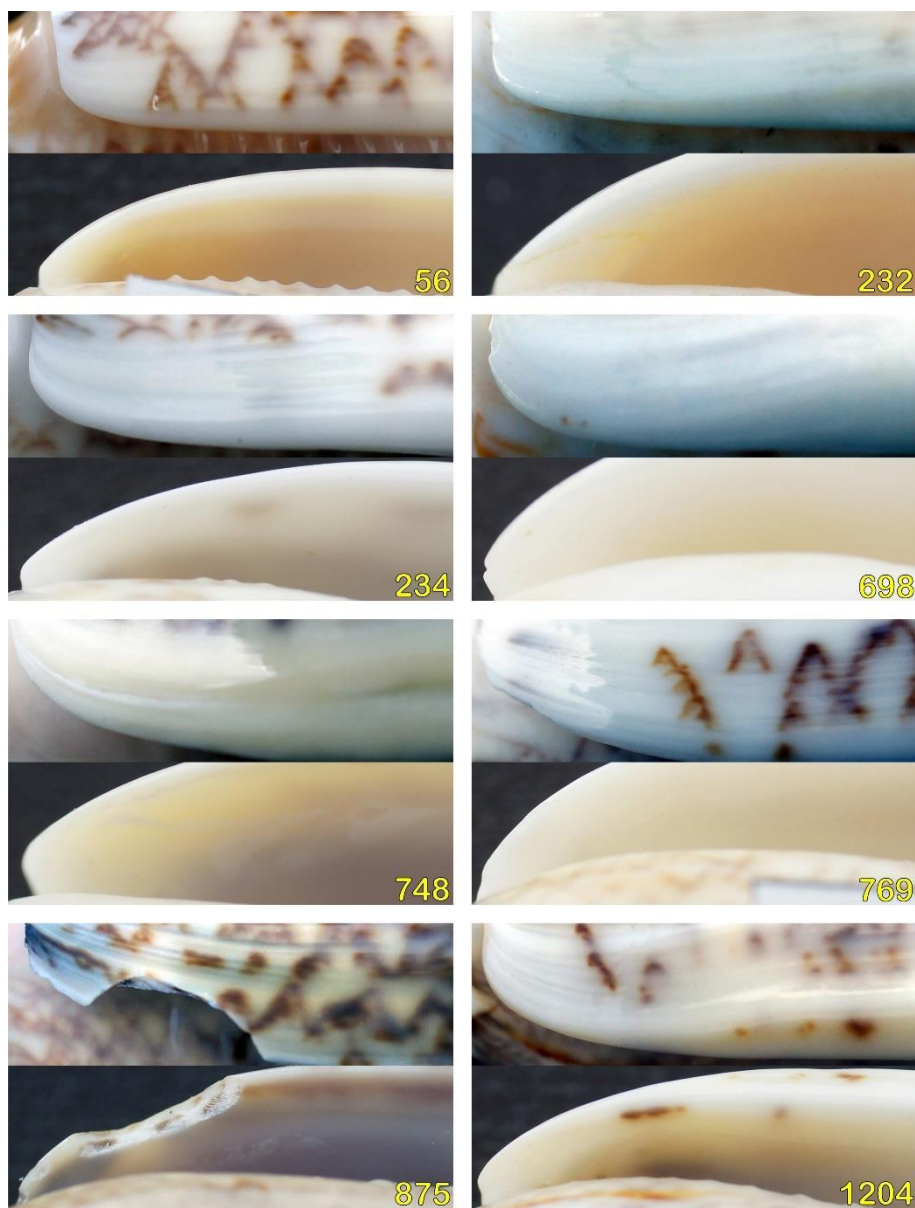

Figure 6. Thick-lipped specimens. The number refers to specimen # in Table 1. For each specimen, a couple of images (below: internal side, above: external side) of the adapical termination of the lip is provided.
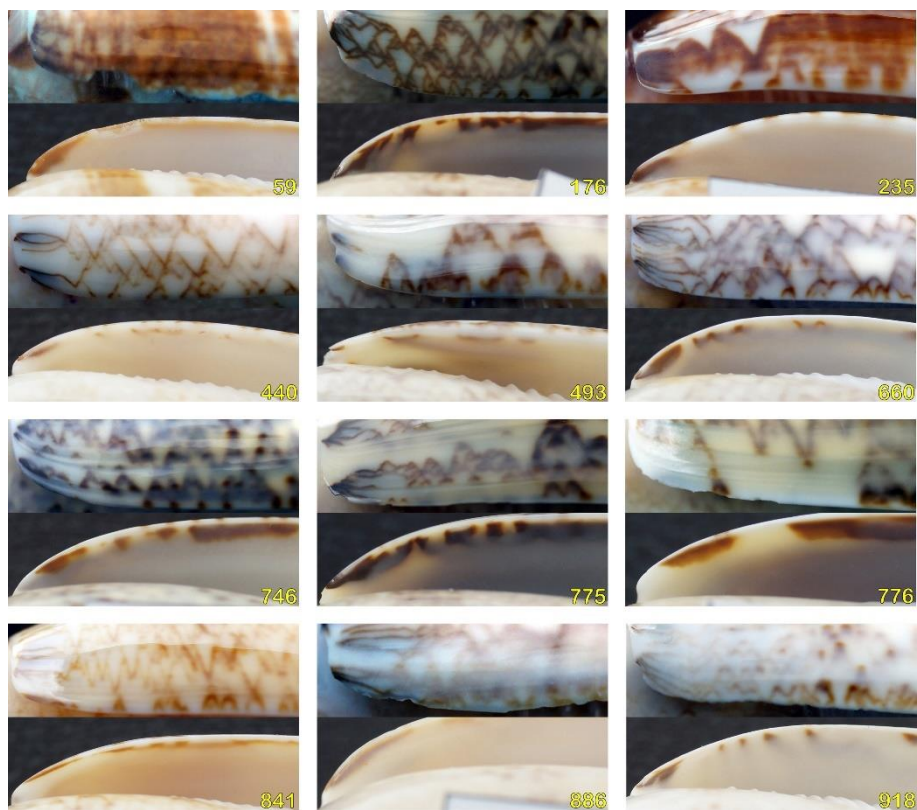
Figure 7. Sharp-lipped specimens. The number refers to specimen # in Table 1. For each specimen, a couple of images (below: internal side, above: external side) of the posterior termination of the lip is provided. The sharpest sections of the lip are mostly dark brown.

Figure 8. Specimens in intermediate stages of lip thickness. The number refers to specimen # in Table 1. For each specimen, a couple of images (below: internal side, above: external side) of the posterior termination of the lip is provided.

The three competing hypotheses include:

- Completely decoupled time frames: the appearance of AS features is totally unrelated with rapid growth phases. The hypothesis is ruled out by the recurring coincidence between termination of an AS feature and the clues of relented/interrupted growth. Furthermore, when observable, lip thinning is generalized and not limited to the subchannel area: differentiation of growth strategies at different lip latitudes would result in severe lip distortion, that was never observed;

- Partially coupled time frames: only some AS features coincide with the rapid growth phases. The hypothesis may look reasonable, considering the distinction between major and minor events as proposed by figures 14 and 15 but, in apical view, the minor and intermediate events are more or less evenly spaced at roughly equal angular distances, weakening the idea that minor and intermediate events do not coincide with shell growth phases;

- Common time frame: all the AS features mark a rapid growth phase and consequently should be included among the rapid growth phase markers. The hypothesis seems verified, looks parsimonious, but cannot be conclusively established without destructive investigations.

Taking evidence at face value, Figure 9 illustrates a typical AS pattern. Decreasing and increasing thickness seem respectively correlated to the ascending and descending stem-line slopes. The fading-in, full development and fade-out of the most complex AS patterns may also coincide with the momentary revelation of medium layer patterns (as per Tursch & Greifeneder, 2001), depending from the thinning-down and thickening-up of the lip. Yet, there is no doubt that subchannel area strokes and cloak pattern lines occupy the same external layer where they also may interact, as illustrated when describing the children-lines phenomenon. In a context of constrained progradation of the lip edge, where no pattern element can regress counterclockwise, reverse or proverse (lipwise) flexion of the paraxial strokes may be the effect of the flexion of the SGE adapical extremity in the scenario of coordinate distortion by Tursch & Greifeneder (2001). Ascertaining *in vivo* the actual position of the mantle edge during the growth phases would require high quality video imagery for a prolonged period of time, a very complex challenge to overcome.

Talking about growth cycles, it may be interesting to remind the reader that Olividae is one of the families that exhibits resorption (dissolution) of the inner volutions of the teleoconch (Kohn et al., 1979), as described by Sterba (2003) and Tursch & Greifeneder (2001). The absence of a proper columella grants an increased internal volume, providing refuge to the mollusk, as well as more space for its growth – both can safely be considered as evolutionary advantages. In the case of the genus *Oliva*, resorption takes also the form of a continuous shift of the parietal callosity (see e.g. page 20 in Sterba, 2003, not reproduced here for copyright reasons), that follows the spiral movement of the growing lip. Besides the creation of new portions of the shell, also a constant recycling and reshaping of the existing shell material occurs, and the system works only in a coordinated fashion: redeposition implies a previous resorption, the spiral translation of structures such as the parietal plications implies both. But, obviously, with the same SGE that takes care of both, the parietal callosity cannot outrun the lip, nor vice versa: the different facets of the Olivinae growth may not be perfectly synchronous, but can neither be independent nor happen randomly. This digression is grist to the mill of a common, coordinated time frame among all the growth-related phenomena, including the generation of the AS features.
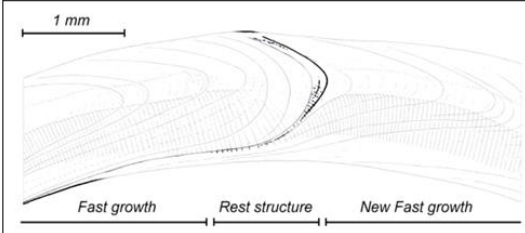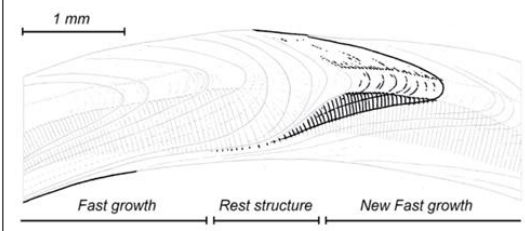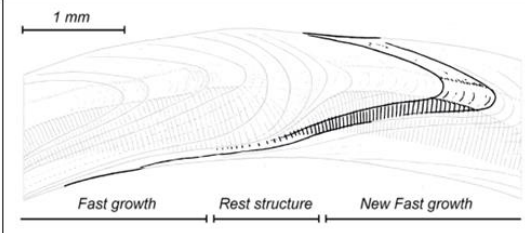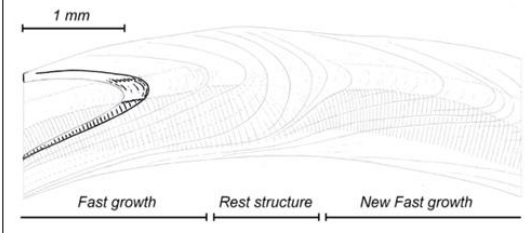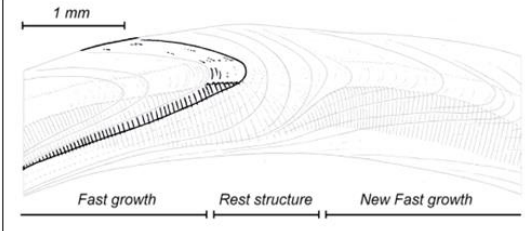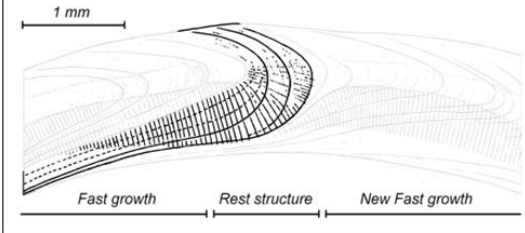
Lip Growth Stage	Phase	Stem-Line Incline	Relevant Examples	Photo
	Early Thinning	Emerging / Ascending	Figure 8 (#439, #580, #726, #727), Figure 7	
	Late Thinning	Ascending		
	Maximum Thinning	Horizontal	Figure 7	
	Early Thickening	Descending	Figure 7, Figure 8 (#62, #64, #240, #729, #825)	
	Late Thickening	Descending / Vanishing (including Lip Contour Straight-strokes)		
	Rest Phase	(no stem-line, back to slow-growth pattern)	Figure 6	

Figure 9. Analogy between growth stages by Strano (2017) and AS feature development. From left to right, exemplifying image from Strano (2017) (modified with permission by the author), based on spiral mid-axial sections of *O. mustelina* Lamarck, 1811; Phase description; Stem-line incline ("Ascending" towards the channel edge – "Horizontal" = coincident with the channel edge - "Descending" away from the channel edge); list of images in Figures 6,7,8 that can (approximately) be referred to each phase; 300% laterally stretched and 90° rotated AS feature from #1205, an undetermined specimen from the *A. reticularis* group from Martinique. Channel edge is highlighted in red.

3.4 Recursion Time of Subchannel Features, Including AS features

Regardless whether AS features are rapid growth markers or not, their periodical recursion is unquestionable. A passing look at Figures 20 and 21 allows to observe that, on average, around a dozen well-formed and more or less regularly spaced features can be observed in the last whorl of most specimens. Even if a direct correlation with rapid growth phases is established, there is no conclusive evidence that the indicatively yearly growth cycle, proposed by Strano (2017) for *O. mustelina* may apply also to *Americoliva*. In that case, the last whorl may cover up to 12 years, an idea compatible with the opinions by Tursch & Greifeneder (2001) about the lifespan of Olivinae: at page 63 they hypothesize a 20 years lifespan, and at page 206 they report the data by Tursch et al. (1985) who measured an average growth rate of 0.38 whorls/year for *Oliva oliva* (Linnaeus, 1758) (resulting in a minimum possible age of 10 years for adults with four teleoconch whorls), and who cite the report by Stohler (1969) of a 10-12 years lifespan for *Olivella biplicata* (Sowerby, 1825) – a species now under the genus *Callianax*.

As a note of caution, while the assumption of a yearly recursion for complex features such as the AS seems plausible, it would be very inconsiderate to conclude that any Olivinae subchannel feature appears yearly – suffice to think to the many *Oliva* species such as *O. todosina* Duclos, 1840 or *Felicioliva peruviana* (Lamarck, 1811), whose last whorl may include a few tens of distinct, simple subchannel marks.

Neither the hypothesis that the intervals between consecutive AS features necessarily mark the same duration of time is conclusively demonstrated: the recursion of subchannel marks may be occasional, affected by transitory factors, including prey availability (growth on prey consumption). Besides being obvious, the direct relation between food availability and shell growth was studied for Gastropods e.g. by Palmer (1983), Leighton & Boolotian (1963), Leighton (1961) and Ino (1949).

But, especially if regular, recursion can be better correlated to extrinsic, astronomical cycles (years, seasonal events, lunar months, special tide conditions...). It's perfectly plausible that more than one condition is required to promote the appearance of a subchannel feature: a fit, adult, well fed individual may react to the trigger event while an ailing or subadult individual can't. It's also evident that each species may react to a different combination of conditions.

3.5 The Creation of AS Features: a Tentative Account

Figures 9 and 10 provide some hints to reconstruct the steps of the creation of an AS feature: a dark blotch, apparently originating in the intermediate layer, is clearly visible at the lip's edge, or can be made out through the outer layer, at varying distances from the posterior tip of the lip. In all the sharp-lipped specimens the blotch is clearly exposed exactly at the apical tip of the lip, covering most of the tip, while in several specimens in intermediate stages of lip thickness a smaller version of the same, or of a very similar, blotch can be made out, slightly displaced anteriorly, through a more or less thick external layer. Both the observations seem to imply an unveiling of intermediate layer, consistent with Strano's lip growth model and with the hypotheses by Tursch & Greifeneder.

By reviewing Figure 9 in light of those observations, it can be hypothesized that the ascending stem-line follows the channel-wise movement of the dark blotch, and that its movement in discrete steps triggers the appearance of the ascending strokes. As soon as the dark blotch is at posterior tip of the lip, which at the same time is the external wall of the filament channel, the lip is at its sharpest: its posterior tip leaves its mark (dot or dash) on the channel wall and, often, the thin protein foil mark. During the lip thickening phase, the dark blotch evolves into the lip contour straight-strokes and in the more sparse and undecided strokes that mark the adapertural part of the feature (Figure 10).

Some unclear points remain, including:

- whether the dark blotch actually moves or simply enlarges channel-wise;
- which layers are engaged during the formation of the AS feature;
- whether strokes in the external layer are triggered by the unveiling of the medium layer.
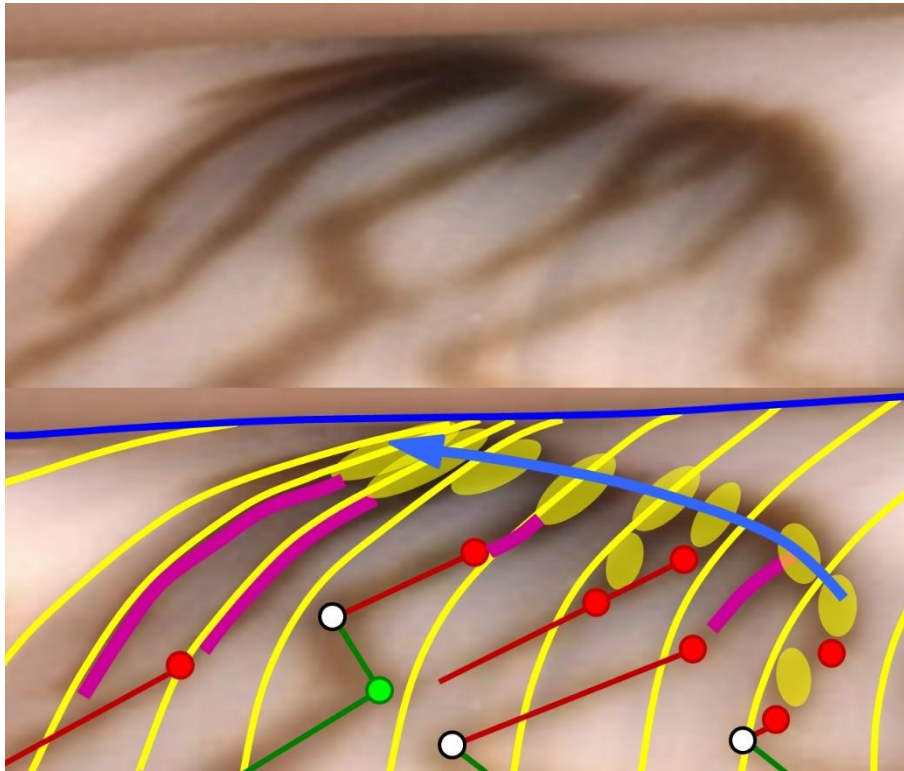

Figure 10. AS Feature from #1205 with 160% lateral stretch. Possible stages in the creation of a typical AS feature. Yellow isochrones mark roughly equidistant lip contours ("Lip Snapshots"). In the Transition Zone, dots mark CHP-style phenomena including children-lines initiation (red), chevron initiation (green), mutual elision on collision (white). The yellow shaded ellipses allow to follow the route of the dark blotch at the lip edge (from which strokes, highlighted by purple lines, originate) to its final destination at the channel edge (blue), where the dark blotch evolves into proper lip contour straight-strokes.

3.6 The Individual Variability of AS Patterns: Event Intensity, Age, Rest Patterns

Individual variability in the subchannel area is the expression of intrinsic and extrinsic factors:

- **Intrinsic (subchannel area peculiarities):** if compared to the cloak, the subchannel area is subject to a higher number of constraints, including reference grid distortion and paradigm conflict in the transition zone, and consequently to a higher variability: as an indirect proof of this complexity, based on the author's 50-year experience in software development, while the CHP can be simulated by a rather simple computer program generating more or less life-like renditions of the cloak pattern (an impression corroborated by the excellent book by Meinhardt, 1998), that's not the case for AS patterns. Besides showing some degree of interaction with the cloak pattern in the transition zone, they seem controlled by a fuzzier and more complicate set of rules, some of which still defy comprehension. It should not be forgotten that the cellular automata used for the simulation of mollusk shell pigmentation incur in a range of "undecidable" behaviors consisting in an erratic mixture of predictability and chaos, where a complex interplay of external "noise" and endogenous processes causes a mode switch between regular and perturbated pattern, depending on the perturbation site and on the overall structure at the time of perturbation (Kusch & Markus, 1996). In that sense, when compared with the cloak area, the extremities (shoulder zone and anterior zone) of the SGE are obviously predestined to perturbation, for the aforementioned spatial constraints, before the onset (when possible) of pattern repair as described by Meinhardt & Klinger (1988).

- **Extrinsic (individual life history):** individual life history impacts growth rate and color pattern generation, as repeatedly observed in many Olivinae e.g. by Tursch & Greifeneder (2001), who describe the quick adaptation of shell color to substrate color. Even small local environmental and ecological variations may, in time, affect AS patterns. Food availability is another extrinsic factor: among the researchers who explored the relation between food and gastropod shell ornamentation, one may cite Ino, 1949 and Leighton, 1961.

As a sobering reminder of the resulting complexity, hereafter some exceptions and corollaries to the general description provided in the Results section are listed.

- **Dark-colored species and populations or melanistic individuals:** needless to say, any pattern may be more or less completely obliterated by an overall dark color. More frequently, as in the case of the illustrated specimens of *O. nivosa clenchi* and of *O. fulgurator*, the AS features show faintly through the dark external glaze.
- **Prolonged sharp-lip phases:** long sharp-lip phases exist in which the AS feature may engage twenty or more degrees of the last whorl, as shown in Figure 11.
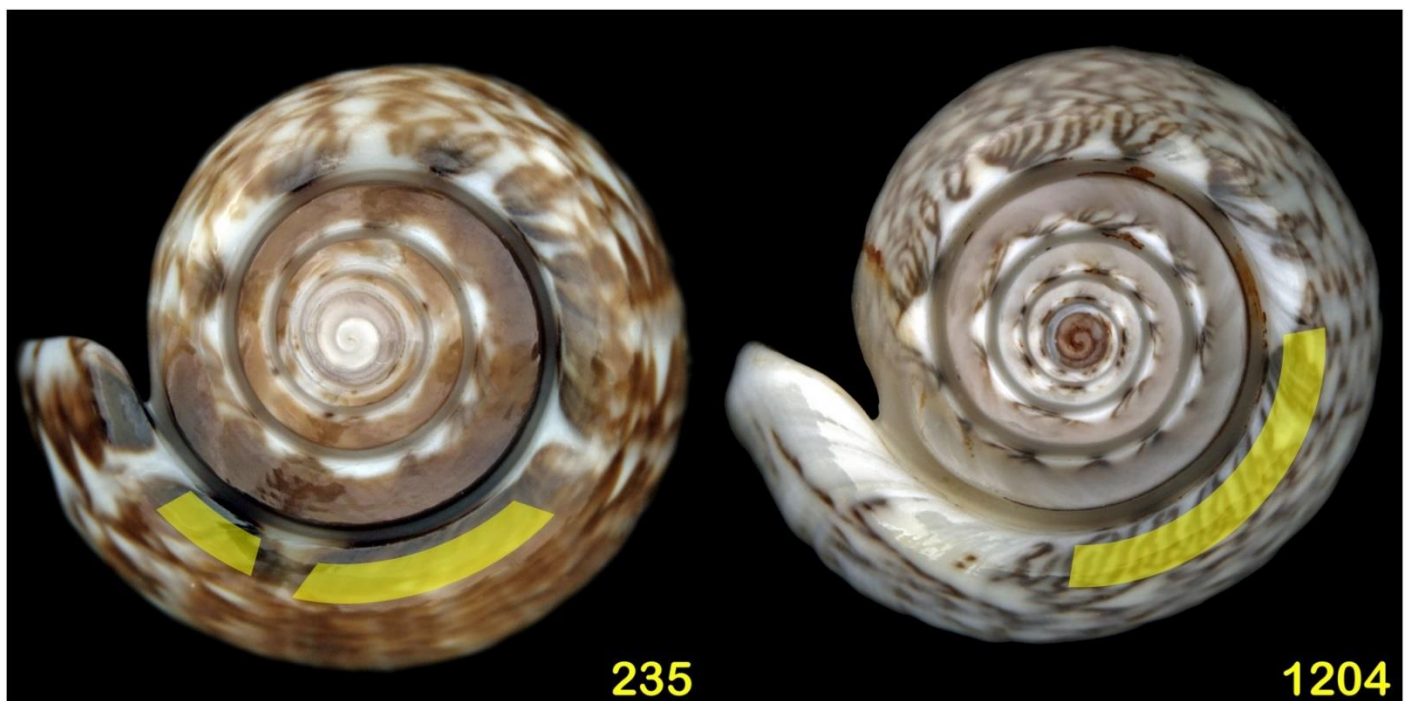
Figure 11. Two examples of AS where lip thinning (as proved by the length of the channel edge segment of the stem-line) appears prolonged.

- **Age-related AS features:** as observed by Strano (2017), sometimes adult or gerontic specimens, such as those illustrated in Figure 12, display a tendency to rarefaction, simplification and reduction of AS features, up to their complete disappearance. But in earlier life too the shape and the number of AS features ("feature mode") may vary with time.
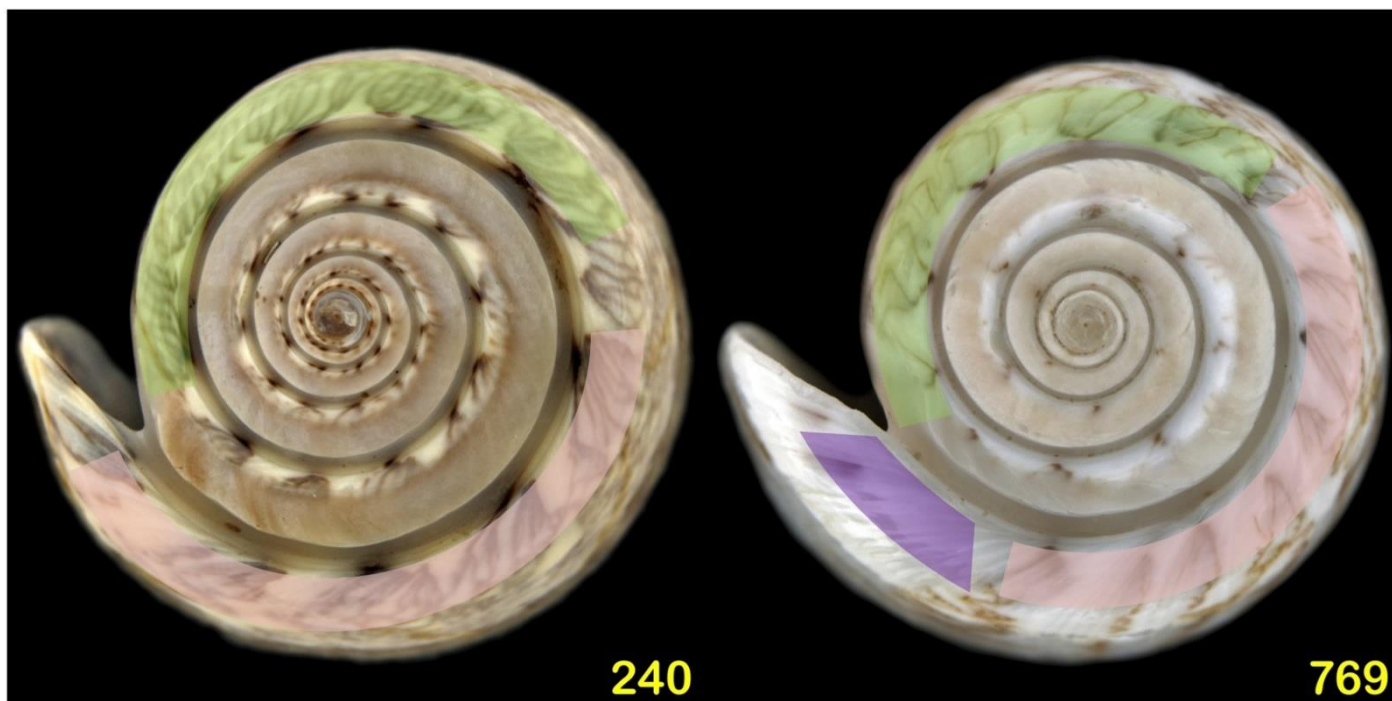
Figure 12. Two examples of AS where age-related variation can be observed. Green shading, feature mode 1 (#240: wide "open hand" features, #769: thin cloak pattern elements, very few strokes); red shading, feature mode 2 (#240: narrower, more proverse features; #769: tightly fasciculate, proverse features); purple shading: gerontic lip.

The uneasily-defined "rest pattern", that includes all the AS ornamentation except the fully developed features, may consist of no pattern at all, or be reduced to the following categories, that can coexist in the same specimen: isolated strokes, minor events, cloak pattern elements.

- **Isolated strokes:** single, unorganized strokes with no apparent relation with other similar strokes: see Figure 13.

Figure 13. Two examples of AS where isolated strokes (shaded in yellow) can be observed.

- **"Minor events":** In several cases, as exemplified in Figure 14 and 15, complexity and completeness of successive AS features may vary. Some of the AS features in the last whorl may look vestigial or incomplete. Compared with fully developed AS features (or "Major events"), these "Minor events" are easily recognizable by at least one of the following parameters:
  o the stem-line doesn't not reach the channel edge;
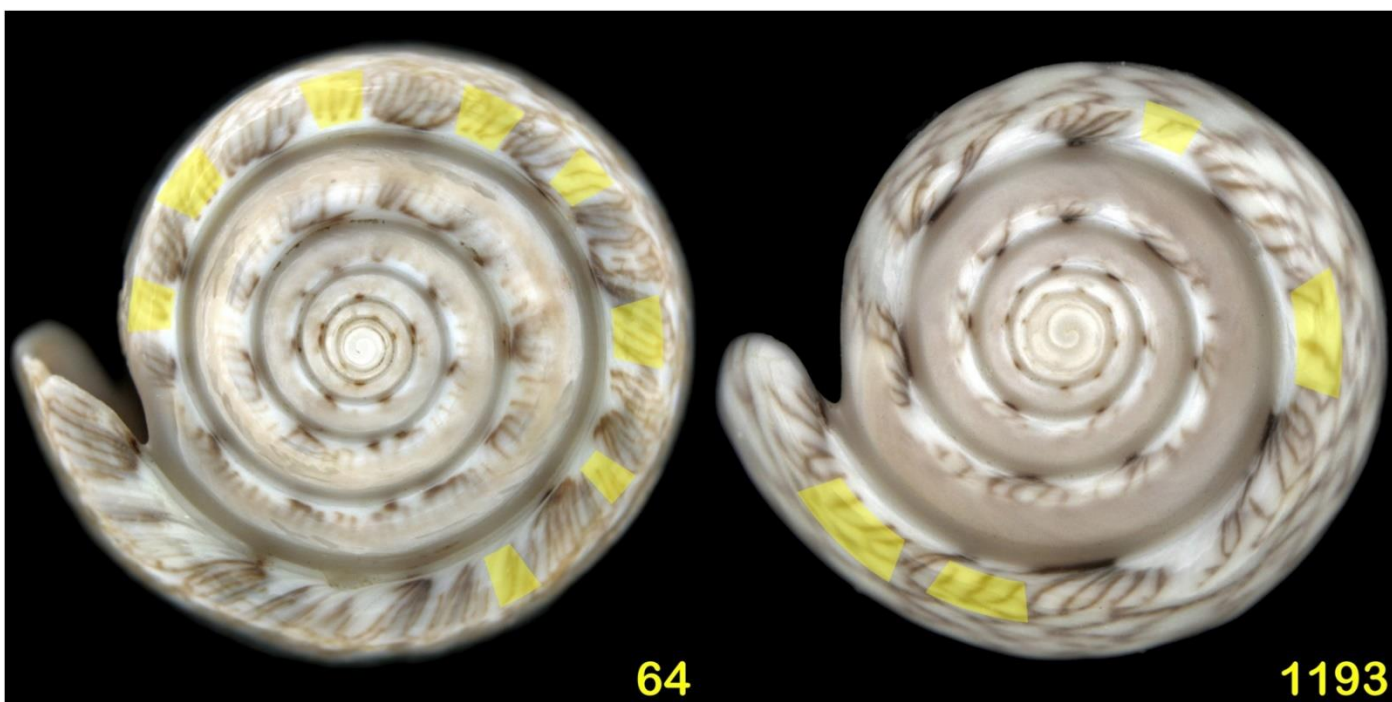 o in the last whorl, the dark spot on the channel edge marking the culmination of the sharp-lip phase is present in some (Major) features, and absent in other (Minor) features;
  o cloak pattern disruption may be almost absent (Minor events) or visible and intense (Major events).
  Intergrades ("Intermediate events") exist. Event intensity is – at least partly – age-related: alongside the gerontic lip, narrow vertical stripes of cloak pattern can often be observed, separated by equally narrow, contrasting pattern-free stripes. But in the shells of non-gerontic adults, intensity variation may occur irregularly: it can easily be imagined that there are good years and bad years in the animal life, and that the intensity of the growth bouts, marked by lip progradation and AS feature deposition, may be directly proportional to the availability of trophic resources in the preceding year (again, Ino, 1949 and Leighton, 1961 should be cited for their work on the influence of food on shell ornamentation).
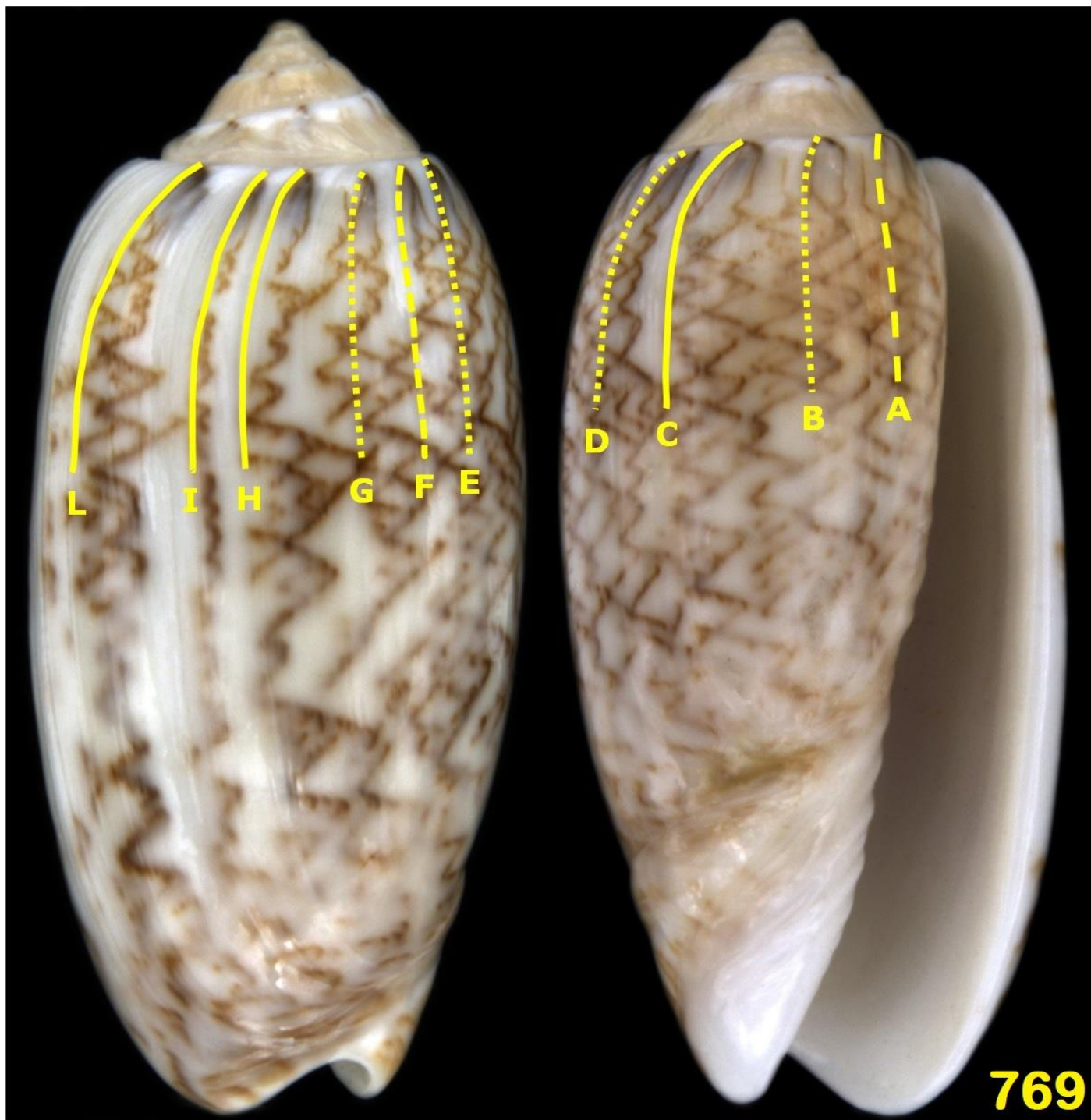
Figure 14. Minor (dotted line), Major (solid lines) and Intermediate (dashed line) cloak pattern disruption events. The ventral view of this specimen of *O. bifasciata*, also appearing in Figure 15, shows how linear elements originated in the cloak can penetrate the subchannel area.

- **Propagation of cloak pattern elements in the subchannel area:** The existence of a transition area implies that – even when the typical subchannel pattern are absent – some degree of cloak-style pattern generation may occur, as shown in Figure 15.
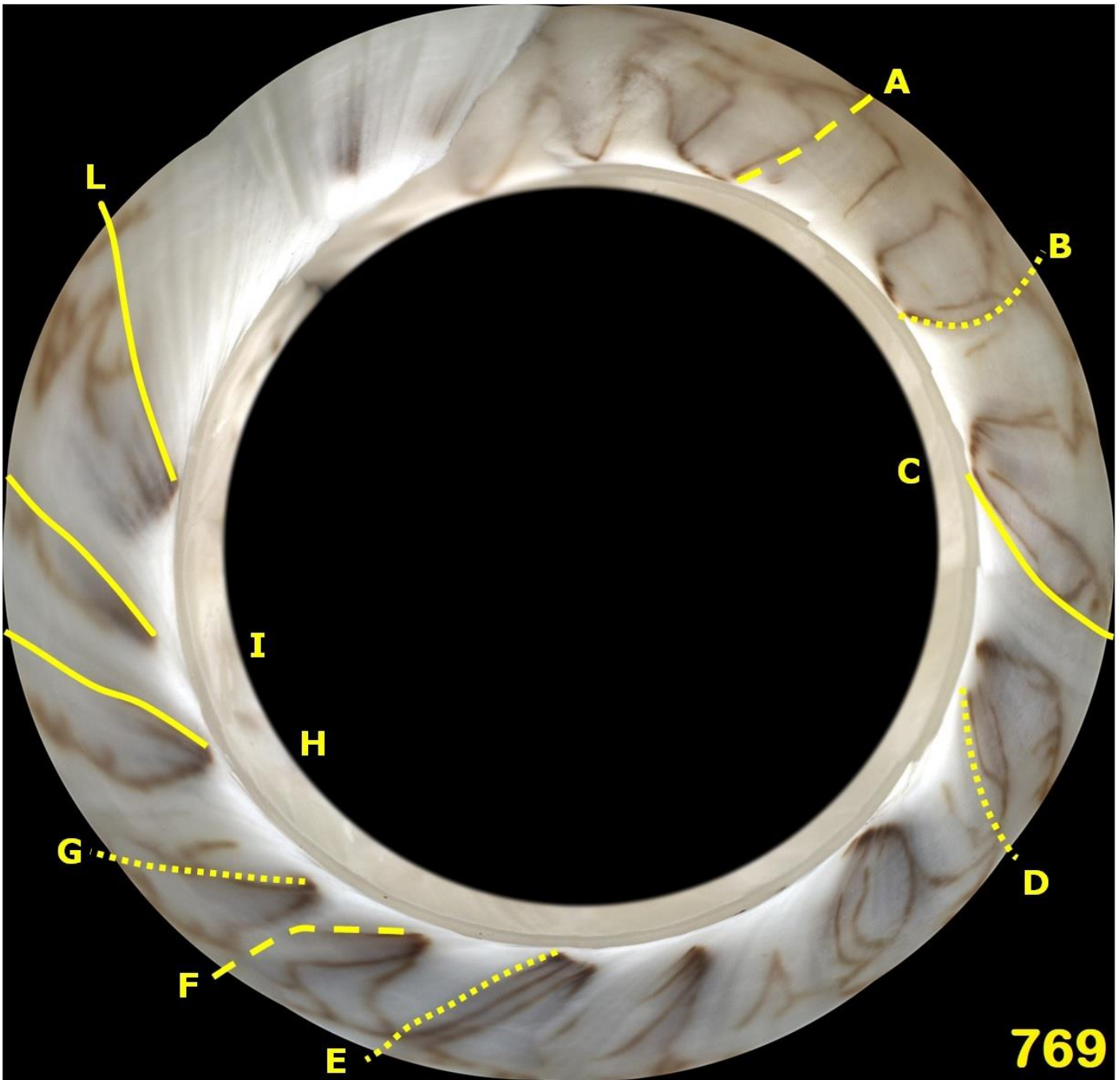
Figure 15. The events in Figure 14 as observable in a peripheral composite photo of the subchannel area, showing: 1) pervasive elements apparently originated in the cloak, or merged with antler-like offshoots from the cloak, almost reaching the channel edge (A-D arc), and 2) the different range of intensity of lip remodeling phases. Letters refer to Figure 14. Minor, Major and Intermediate events are respectively marked by dotted, solid and dashed lines.

- **Monotonous pattern:** in the *Americoliva nivosa* group (see more under), as exemplified by *A. nivosa maya* (Figures 16 and 17) fasciculation may be feeble and inconspicuous. Many, or most of, the lip remodeling events, excluding those in late life, look "minor" and cloak pattern disruption may be minimal: some attention is required to see a disruption that can be observed only in the paraxial alignment of chevron /flammule tips.

Figure 16. The monotonous AS of *A. nivosa maya*: faint discontinuities marking the arrested growth phases. The absence of shaded areas or reference lines is intentional.

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Figure 17. The monotonous AS of *A. nivosa maya*, as seen in peripheral composite photography. Lip is at the top. Compare with Figure 18 to appreciate the different level of feature accentuation. The penultimate feature before the lip edge was partly replicated in the image alignment phase. The absence of shaded areas or reference lines is intentional.
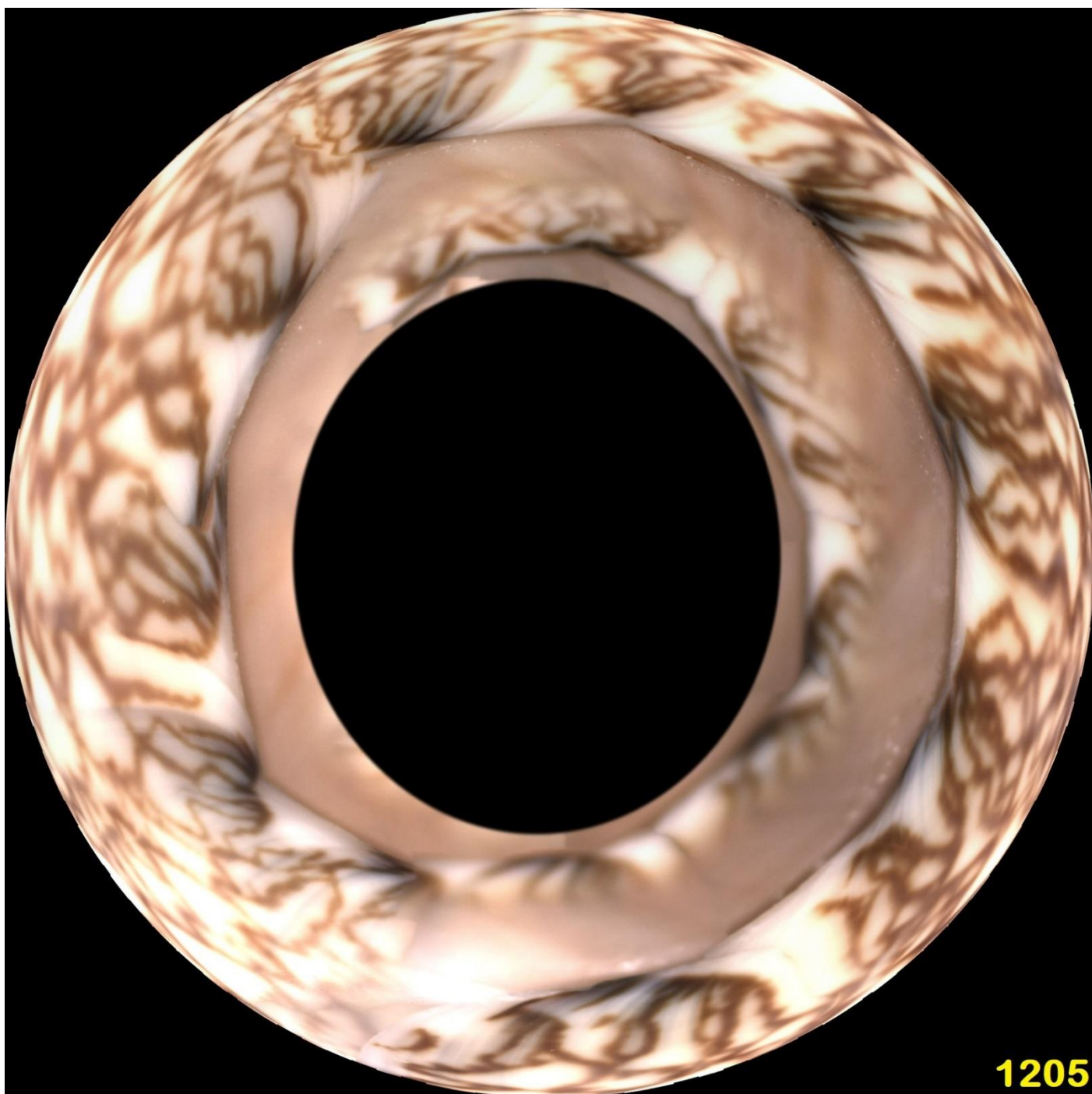
Figure 18. The peripheral composite view of a consistent, well-sculpted AS pattern where all the events are evenly spaced, marked by fully-developed features showing no significant variation for the entirety of the whorl. Lip is at the bottom. #1205 is an undetermined specimen from the *A. reticularis* group, from Martinique, originally attributed to *Americoliva lilacea* Paulmier, 2013.

3.7 The Interspecific Variability of AS Patterns

The intraspecific variability of the subchannel area reverberates at the interspecific level where, along with consistent, unifying traits, also an increasing range of small variations appears, hampering any attempt to group AS patterns unambiguously, meaningfully and consistently. The AS features from different species may share some common traits and differ radically in others or in the way in which they are organized: depending from the perspective, the same combination of characters may be potentially species-specific or may be shared by more species. As documented by Figures 19-21, the "family look" of each species amounts to the combination of a few, sometimes fuzzy, characters that appear as unifying factors only when the shells of similar species

are observed side by side. The at first glance subdivisions proposed hereafter, that may include some flimsy biogeographical inductions, can only be informal and tentative, as mere suggestions that individual and population variability may disavow: a careful examination of the figures will hopefully allow the reader to form his/her own opinion.

- **Cloak Pattern reaching the channel edge:** in *A. sayana* the subchannel pattern is reduced to a barely visible thin stripe at the channel edge, and the cloak pattern extends up (posteriorly) almost to the point of touching the channel. Also, in many *A. bifasciata* the cloak pattern, frequently reduced to a few thin lines, may almost reach the channel (see e.g. #62 in Figure 19 and 20) with branching, antler-like offshoots, but a proper transition zone exists, where typical subchannel strokes may coexist and interact in unclear relation with the cloak pattern elements. Considering the heterogeneity of this subdivision and the widespread range of *O. bifasciata*, no biogeographic relevance can be annexed to this grouping, also considering some similarities with *A. goajira* and *A. circinata*.

- **Disperse strokes pattern ("Hebrew character"-style):** *A. olivacea*, *A. barbadensis* and *A. lilacea* share some similarities, such as a low number (very few in *O. lilacea*) of disperse strokes, that may include lip contour straight-strokes developing in semicircular fashion. Fasciculation is irregular, transition zone is well-developed and well-separated from the channel. Observed in species from Barbados, St. Vincent and Martinique, it may be typical of the southern Antillean Subprovince.

- **"Hispaniola patterns":** the identification of at least one of the *A. jamaicensis* is questionable, especially considering the radical differences in the subchannel pattern. Anyway, quite regular, "sharp-tipped" fasciculations can be observed, with a wide and quite undisturbed transition zone. With declared provenance from the same Antillean latitude (Dominican Republic, Puerto Rico and Haiti for the two *A. zombia*), also this kind of pattern may bear some biogeographical significance.

- **The *A. nivosa* pattern:** the default pattern of this complex, biogeographically diverse subspecies group is made by a dense, almost uninterrupted series of thin paraxial, roughly equidistant strokes and includes many "minor events" (see the preceding pages) where almost complete features don't reach the channel edge. Despite the numerous similarities with *A. goajira* from the Colombian Subprovince, the subchannel pattern of *O. nivosa* sets this species apart. The transition zone is distant from the channel edge and interferences from the subchannel pattern only rarely disrupt the "fence" of regular strokes.

- **The many flavors of *A. reticularis*:** with an extended distribution and a high intraspecific variability, *A. reticularis* is a candidate umbrella species hiding several undescribed taxonomical entities. It's no surprise that, with extreme shape and size variations, also the subchannel pattern is far from consistent. As an example, the stem-line of the AS feature may, or may not, be visible, and its thickness may vary. Once that such a variability is taken into account, the AS loses species-specificity. As an example, two specimens from Martinique, that initially were assigned to A. *lilacea*, look much more akin *A. reticularis* when the AS is considered.

- **Aruban shoulders**: *A. fulgurator* and *A. reclusa* both show well-separated, lightly shaded AS features made of very thin, undecided strokes, no visible stem-line, with more or less pronounced lip contour straight-strokes. Cloak pattern reaches near the channel, with a wide transition zone.

- ***A. goajira* and *A. circinata* – "separated at birth"**: *A. goajira* and *A. circinata*, besides occupying adjacent provinces, share a number of commonalities in their AS patterns that can only be explained in terms of common ancestry and synapomorphy, especially when considering the very similar cloak ornamentation. As in the case of *O. sayana* and *O. bifasciata*, the cloak pattern may occasionally almost reach the channel edge, contending a wide transition zone with the AS features, that usually are well-developed, evenly spaced, and with very few minor events. Lip contour straight-strokes are not particularly relevant, and stem-line segments may, or may not, be visible.

- **Venezuela and Colombia – trouble at the border:** the specimens of *A. porcea* and *A. bewleyi* (including one putative) didn't fall squarely in any of the preceding tentative categories, but share common features with other Colombian / Aruban species including more or less thin transition zone very near the channel edge, so that the cloak pattern may almost reach the channel edge. One may include both species and the very similar Colombian *A. obesina* Duclos, 1840 in the poorly understood

(and improperly named) "*A. tisiphona* complex".

Summarizing, even though it cannot be used as the main, or only, criterion, extended similarity in subchannel pattern provides one relevant additional character to consider in specific determination. Figure 19 shows AS thumbnail images arranged according to the proposed groups, while Figures 20 and 21 show normalized apical views of all the specimen cited in this study, also arranged in order of appearance of each species in Figure 19.

Figure 19. AS thumbnail images grouped following the tentative categories proposed in the text. The specimens of uncertain taxonomical position are outlined in red.

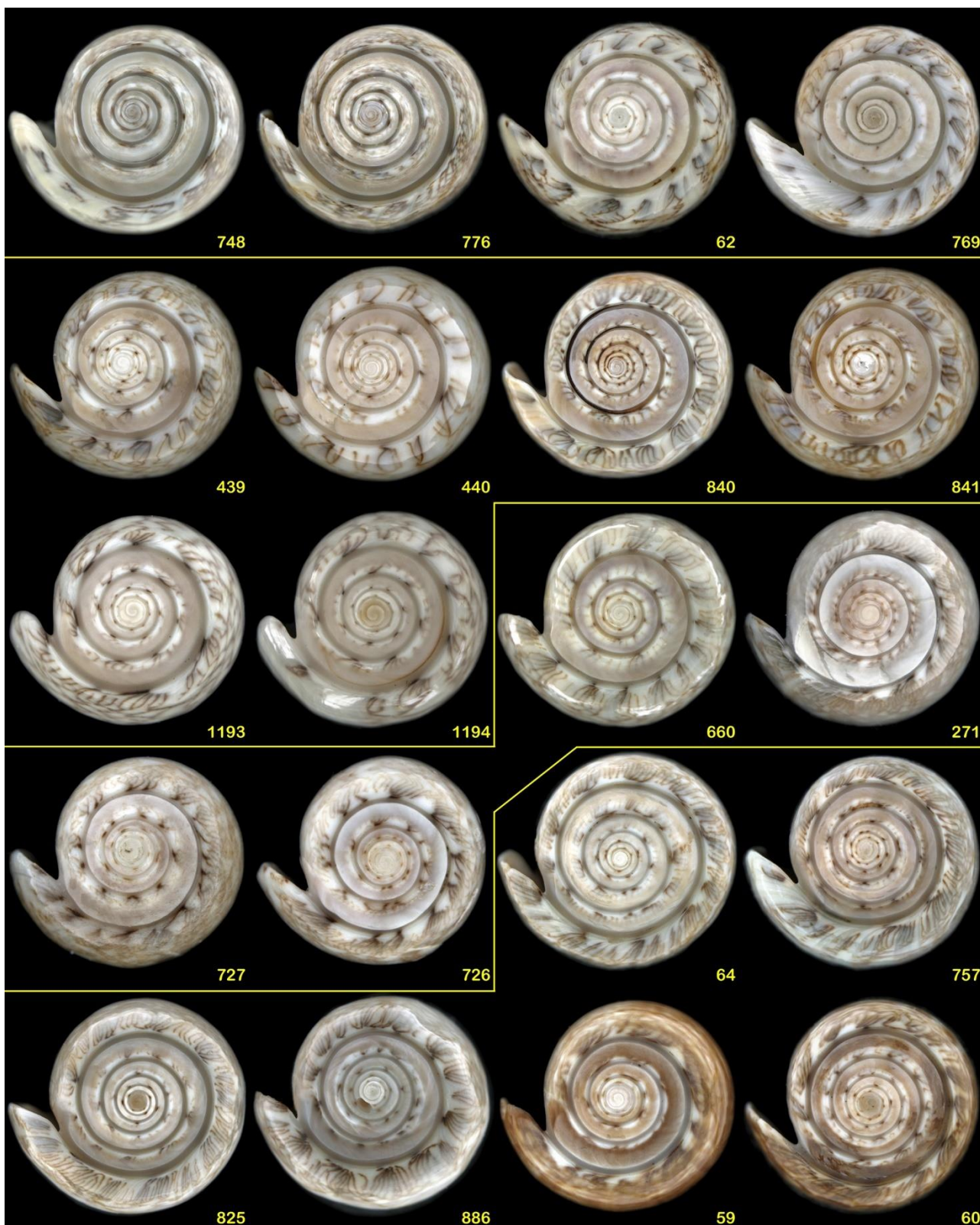**Figure 20.** First group of full apical views grouped following the tentative categorization proposed in the text. For species identification, check text and Table 1.

Figure 21. Second group of full apical views grouped following the tentative categorization proposed in the text. For species identification, check text and Table 1.

4 Results

4.1 American Shoulder and Growth Cycles

In *Americoliva*, the appearance of AS features is coincident with lip thinning phases. Robust, parsimonious but indecisive evidence hints at their coincidence with a rapid-growth phases, a conclusion that needs to be corroborated by destructive investigations. AS features look like promising rapid growth phase markers: their disappearance or rarefaction, marked by some degree of lip thickening, very probably corresponds to periods of slower growth. Periodical variations in trophic resources may influence both the frequency and the degree of development of the features.

4.2 A General Description of the American Shoulder

The following description is given in right to left (leiotropic growth) direction and refers to the most typical case of complete AS feature.

With the exception of populations or individuals with faintly colored or absent ornamentation, more or less regularly distributed elements including fasciculate features or isolated strokes (AS Features) can be observed in the subchannel area of *Americoliva* specimens. With variable rapidity after an interruption or rarefaction, subvertical/paraxial strokes reappear, in more or less rapidly increasing length, and at more or less rapidly decreasing distance from the channel edge: in the apex-up iconographical convention, this progression is defined as ascending. The ascending "stem-line", uniting the upper (posterior) tip of the strokes, apparently follows the adapical movement of a dark blotch appearing at the lip posterior tip (see Figure 7, 8 and 10). The stem-line may be an abstraction, or may be clearly marked by the coalescence of the adaperturally arched upper tips of the strokes. The ascending tract may be the only visible part of the stem-line.

The progression to the channel edge, that constitutes the abapertural (rightmost) part of the fasciculate feature, is marked by an extremely variable number of strokes. In any case, repeated observations confirm that the ascending progression coincides with the lip thinning phase. It can be easily expected that a multi-layered structure such as the Olivinae shell is extended starting from its interior layers, subsequently covered by the outer layers. The initial lip protrusion act is marked by the advance of a dark layer, that may or may not coincide with the white activation layer by Strano (2017), initially uncovered, then progressively covered by an increasingly thicker outer layer. The dark blotch cited above appears to be an artifact of such thinning, and may coincide with the unveiling of a deeper color pattern, as advocated by Tursch & Greifeneder (2001). The generally darker color of the medium layer exposed during the thinning phase may show through behind the upper part of the strokes, as frequently observed in the last part of the ascending (and often in the first part of the descending) tract of the stem-line.

At some point, the series of strokes reaches the channel edge, the posterior/upper external border of the last teleoconch whorl, untraversable by the SGE tip: at that point, the lip is at its thinnest state and the tip of the fasciculate feature appears, in some cases with an intense darkening of both the sides of the external wall of the filament channel. The duration of the stay at the channel edge may vary greatly between different species but also during the lifecycle of any individual: when the stay is short, in other words when the thickening caused by the deposition of the external layer is quick, the fascicule tip can be assimilated to a point, fascicules are triangular, fan-like and tend to be symmetrical, as in the case of the Pacific *Americoliva* that in apical view show the namesake "cogwheel pattern". It may be significant to observe that such a pattern, generated by symmetrical features, is particularly well-developed in relatively thick-lipped species like the Pacific *A. polpasta* Duclos, 1833, *A. truncata* Marrat, 1867 and *A. olssoni* (Linnaeus, 1758). Longer stays result in a dash-like horizontal stem-line that - like the ascending tract - may be the only visible trace of the stem-line. When a horizontal stem-line is visible, the resulting feature is vaguely similar to a human right hand in dorsal view, with the wrist at the channel edge.

Since the contact with the channel edge, paraxial strokes (often, of increasing length) begin to follow the contour of the upper/posterior part of the lip with increasing accuracy, even though it cannot be granted that they mark exactly the lip edge. Where present, one or more adaperturally-arched, thicker lip-contour straight-strokes departing from the channel edge provide a reliable track of the lip shape and position, especially when

they coincide with discontinuities in the cloak pattern or other clues about past lip position (Fig. 10). Their coalescence marks the descending tract of the stem-line.

The descending tract, generated during the shorter or longer lip thickening phase, constitutes the adapertural (leftmost) part of the fasciculate feature: it may miss altogether, and is apparently even more variable than the ascending portion. Usually, during and after the descending phase, strokes rarify, get shorter and increasingly farther away from the channel, then fade into the rest pattern, giving raise to another interval between adjacent features. Intense and apparently irreversible lip thickening was observed only in gerontic specimens, and a very blunt lip is rarely observed.

Generally, thicker lip coincides with temporary rarefaction or disappearance of any pattern, but there are species, including *Americoliva nivosa maya* Marrat, 1871 and *Americoliva nivosa bollingi* Clench, 1934, where fasciculation is quite inconspicuous and stroke rarefaction is both infrequent and irregular. In those cases, it can be stated that the subchannel pattern creation is only marginally affected by lip-sharpening events, or that such events are frequent and inconspicuous.

Species-specificity of the AS is low, especially considering that the individual variability of the subchannel features is very high (in Figure 20, compare e.g. the two *A. nivosa maya* #886 and #825, the two *A. barbadensis* #840 and #841, the two *A. porcea* #580 and #746), and even the last whorl of any individual shell can show differently developed features, including radical differences (see e.g. the age-related variations in Figure 12). Furthermore, similar features occur in different species - devoiding the AS patterns of a reliable use as the sole specific character. This notwithstanding, some degree of family look among the AS of conspecific individuals can be observed, more in general than in particular terms. As an example, the presence and the extension of the subchannel area and of the transition zone is species-specific, and extension and some recurring detail exist, as e.g. what stated above about the inconspicuousness of fasciculations and the high density of thin strokes in *A. nivosa maya* and *A. nivosa bollingi*.

Figure 22 and 23 are examples of "AS analysis", relative to eight specimens of six different species, in application of the concepts above illustrated: a Pacific species, *Americoliva spicata* (Röding, 1798), is also included to test the applicability of the general description also to specimens outside the study area.

5   Conclusions

This work, limited to a few species of *Americoliva*, besides providing a more exhaustive description of the diverse and complex "American Shoulder" phenomenon, sets a robust correlation between, on one side, lip thinning/thickening and, on the other side, the creation and the structure of the typical AS features, in particular of coalescent/fasciculate features at the filament channel edge. Works as Tursch & Greifeneder (2001) and Sterba, 2003 and, more recently end exhaustively, Strano (2017), clarify how the occurrence of lip thinning obligatorily marks periodical (indicatively, yearly in *Musteloliva*) growth phases. The alternation of rapid and slow phases in the Olivinae growth cycles, coincident with cyclical, extensive remodeling of the shell provides the most parsimonious explanations for periodical events such as the appearance of significant pattern features. Transitively, in a biological frame AS features may most parsimoniously be related with the rapid growth/sharp lip phase observed by Strano (2017) in *Musteloliva*.

Three alternative hypotheses were proposed about the nature of such a correlation, with robust support for a full coincidence between AS features and rapid growth phases, but conclusive evidence will only be reached by applying the methods by Strano (2017) to multiple spiral sections of each specimen in a relevant sample of *Americoliva* shells. Metaphorically, the attention of Strano, 2017 was concentrated at the shell's equator, while this is a study at arctic latitudes: the author leverages the discoveries by Strano and confirms their value even outside their original scope of application. If the relation of subchannel pattern features and growth cycles is established for more than one genus, it can be hypothesized that it's a subfamily, or family, character. In that case, future studies may ascertain whether the subchannel pattern can be regarded as a reliable age indicator for all Olivinae, and may try to define the general criteria for its translation in proper time units, in which case

the concept of clockwise growth would cease to be a metaphor – the dial provided by the apical view would in fact allow a precise age reading of any Olivinae shell by a simple count of the subchannel features.
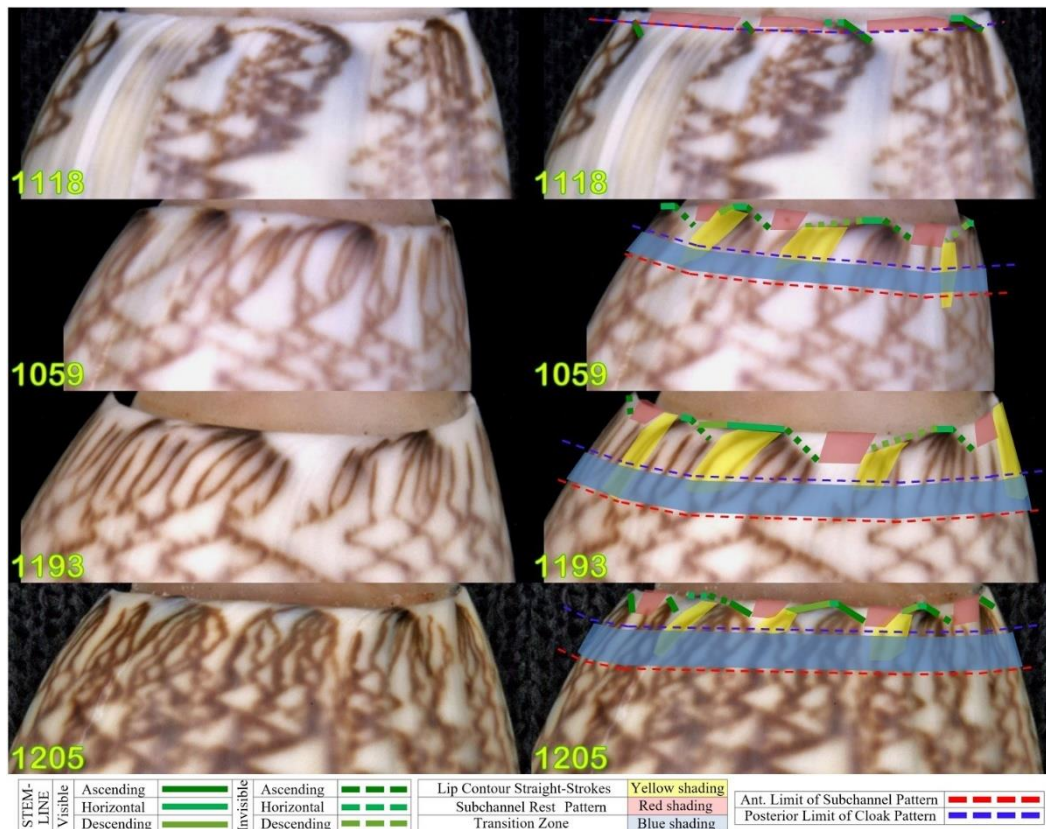

Figure 22. Highlighted elements of the typical AS pattern. #1118: *A. sayana sarasotensis* Petuch & Sargent, 1986 (Sarasota Bay); #1059: *A. reticularis ernesti* Petuch, 1990 (East Panama, unconfirmed); #1193: *A. lilacea* Paulmier, 2013 (Martinique); #1205: *Americoliva sp.*, akin to *A. lilacea* (Martinique)
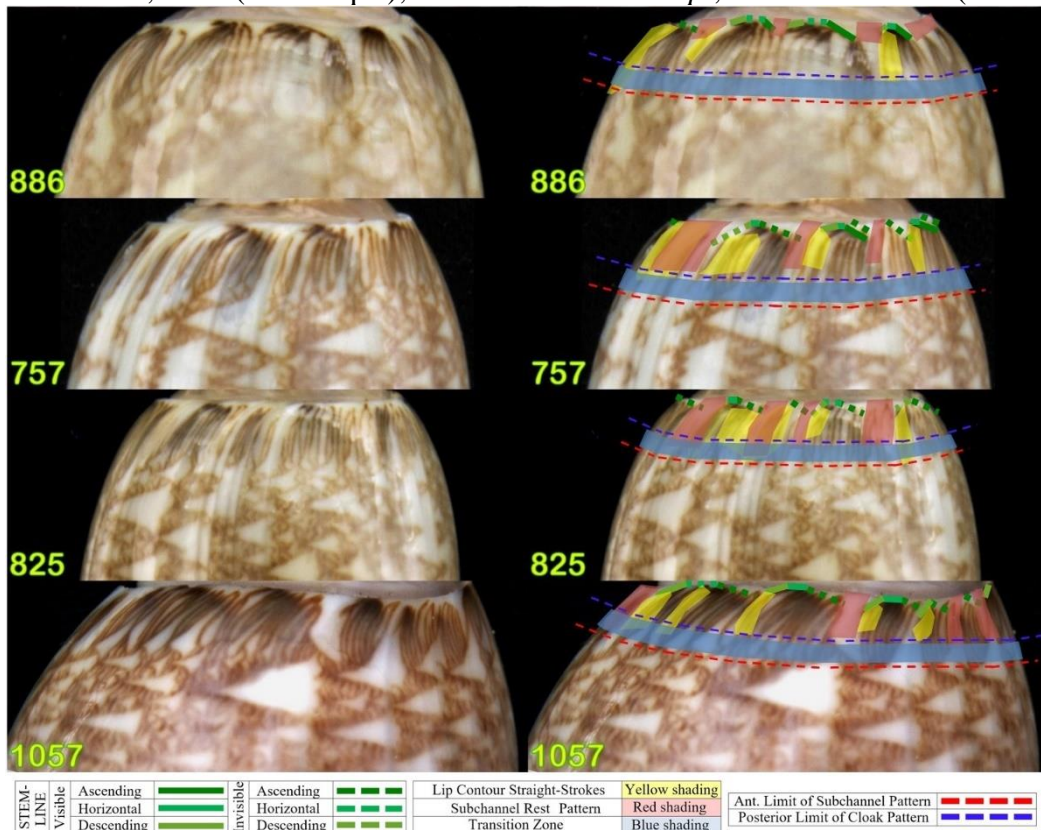
Figure 23. Highlighted elements of the typical AS pattern. #886: *A. nivosa maya* Petuch & Sargent, 1986 (Yucatan); #757: *A. nivosa bollingi* Clench, 1934 (Tampa Bay); #825: *A. nivosa maya* Petuch & Sargent, 1986 (Cabo Catoche, Yucatan); #1057: *A. spicata* (Röding, 1798) (San Carlos Bay, West Mexico).

The applicability of the Chevron Paradigm by Tursch & Greifeneder (2001) to the subchannel area of *Americoliva* was questioned on solid bases, and an alternative hypothesis was outlined, based on the still elusive concept of "stroke", a definition needing much refinement, but indispensable to provide an accurate description of the subchannel features. While those features were treated extensively, and the context of their appearance was exhaustively outlined, the moment-by-moment description of their creation is still sketchy, because of an incomplete knowledge of the events in the subchannel area, due to the purely conchological nature of this study and to the limited number of specimens considered.

With regard to species-specificity, in a general sense the AS patterns show a higher degree of variability than desirable, both at specific and (sub)generic level. The common-sense statement about the high intraspecific variability and low interspecific variability of Olivinae, and of *Americoliva* in particular, is once again confirmed. Anyway, provided that it's not used as the only criterion, the subchannel pattern may concur to species determination, particularly for the Western Atlantic / Caribbean / Gulf of Mexico *Americoliva* shells. For that reason, the author recommends that any nomenclatural act related with Olivoidea, with particular reference to the description of new taxa of Olivinae, includes a more accurate an extensive description of the subchannel features, based on an adequate number of specimens. After all, as Sterba (2003) warns, «Key-determination features are the pattern of the body whorl directly below the filament channel and the fasciole».

To close with an American analogy, the truth about the American Shoulder is half concealed, half disclosed - like the unveiling medium layer at the beginning of the growth cycle or, much better!, like some notable banner under a fitful breeze. The dim-sighted author, whose reluctance to sacrifice specimen shells resulted in an indecisive solution, wishes the best of luck to whomever, after venturing in the lingering mist, will be there to catch the gleam of a glorious, full disclosure (Key, 1814).

6   Acknowledgements

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8   Appendix 1 – Glossary

Note: see also Figure 1.

ANTERIOR BAND = the anteriormost, ribbon-like ornamented band of the body whorl.

ABAPICAL = pointing away from the shell's apex.

ADAPICAL = pointing at the shell's apex.

AXIS = the adapical/abapical longitudinal coiling axis of the shell, usually marked as "Y axis".

AXIAL = the direction marked by the axis.

CHANNEL EDGE = the edge of the filament channel, marking the posterior limit of the body whorl.

CHEVRON PARADIGM (CHP) = the idealized model of cloak pattern generation by Tursch & Greifeneder (2001) (see also Fig.2 and its caption), based on the asynchronous coordinated activation of adjacent glands in the SGE by the wavelike propagation of special chemical signals. Diachronically, the propagating signal determines the appearance of the well-noted reticulate and flammulate patterns. Mutual elision on collision occurs whenever two chevron lines collide in the same reference grid cell: physiologically, the involved gland at the intersection of two propagating waves enters quiescent state after discharge, and stops further signal propagation.

CLOAK = the area covering the last whorl, excluding its anteriormost and posteriormost parts.

CLOAK PATTERN = the typical pattern of the cloak.

COALESCENT = attribute of the strokes that appear connected in a feature.

CONVERGENT = attribute of the strokes that appear to converge to / diverge from a point.

DOWN, LOWER = improper synonyms of anterior, with reference to the "apex-up" seashell iconography.

FASCIOLE = the band-shaped structure that lies belt-like on the anteriormost part of the body whorl, engaged in the siphonal canal and partially covered by the parietal callus. In Olivinae, it is divided into anterior and posterior band.

FEATURE = an "AS Feature" is the peculiar coalescent multi-stroke pattern, as opposed to the featureless "Rest Pattern".

FILAMENT = by antonomasia, the posterior mantle filament of the *Oliva* animal, a narrow muscular and glandular structure of uncertain, most probably multiple role that may be both sensory and defensive or that, as Sterba (2003) supposes, may concur to the formation of the spiral callus. At rest, it's housed in the filament channel. Oliva animals are also endowed with an anterior mantle filament, that protrudes from the anterior notch of the shell and is kept wrapped at the base of the siphon. Its function is ignored.

FILAMENT CHANNEL = the spiral recess that marks the spiral suture in the Oliva shell and that houses the filament at rest.

ISOCHRONE = an imaginary line that unites all the point of the shell surface, created at the same time. In the majority of the cloak pattern, isochrones are paraxial and do not coincide with lines, but at its outskirts (subchannel area and anterior band) the anteriormost/posteriormost part of an isochrone may coincide with a

stroke.

LINE = a diachronic (dot-by-dot) linear feature generated under the CHP.

PARAXIAL = parallel to the shell's coiling axis.

PARIETAL CALLOSITY = the callus facing the lip. It's the site of the parietal plications.

PARIETAL PLICATIONS = the plicae ("folds") occurring on the adaxial surface facing the lip, also called "columellar plications", an improper definition for the Olividae, that lack a columella because the internal teleoconch whorls are dissolved as the shell grows.

REST PATTERN = the pattern of the subchannel area between two consecutive features.

SHELL GROWING EDGE (SGE) = a synecdoche that refers to the linear paraxial arrangement of pigment-secreting glands at the mantle edge, laying down the small dots that compose lines and other more complex pattern features.

SPIRAL = the transversal direction perpendicular to the shell's coiling axis.

SPIRAL CALLUS = the callus following, and partly covering, the posterior spiral filament channel.

STEM-LINE = a linear pattern element usually generated by coalescence of strokes, from which the strokes seem to depart. May be partly, or entirely, invisible.

STRAIGHT-STROKE = a stroke that is laid down all-in-one-shot. As such, it lays on an isochrone.

STROKE = a linear pattern element limited to the subchannel zone, laid without the constraint of the CHP. The term is coined with reference to a brush stroke in a painting. Stroke generation may imply the simultaneous activation of adjacent pigment-depositing cells, or other violations to the CHP and – while not necessarily instantaneous – may require a much shorter time than an equally long, dot-by-dot line. Strokes are usually clearly different in thickness and color from the cloak pattern lines, and do not develop into chevrons or flammules.

SUBCHANNEL AREA = the posteriormost strip of the body whorl, adjacent to the channel edge.

SUBCHANNEL PATTERN = the pattern of the subchannel area.

TRANSITION ZONE = the area of the body whorl between the subchannel area and the cloak, where cloak pattern and subchannel pattern overlap and interfere. "Thin" or "thick" refer to its antero-posterior extension.

UP, UPPER = improper synonyms of posterior, with reference to the "apex-up" seashell iconography.