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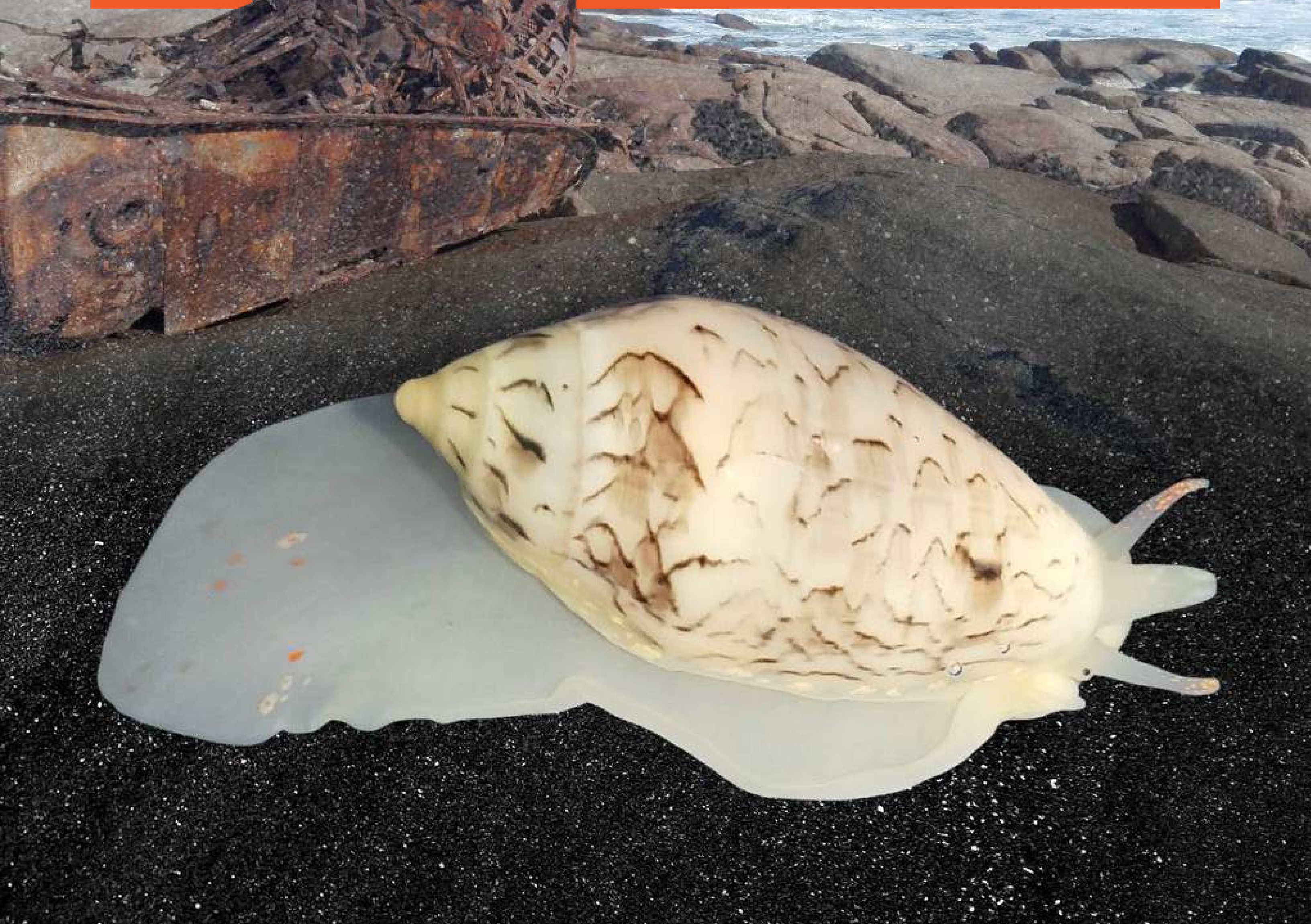

Cuspivolva from Australia

"Clockwork Olive"

Diet and Growth of *P. macroptera*

Dissona from Indonesia

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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 presence in the American olives) 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 peculiar pattern 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 exhaustive descriptions of American Shoulder patterns in new nomenclatural acts involving the (sub)genus *Americoliva*.

KEY WORDS *Americoliva*, **"**American Shoulder" patterns, "Chevron Paradigm"

INTRODUCTION

Terminology and abbreviations

A glossary is proposed in Figure 1 and under Appendix 1. Terminology is mainly from Tursch & Greifeneder (2001), with modifications and integrations. The nomenclature of shell layers by Sterba (2003) 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). Starting from the innermost, 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 (except in the case of *Vuilletoliva splendidula* (Sowerby, 1825), which is endowed with one more outer layer), 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).

Aims of this study

This contribution on the *Americoliva* shoulder patterns is aimed at:

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

The distinctive ornamentation of the Olivinae shells has attracted the attention of many authors: among the outstanding works of the last decades, Tursch & Greifeneder (2001) should be cited first. Their "chevron paradigm" (CHP), mathematically supported by computer based algorithms, evolved from those by Meinhardt (1998), elucidates the mechanism of generation of any color pattern observed on the surface of the cloak of an Olivinae shell. While in their entirety those patterns 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 restricted to the posterior part of the whorl (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.

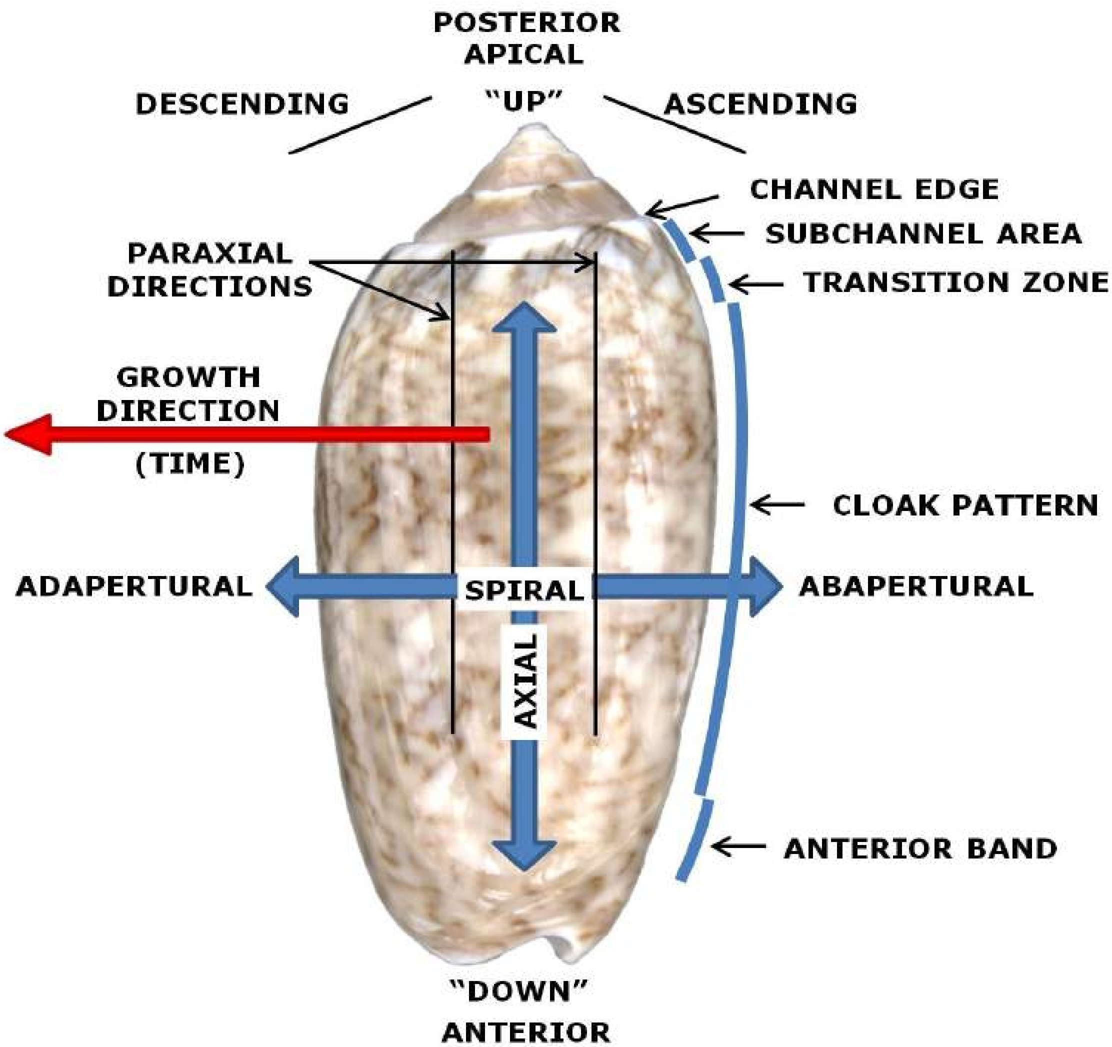

Figure 1. Olivinae shell topology as adopted in this paper. See also the Glossary.

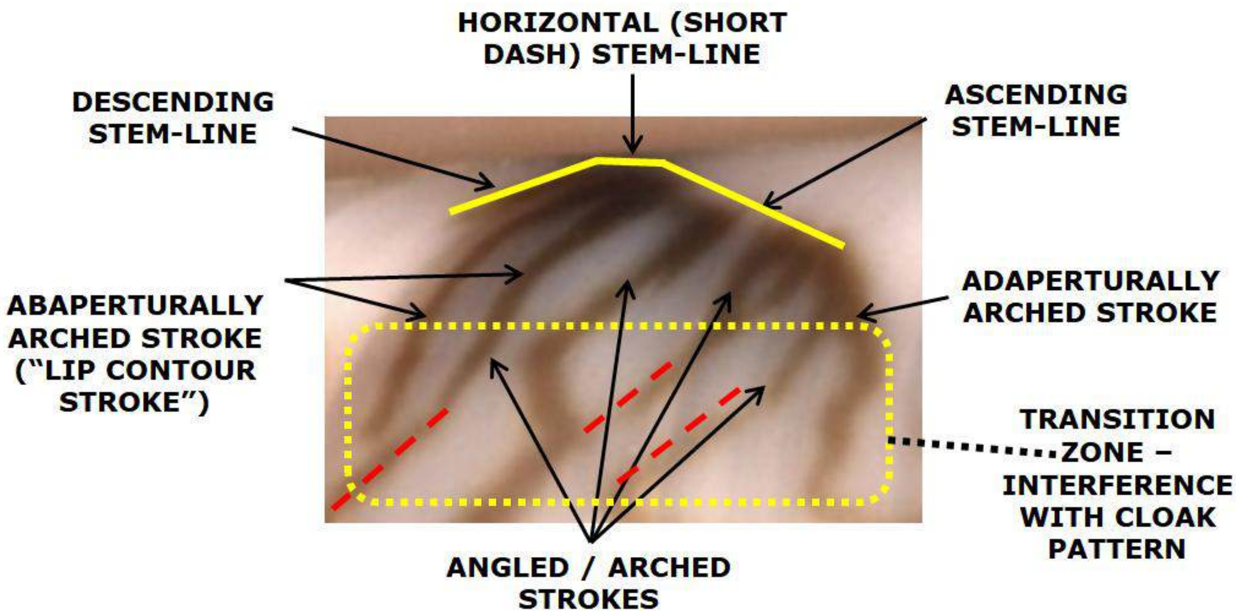

Figure 2. A typical AS Feature (of specimen $1205) – observe how the strokes' lower (posterior) tip may trigger the propagation in the transition zone of "children-lines" compliant with the CHP (red dashed lines). #1205 is an undetermined specimen from the *A. reticularis* group,

Americoliva (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 as a synonym of *Oliva* Bruguière, 1789 ([https://www.marinespecies.org/aphia. php?p=taxdetails&id=815486](https://www.marinespecies.org/aphia.php?p=taxdetails&id=815486)), 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 as including all the species formerly included in *Strephona* Mörch and the newer species created after the formal institution by Petuch (2013) ([https://www.olivirv. myspecies.info/en/ taxon-pages/americoliva](https://www.olivirv.myspecies.info/en/taxon-pages/americoliva)).Type species is *Oliva sayana* Ravenel, 1834) includes species from the Western Atlantic / Gulf of Mexico / Caribbean Area, from the Pacific Central American provinces, and from Eastern Atlantic: all the species show peculiar shoulder patterns known as "American Shoulder" (AS), still lacking an exhaustive description. This study will throw a first shoulder shove to this issue. Figure 1 and the glossary provide the basic concepts needed for the discussion: 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.

Coordinate distortion at the cloak's edge

The area of increased adapical shell curvature known as "shoulder" is 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) developed a computer-based model both for Oliva growth and for pattern generation, reminiscent of, but different from, the more random-based software by Meinhardt (1998). Their subchapter "Special cases. shoulder patterns" demonstrates 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. The movement of the SGE in the distorted shoulder reference grid is the purely geometrical reason of pattern differentiation in that area. At sub-points 9.7.1 and 9.7.2, Tursch & Greifeneder (2001) 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 pattern in the subchannel area including paraxial, vertical or subvertical elements (the copyright-protected, detailed images by Tursch & Greifeneder (2001) are not reproduced here also because for their full understanding the entire accompanying text would also need to be reproduced). Such unquestioning reliance on the CHP as a diagnostic character is analyzed and criticized below.

Specimen			**Species of *Oliva* (*Americoliva*)**		**Locality**	**Lip Condition**		
Count	**#**	**Size mm**	**Sp. #**	**Name**		**Thin**	**Intermediate**	**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				☐	☑	☐

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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 Peninsula, East Mexico	☐	☑	☐
21	886	54.1			Yucatan Peninsula, East Mexico	☑	☐	☐
22	439	31.3	12	*olivacea* Marrat, 1870	Rapid Point, Union Island, 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.

The Oliva growth model by Giorgio Strano

Ornamental pattern evolution 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 that periodically impact both the ornamentation and the structure of the shell, marking relatively rapid phases of shell restructuring interspersed among longer rest phases, with an indicatively yearly recursion. Rather than a juvenile character, the sharp lip is demonstrably a recurring if infrequent condition, Strano (2017) suggested caution when applying this character 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, even though the tightening of rest-structures in the lip of gerontic specimens may impede their counting. By the way, the last whorl of 13 specimens of *O. mustelina* Lamarck, 1811 and *O. mustelina virgata* Sterba, 2005 from the author's collection brings from 9 to 13 (on average, 11) simple subchannel features, consistent with both the last whorl's number of years in the statistic growth curve in Figure 3 by Strano (2017), and the average number of AS features in the last whorl of the 38 specimens figured in this paper.

Strano (2017) worked with mid-axial full-girth sections, at the SGE center, without any special attention to the subchannel area. Yet, the relevance of Strano (2017) for the aims of this study stems from the obligatory association between lip thinning and rapid growth: no evidence of lip thinning without shell rapid growth, nor of shell rapid growth without lip thinning was reported by Strano (2017).

Transitively, other phenomena coincident with lip thinning, including the generation of the coalescent/fasciculate AS features, 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, can corroborate the possible relation between growth cycles and the AS.

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. A set of 38 Western Atlantic (including Gulf of Mexico and Caribbean) *Americoliva* 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 below. 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 availability and quality, with no particular concern about systematics. The author is solely responsible for any misidentification of the specimens, some of which were unaccompanied by reliable locality data, a minor shortcoming to the purpose of this study. 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 specimen was included to investigate pattern consistency.

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.

To explore the correlation between lip thinning and the creation of AS features, separate pictures of the inside and the outside of the apical lip extremity were taken, with an 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 where 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 14, 16 and 17) 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.

DISCUSSION

The paradox of the AS and the crisis of the Chevron Paradigm

Due to its the complexity, the subject of the AS was avoided even by keen investigators with huge collections and decades of experience, such as Tursch & Greifeneder (2001). Rather than providing a structured description of the AS, authors get by with just a few drawings and some general examples. When addressing this recalcitrant problem from the heights of his 38 specimens, the author is so reckless to start by questioning the conclusions by Tursch & Greifeneder (2001). In fact, one of the reason 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, dot-by-dot 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

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layer is involved and regardless of reference grid distortion (the latter may account for curvature, not for convergence). In Figure 3A-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 3E shows the standard application of the CHP in translational sweeping mode (right to left) with successive generation of three chevrons (as exemplified in Figure 2) while Figure 3F 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 3F 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.

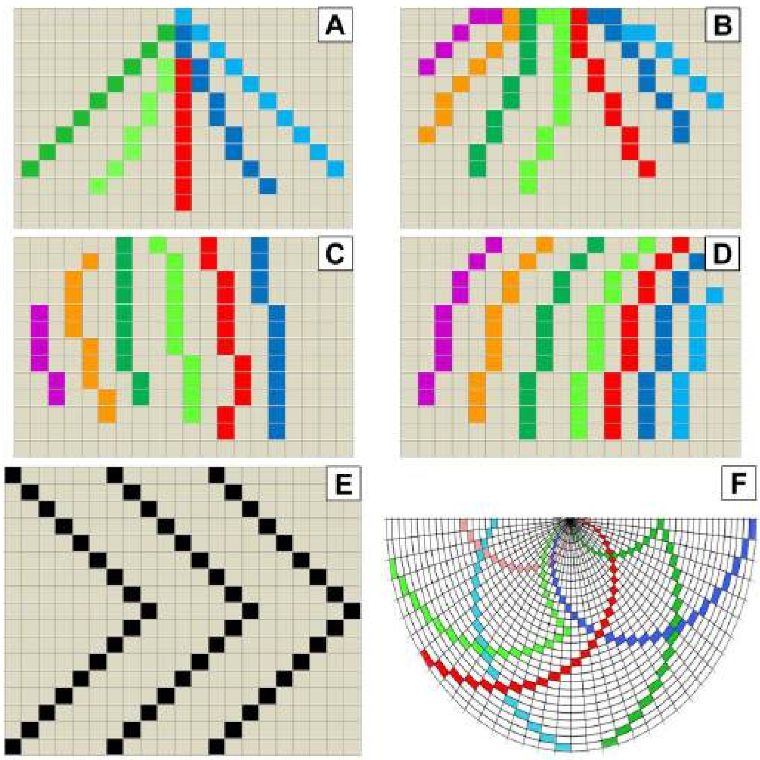


Figure 3. Incongruence between the Chevron Paradigm and the shape of AS features. A: "Cog tooth" (Pacific *Americoliva*, but also partly visible in e.g. #726); B: "Open Hand" (e.g. #1205); C: "Fence" (e.g. #825); D: "Lip contour straight-strokes" (e.g. #757); E: translational CHP; F: Rotational CHP.

It can be easily understood that there is no way to reconcile the two flavors of the CHP, 3E and 3F, with the lines composing the four reference AS features. Moreover, even hypothesizing that the CHP had some secret way to circumvent its own rules, and were capable to retrogradate or to follow isochrones, the application of the CHP to fasciculate features such as Figure 3A and 3B 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, the glossary and Figure 2 disclosed the term "stroke", a concept flexible enough to accommodate both the author's many uncertainties and his few certainties (also some anterior band features which is outside the scope of this paper, observed in *Americoliva* as well as other genera of Olivinae, could be defined as strokes).
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;
- 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 dot-by-dot 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 shown in Figure 2 and 9, by examining the lower (posterior) part of an AS feature it's frequent to observe diachronic "cloak-style" lines obviously triggered by the anterior tip of a stroke ("children-lines"). The reverse wasn't observed, maybe because reverse stroke generation triggered by the 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, 19, 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 4.

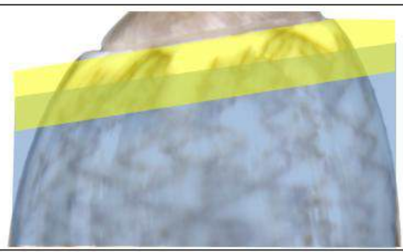
Position	Acronym	Name	Kind of pattern element	Mode of generation	Chevron Paradigm applies?
	SA	Subchannel Area	Stroke	Quick / instantaneous	NO
	TZ	Transition Zone	Anterior (lower) tip of strokes Occasionally, Lines	Occasionally, strokes may trigger lines Occasionally, line generation may occur	Partly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

Figure 4. Pattern Generation Modes in the Subchannel area.

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.

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 6.

Figure 6 shows both sides of the adapical extremity of the lip 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 19 and 20 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 7 shows both sides of the adapical extremity of the lip, 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.

AS features and growth cycles

The obligatory association between lip sharpening and rapid growth established by Strano (2017) allows to hypothesize that the AS features may mark rapid growth phases. The detail of the lip shown in Figures 5-7 is too small to observe overall color discontinuities or color bands inside the aperture, but can be used

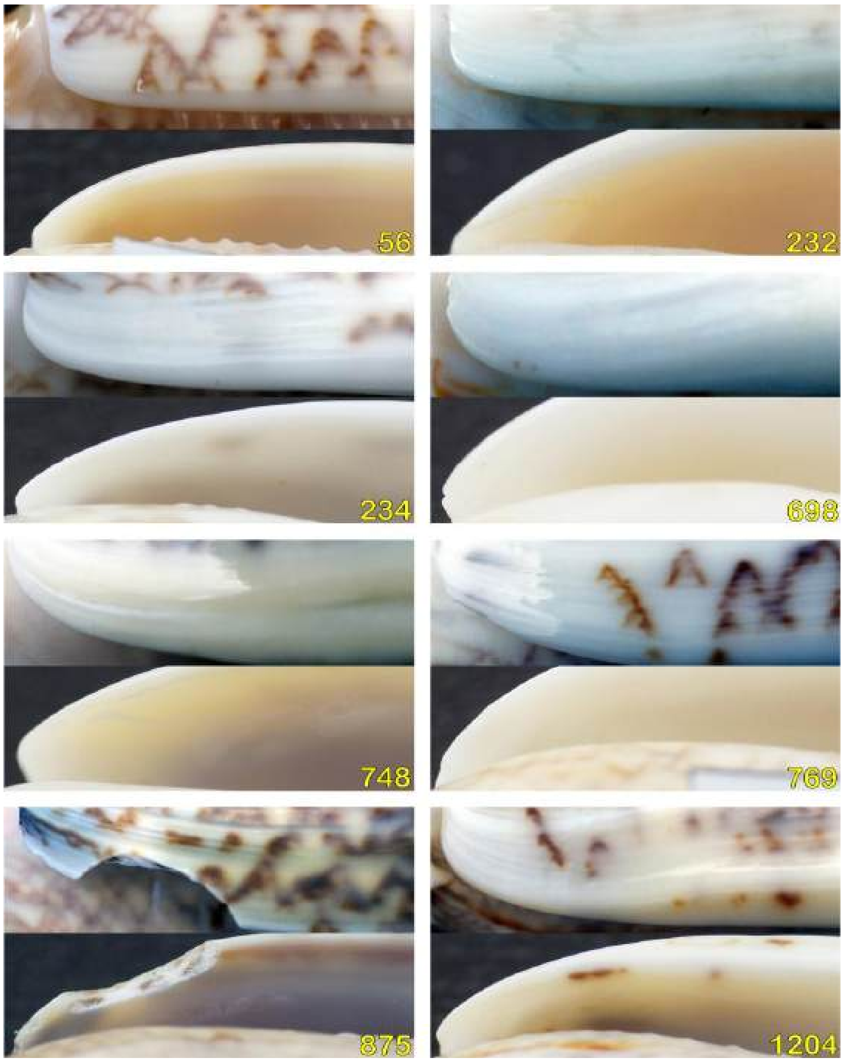


Figure 5. Thick-lipped specimens. The number refers to specimen # in Table 1. For each specimen, a couple of images (below: internal side, above: external side) of the adapical termination of the lip is provided.

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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 5 (#875)
  - Figure 6 (#176, #746, #776)
  - Figure 7 (#64, #757, #825)
- Cloak pattern disruption (see also "Minor events" more under):
  - Figure 5 (#56, #234, #769, #1204)
  - Figure 6 (#176, #235, #746, #775, #776)
  - Figure 7 (#62, #64, #240, #271, #497, #726, #727, #757, #825, #843, #1194)
- Bulging lip:
  - Figure 5 (#234, #698, #748, #1204)
  - Figure 6 (#493)
  - Figure 7 (#497, #757, #840, #1194)

The case for AS features as rapid growth markers 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.

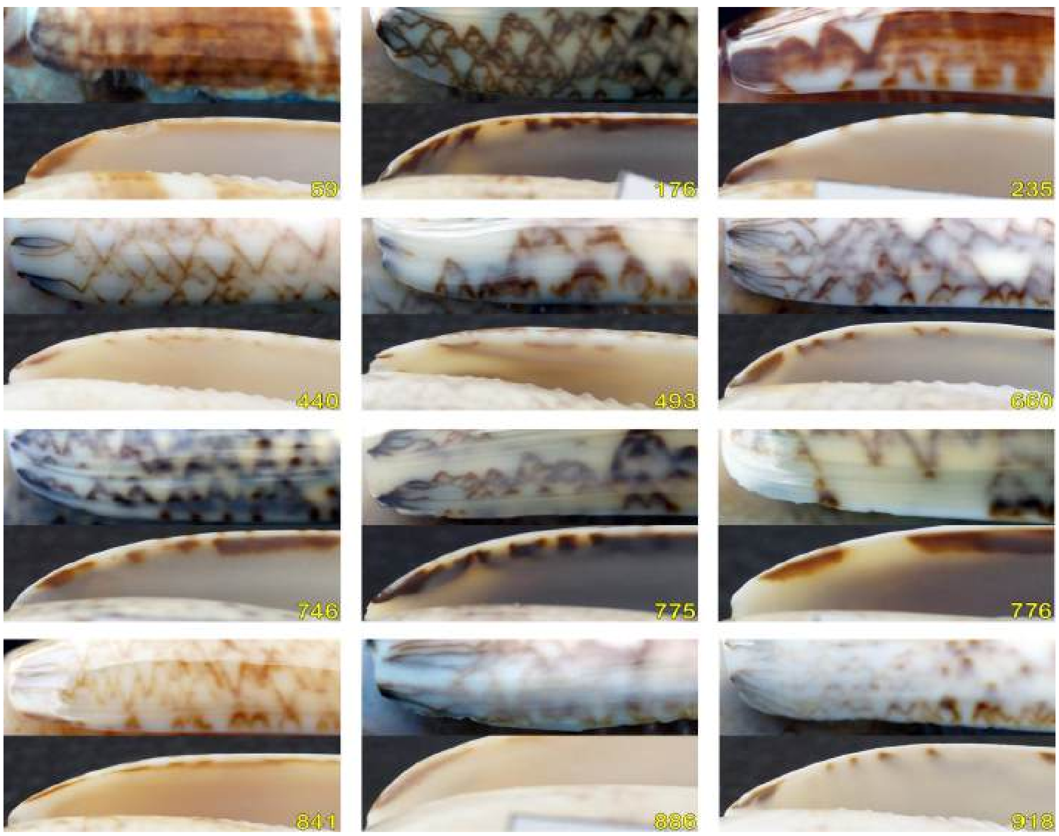

Figure 6. Sharp-lipped specimens. The number refers to specimen # in Table 1. Images show the adapical termination of the lip, mostly dark brown.

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 13 and 14 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 8 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.

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 19 and 20 allows one 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, established by Strano (2017) for *O. mustelina* may apply also to *Americoliva* (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 subchannel marks), in which case the last whorl may cover up to 12 years.

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Figure 7. 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.

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). 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.

The creation of AS features: a tentative account

Figures 6 and 7 provide some hint 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.

By reviewing Figure 8 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 the 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 9).

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.

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):** when compared to the cloak, the subchannel area is subject to an higher number of constraints, including reference grid distortion and paradigm conflict in the transition zone, and consequently to an higher variability. As an example, while the CHP can be simulated by a rather simple computer program that generates life-like renditions of the cloak pattern, that's not the case for AS patterns that (besides showing some degree of interaction with the cloak pattern in the transition zone) seem controlled by a fuzzier and more complicate set of rules, some of which still defy comprehension.

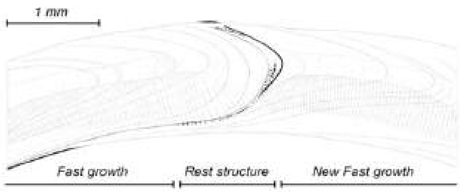
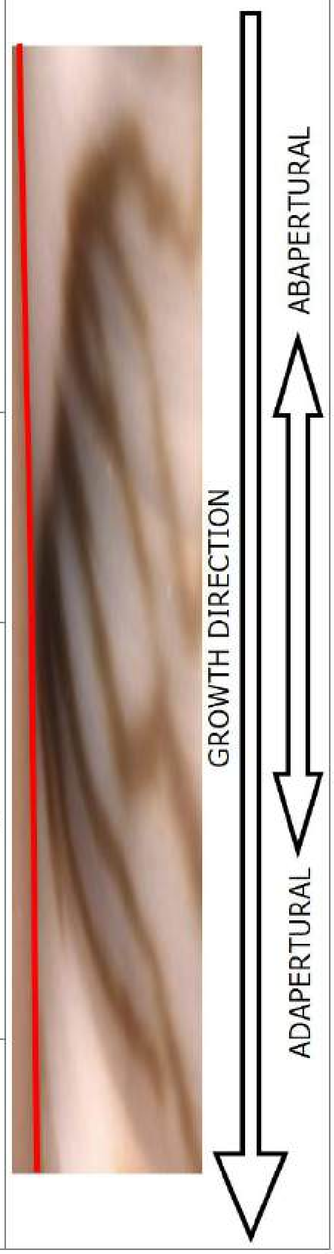
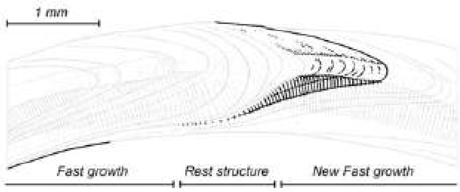
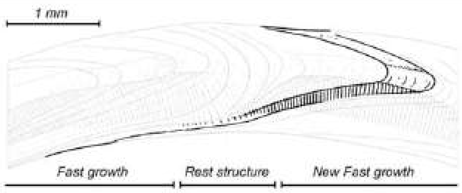
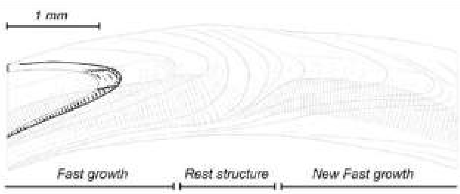
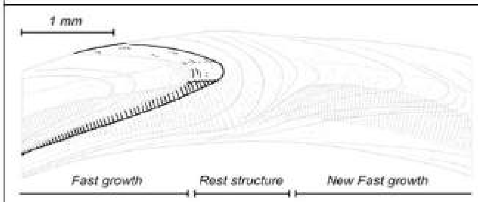
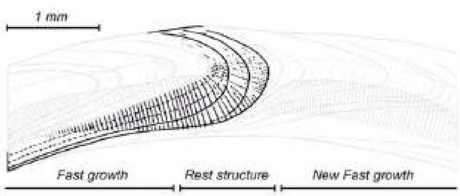
Lip Growth Stage	Phase	Stem-Line Incline	Relevant Examples	Photo
	Early Thinning	Emerging / Ascending	Figure 7 (#439, #580, #726, #727), Figure 6	
	Late Thinning	Ascending		
	Maximum Thinning	Horizontal	Figure 6	
	Early Thickening	Descending	Figure 6, Figure 7 (#62, #64, #240, #729, #825)	
	Late Thickening	Descending / Vanishing (including Lip Contour Straight-strokes)		
	Rest Phase	(no stem-line, back to slow-growth pattern)	Figure 5	

Figure 8. 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 5,6,7 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.

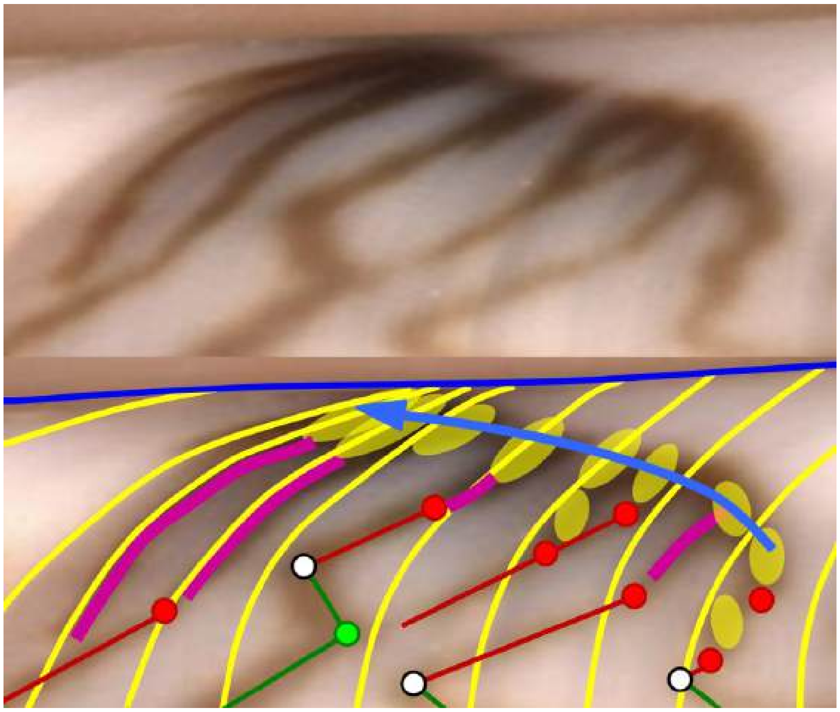


Figure 9. AS Feature from #1205 with 160% lateral stretch. Possible stages in the creation of a typical AS feature. Yellow isochrones mark roughly equidistant lip contours ("Lip Snapshots"). In the Transition Zone, dots mark CHP-style phenomena including children-lines initiation (red), chevron initiation (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.

- **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.

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 10.

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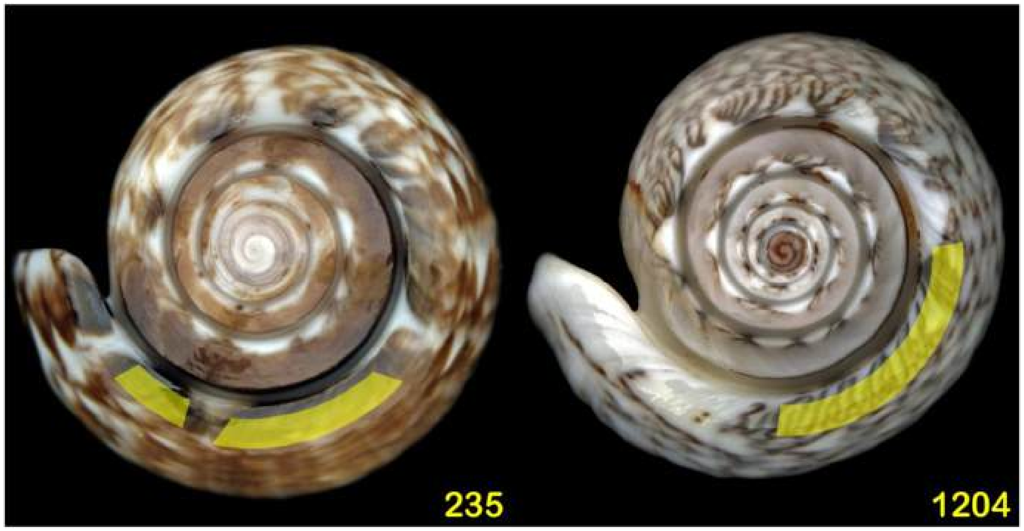

Figure 10. Two examples of AS where lip thinning (as proved by the length of the channel edge segment of the stem-line) appears prolonged.

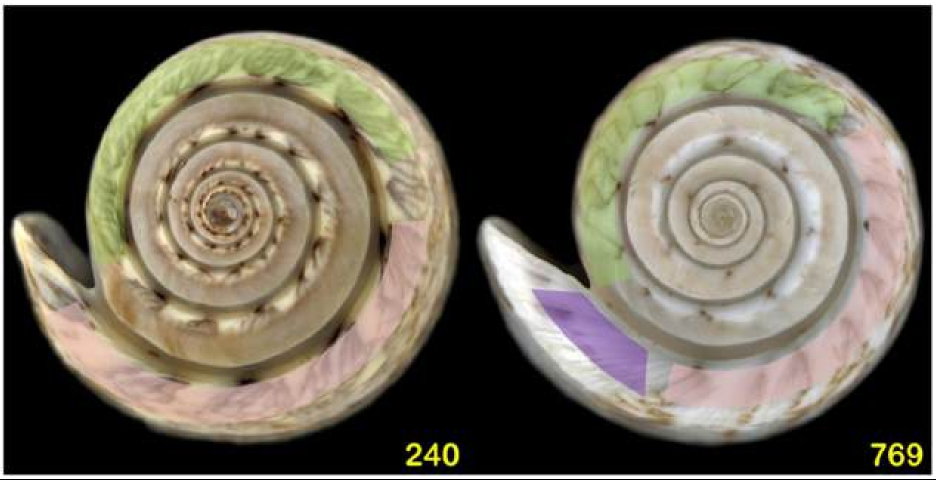

Figure 11. Two examples of AS where age-related variation can be observed. Green shading, feature mode 1 (#240: wide "open hand" features, #769: thin cloak pattern elements, very few strokes); purple shading, feature mode 2 (#240: narrower, more proverse features; #769: tightly fasciculate, proverse features).

- **Age-related AS features:** as observed by Strano (2017), sometimes adult or gerontic specimens, such as those illustrated in Figure 11, display a tendency to rarefaction, simplification and reduction of AS features, up to their complete disappearance. But also in earlier life the shape and the number of AS features ("feature mode") may vary with time.

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Figure 12. Two examples of AS where isolated strokes (shaded in yellow) can be observed.

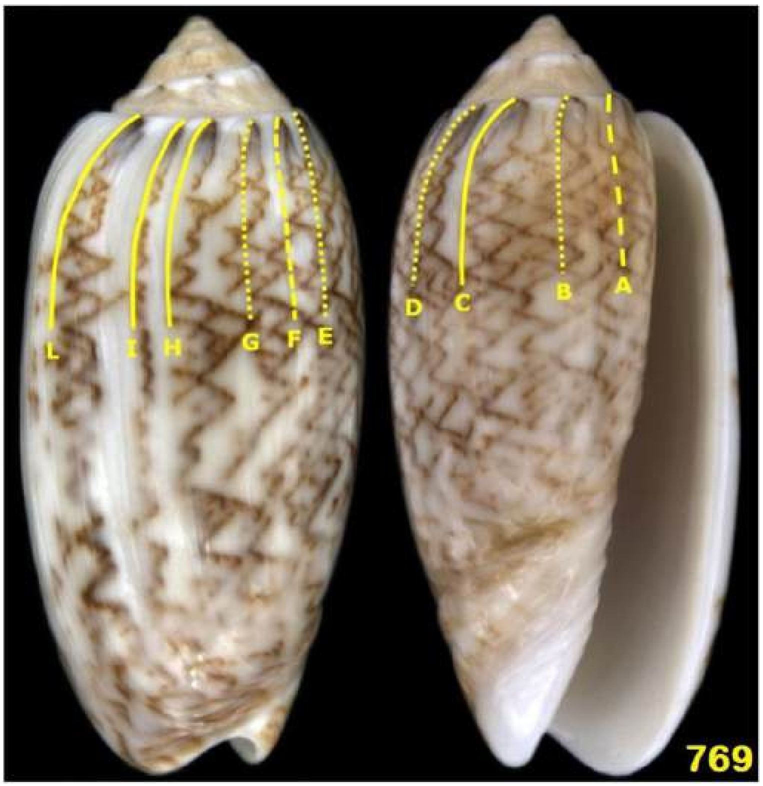

Figure 13. Minor (dotted line), Major (solid lines) and Intermediate (dashed line) cloak pattern disruption events. The ventral view of this specimen of *O. bifasciata* , also appearing in Figure 14, shows how linear elements originated in the cloak can penetrate the subchannel area.

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 12.
- **"Minor events":** In several cases, as exemplified in Figure 13 and 14, complexity and completeness of successive AS features may vary. Last whorl AS features 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:
  - the stem-line doesn't reach the channel edge;
  - in the same last whorl, the dark mark on the channel edge that marks the culmination of the sharp-lip phase is present in some (Major) features, and absent in other (Minor) features;
  - cloak pattern disruption may be almost absent (Minor events) or visible and intense (Major events).

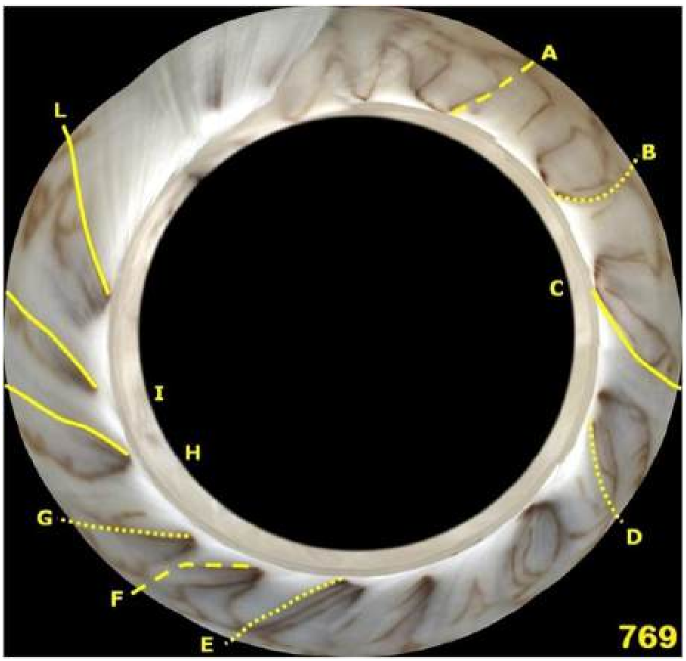

Figure 14. The events in Figure 13 as observable in a peripheral composite photo of the subchannel area, showing: 1) pervasive elements apparently originated in the cloak, or merged with antler-like offshoots from the cloak, almost reaching the channel edge (A-D arc), and 2) the different range of intensity of lip remodeling phases. Letters refer to Figure 13. Minor, Major and Intermediate events are respectively marked by dotted, solid and dashed lines.

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 younger specimens intensity variation may occur irregularly: it can easily be imagined that there are good years and bad years in the animal's life, and that the intensity of the growth bouts, marked by lip progradation and AS feature deposition, is directly proportional to the availability of trophic resources in the preceding year

- **Propagation of cloak pattern elements in the subchannel area:** The existence of a transition area implies that – even when the typical subchannel patterns are absent – some degree of cloak-style pattern generation may occur, as shown in Figure 14.
- **Monotonous pattern:** in the *Americoliva nivosa* group (see more under), as exemplified by *A. nivosa maya* (Figures 15 and 16) 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 15. 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 16. The monotonous AS of *A. nivosa maya*, as seen in peripheral composite photography. Lip is at the top. Compare with Figure 17 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 17. 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.

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 18-20, the "family look" of each species amounts to the combination of a few, sometimes fuzzy, characters that appear as unifying factors only when specimens 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, 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 18 and 19) 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, especially considering the similarities between *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) with almost complete features that 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 an 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 constant. 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 looses species-specificity. As an example, two specimens from Martinique, that initially were assigned to A. *lilacea*, look much more akin to *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 between specimen sets provides one relevant additional character to consider in their specific determination. Figure 18 shows AS thumbnail images arranged according to the proposed groups, while

Figures 19 and 20 show normalized apical views of all the specimen cited in this study, also arranged in order of appearance of each species in Figure 18.

RESULTS

American Shoulder and growth cycles

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.

A general description of the American Shoulder

The following description is given in right to left (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 6, 7 and 9).

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 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.

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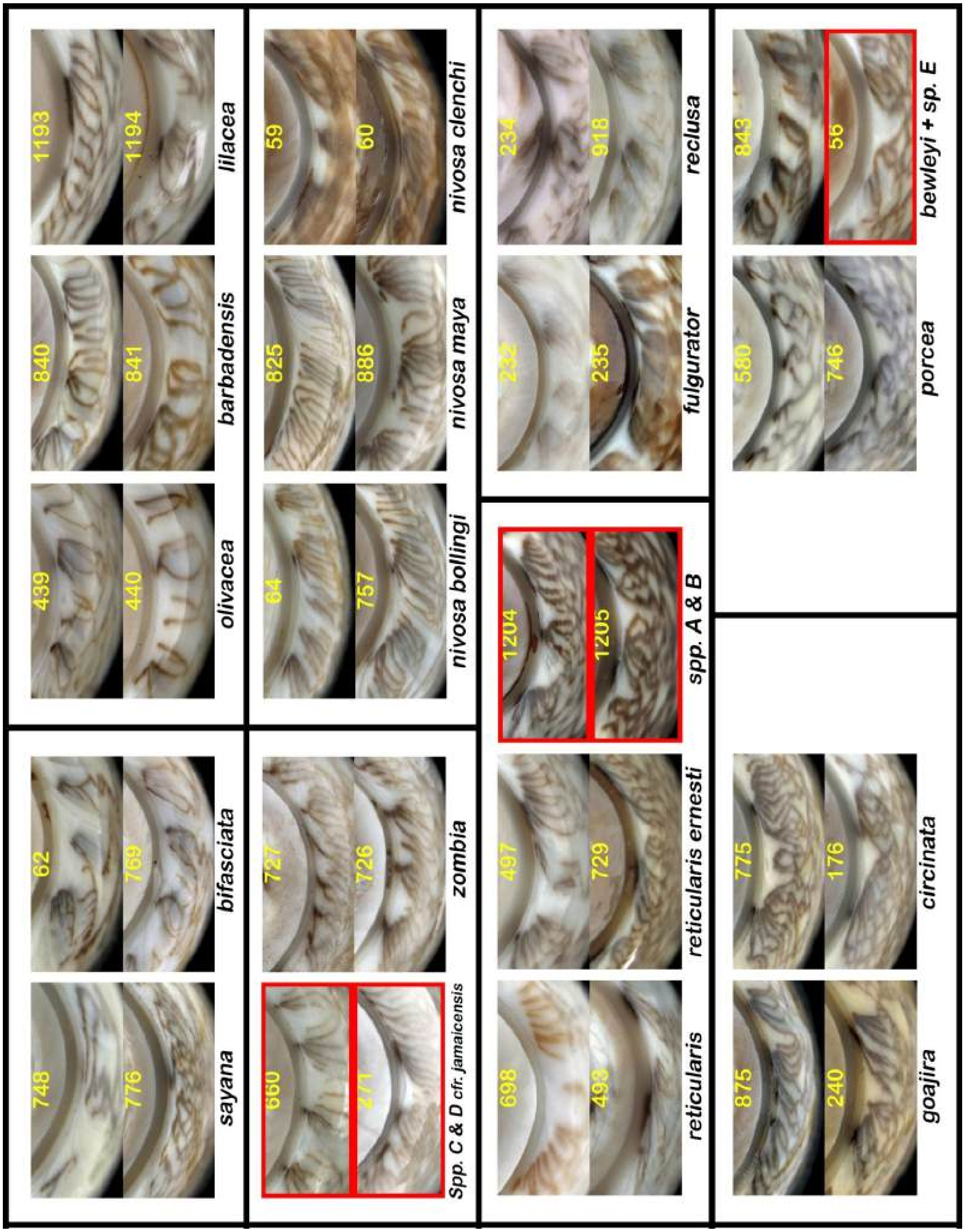

Figure 18. AS thumbnail images grouped following the tentative categories proposed in the text. The specimens of uncertain taxonomical position are outlined in red.

Figure 19. First group of full apical views grouped following the tentative categorization proposed in the text. For species identification, check text and Table 1.

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

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 the cogwheel 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 an 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.

From 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. The coalescence of these stokes marks the descending tract of the stem-line.

The descending tract, generated during the shorter or longer lip thickening phase, constitutes the adapertural 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, a thicker lip coincides with temporary ratification 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.

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 11). Furthermore, similar features occur in different species - devoiding the AS patterns of a reliable use as the sole specific character.

Table 2. Graphic elements used in the right column of Figure 21

STEM-LINE	Visible	Ascending		Lip Contour Straight-Strokes	Yellow shading
		Horizontal		Rest Subch. Pattern	Red shading
		Descending		Transition Zone	Blue shading
	Invisible	Ascending			
		Horizontal		Anterior Limit Of Subch-Pattern	
		Descending		Posterior Limit Of Cloak Pattern	

Notwithstanding these similarities some degree of common pattern 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 21, whose legend is summarized in Table 2, is an example 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.

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 (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.

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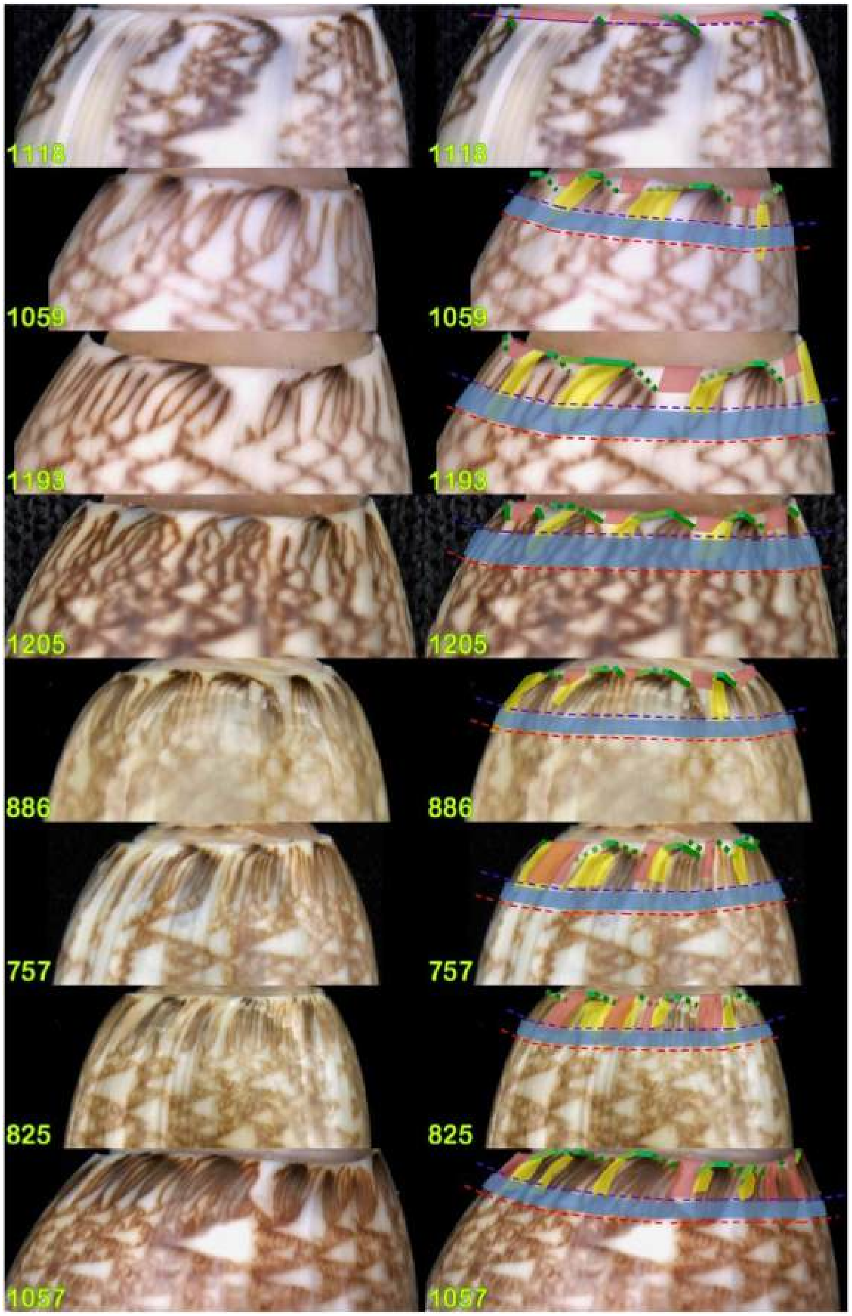

Figure 21. The elements of the typical AS pattern highlighted according with Table 2. #1118: *A. sayana sarasotensis* Petuch & Sargent, 1986 (Sarasota Bay); #1059: *A. reticularis ernesti* Petuch, 1990 (East Panama, unconfirmed); #1193: *A. lilacea* Paulmier, 2013 (Martinique); #1205: *Americoliva sp.*, akin to *A. lilacea* (Martinique); #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).

In that case, future studies may ascertain whether the subchannel pattern can be regarded as a reliable age indicator for all Olivinae, and 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.

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 they were described 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, also due to the limited number of specimens considered.

With regard to species-specificity, in a general sense the AS patterns show an 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 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 references 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.

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.

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I owe much gratitude to Giorgio Strano, both for his inspirational paper of 2017 and for kindly allowing the reuse of one of his illustrations from that article but, much more importantly, for being my patient olivological mentor since more than a decade. I'm also much obliged to Pierre Recourt, for the gift of several *Americoliva* specimens, some of which appear in this paper.

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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) (Figure 2), 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.
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 = improper synonym of anterior, with reference to the "apex-up" seashell iconography.
FEATURE = an "AS Feature" is the peculiar coalescent multi-stroke pattern, as opposed to the featureless "Rest Pattern"
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.
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.
STEM-LINE = a linear pattern element usually generated by coalescence of strokes,

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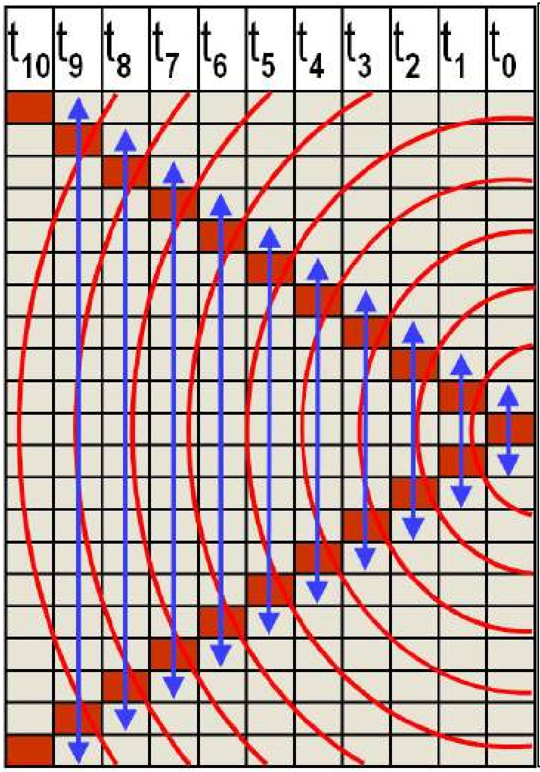
from which the strokes seem to depart. May be partly, or entirely, invisible.
STRAIGHT-STROKE = a stroke that is laid down all-in-one-shot. As such, it lays on an isochrone.
STROKE = a linear pattern element limited to the subchannel zone, laid without the constraint of the CHP. The term is coined with 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 channel edge and the cloak, where cloak pattern and SP superpose and interfere. "Thin" or "thick" refer to its antero-posterior size.
UP = improper synonym of posterior, with reference to the "apex-up" seashell iconography.



The chevron paradigm exemplified: at t_0 an initial active point in the 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 Tursch & Greifeneder (2001). Redrawn and modified after Tursch & Greifeneder (2001).

Figure 22.