

## The microstructure of the shell in the genus *Oliva* (Studies on Olividae. 24)

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**KEYWORDS:** Mollusca, Gastropoda, Olividae, *Oliva*, shell structure, taxonomy.

**SUMMARY.** The microstructure of the shell of 75 taxa in the genus *Oliva* has been examined and compared to that of some Olividae species belonging to other groups. Useful taxonomic characters are obtained even by non-destructive examination of the surface. Implications for systematics are discussed.

**RESUME.** La microstructure de la coquille de 75 taxa du genre *Oliva* a été examinée et comparée à celle de quelques espèces d'Olividae d'autres groupes. Des caractères taxonomiques utiles sont obtenus, même par examen non-destructif de la surface. Les implications pour la systématique sont discutées.

### 1. INTRODUCTION

#### 1.1. Purpose.

Shell mineralogy and microstructure have been sometimes utilised at the higher taxonomic levels (above Family rank) in Gastropods (see for instance LINDBERG, 1986 and McLEAN, 1990), where they have a deep phylogenetic meaning (see HAAS 1981; HEDEGAARD, 1995). Comparative studies at the species level are much rarer, but shell structural characters have been used, for example in the Muricidae (PETITJEAN, 1972) and the Littorinidae (TAYLOR & REID, 1990).

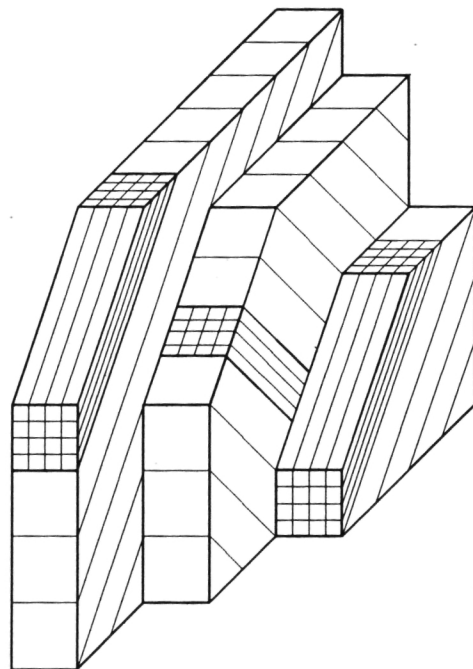
The aim of the present study is to investigate the potential of the structure of the shell to find additional characters for the classification of the genus *Oliva*, where the scarcity of objective taxonomic characters has posed serious problems (see TURSCH & GERMAIN, 1985). Most characters available today are morphometric. Additional, quantitative information might be most useful, especially if it is of a different nature.

#### 1.2. The shell of neogastropods.

Very numerous works deal with the shell structure of molluscs. After the classical work of BØGGILD (1930), general reviews and extensive lists of references will be found for instance in PETITJEAN (1972), TERMIER & TERMIER (1972), VOVELLE (1972) and MAJEWSKE (1974). Only the most basic notions, indispensable for understanding, will be recalled here.

In neogastropods, the shell (without the periostracum) consists mainly of calcium car-

bonate in the aragonite crystal form. Three distinct layers, stacked parallel to the surface are usually present. Each of these layers has a typical *crossed-lamellar structure* (abbr.: *XLM*). This is a lamellate "plywood-like" fabric (TAYLOR & REID, 1990) as depicted in Fig. 1. It shows three large *third order lamellae*, each formed by a series of oblique, parallel *second order lamellae*, consisting themselves in bundles of small *first order lamellae*.

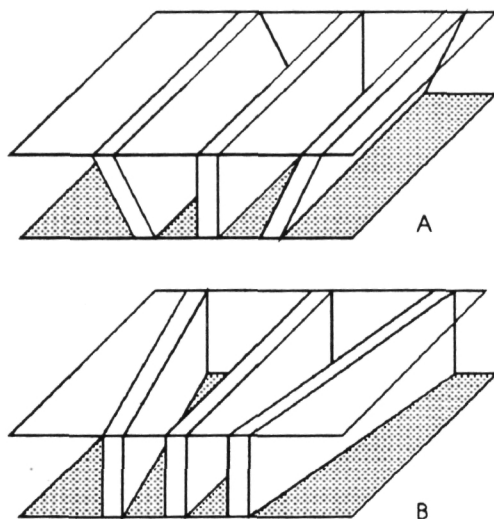


**Figure 1.** Crossed lamellar crystal structure of a neogastropod shell, schematised (see text, section 1.2.).

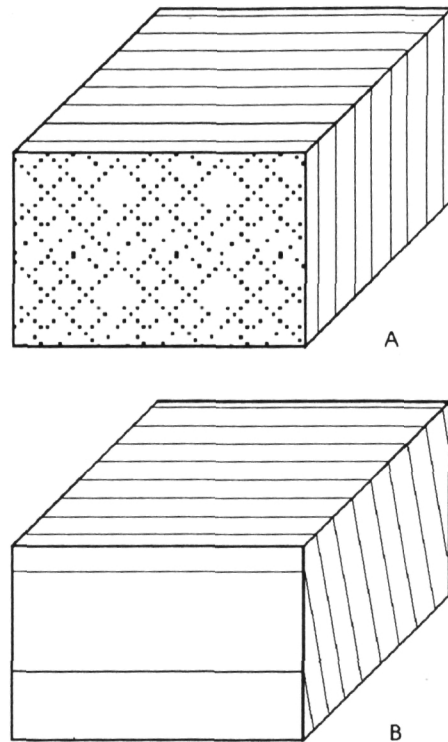
The usual three layers of the neogastropod shell are orientated in different directions. Usually the external and the inner layers are orientated in a transversal direction (third order lamellae perpendicular to the growth lines) and the middle layer is longitudinal (third order lamellae parallel to the growth lines). The three layers are not independent but are fused together at their limits by a gradational transition, as shown by local misorientation and torsion in the pattern. The complex structure of the neogastropod shell (strongly evocative of the composite materials of our modern technology) probably yields greatly increased mechanical resistance.

Within a given layer, the orientation of the stack of juxtaposed, parallel lamellae can be described by their **direction** (*i.e.* the angle formed on the surface of the layer by the trace of the lamella with a given reference line) and their **tilt** (*i.e.* the dihedral angle of the plane of a lamella with the plane of the surface of the layer). These notions are schematised in Fig. 2.

As will be seen below, shells present some variability in the tilt of the XLM. Even a small tilt, as shown on Fig. 3, can considerably modify the aspect of a radial (perpendicular to the surface) section. The expected crossed-lamellar structure will appear only if the lamellae are perpendicular to the surface with an direction parallel to the cut (Fig. 3A). The pattern will appear as parallel lines (Fig. 3A) if the lamellae are tilted even slightly from 90°.



**Figure 2.** Direction and tilt of lamellae. **2A:** three lamellae with same direction and different tilts. **2B:** three lamellae with different directions and same tilt.



**Figure 3.** Effect of the tilt of lamellae on the aspect of radial sections. **3A:** lamellae perpendicular to surface. **3B:** lamellae with slight tilt.

### 1.3. The shell of Olividae.

Only a few, very succinct descriptions of the shells of Olividae are found in the literature. BØGGILD (1930: 315) says: "The shells of different forms of *Oliva*, *Olivella* and *Ancilla* examined by me all show the ordinary structure with three layers. There may, in some instances, be faint traces of an upper, longitudinal layer but it is not formed as a distinct, separate layer. BOWERBANK (1844) places the *Oliva* among the gastropods which have three layers of which the middle one has transverse lamellae; there may, perhaps be other species than those examined by me, which possess the said middle layer". MAJEWSKE (1974, Table 7, p. 79) reports only that the shell of Olividae is composed of aragonite and consists in 3 to 5 cross-lamellar layers. WILMOT *et al.* (1992) have studied the microstructural parameters of the XLM elements of *Oliva sayana*.

At the macroscopic scale, the Olividae share with some other gastropod families (Conidae, Cypraeidae, Ovulidae, Marginellidae) an interesting particularity: the dissolution of the inner, earlier volutions of the shell, to make



place for growth of the animal (KOHN *et al.*, 1979; ZEIGLER & PORRECA, 1969).

Much more complex structures are met in the thickened parts of the *Oliva* shell: the spire, the columella and the fasciolar region. This study is limited to the simpler, central part of the body whorl. We shall concern ourselves only with the largest of these crystalline units and the word "lamellae" will refer here to the third order lamellae, unless otherwise stated.

## 2. MATERIAL

The taxonomy and the nomenclature of the genus *Oliva* are not yet fully stabilised. The status of many of the taxa here below still needs revision and some of the names utilised here will certainly have to be changed later. No collection numbers are given for the shells that have been cut (the specimens are destroyed). They are given for all the shells examined by non-destructive methods. Abbreviations: AM: Zoölogisch Museum Amsterdam; BT: Tursch collection; DG: Greifeneder collection; JS: Senders collection; P.I.: Philippines; P.N.G.: Papua New Guinea.

Genus *Agaronia* Gray, 1839.

*A. acuminata* Lamark, 1811 (NIGERIA).

Genus *Ancilla* Lamarck, 1799.

*A. lienardi* Bernardi, 1858 (BRAZIL).

Genus *Oliva* Bruguière, 1789.

*O. amethystina* (Röding, 1798) (MARSHALL IS.: BT-2771; P.I.: BT-4563, 4564, 4567, 4570).

*O. amethystina* (Röding, 1798) forma *carnicolor* Dautzenberg, 1927 (P.I.: BT-1303, 1463, 3537, 4022, 4637).

*O. arctata* Marrat, 1871 (THAILAND: BT-081, 1232, 3490, DG-7102/6, DG-RWS-X).

*O. australis* Duclos, 1835 (AUSTRALIA: BT-1476, 1478, 3600, 4506, 5301).

*O. baylei* Petuch, 1979 (SOLOMONS: BT-725, 3548).

*O. buelowi* Sowerby, 1889 (P.N.G.: BT-399, 403, 422, 425, 426).

*O. bulbiformis* Duclos, 1840 (INDONESIA: BT-1549, 1551, JS-028, 029; P.I.: BT-1556).

*O. bulbosa* (Röding, 1798) (ABU DHABI: BT-4604, 4605, 4606, 4607, 4608).

*O. caerulea* (Röding, 1798) (MADAGASCAR: BT-4643, 4656; MOZAMBIQUE: BT-1194; SOUTH AFRICA: BT-2909, 2912).

*O. caldania* Duclos, 1835 (AUSTRALIA: BT-1610, 1612, 1614, 4442).

*O. carneola* (Gmelin, 1791) (SOLOMONS: BT-301, 2516, 2548, 2549, 2553).

*O. carolinensis* Conrad, 1863 (U.S.A., FLORIDA, Fossil: BT-3041, 3044, 3049, 3059, 3093).

*O. caroliniana* Duclos, 1840 (MOZAMBIQUE: BT-1567; SOUTH AFRICA: BT-2617, 2618, 3800, 3997).

*O. ceramensis* Schepman, 1904 (P.N.G.: BT-1577, 1582, 1601, 3562, 3563; SOLOMONS: BT-7196).

*O. chrysoplecta* Tursch & Greifeneder, 1989 (P.I.: BT-5005, 5511, 5512, 5514).

*O. circinata* Marrat, 1871 (BRAZIL: BT-1684, 1685, 2107, 2108, 2116, 2554, 5528, 6699, 6700).

*O. concavospira* Sowerby, 1914 (JAPAN: BT-5521, 5522; P.N.G.: BT-557, P.I.: BT-5279).

*O. concinna* Marrat, 1870 (P.N.G.: BT-7094, 7095, 7104, 7116, 7163).

*O. dubia* Schepman, 1904 (P.N.G.: BT-4928, 4929, 4930, 4931, 4932).

*O. elegans* Lamarck, 1811 (P.I.: BT-7225 to BT-7230).

*O. esiodina* Duclos, 1845 (TAHITI: BT-3688, 5298, 6042, 6046, 6048).

*O. faba* Marrat, 1867 (INDONESIA: BT-5385; SRI LANKA: BT-7197, 7198; THAILAND: BT-1330).

*O. flammeacolor* Petuch & Sargent, 1986 (SRI LANKA: BT-6220, 6221, 6222, 6224, 6225).

*O. flamulata* Lamarck, 1811 (GABON: BT-2087, 2088; MAURITANIA: BT-4215; SENEGAL: BT-2127, 4432).

*O. foxi* Stingley, 1984 (COCOS IS.: BT-3326, 5429).

*O. fulgurator* (Röding, 1798) (ARUBA: AM-10, 33, BT-1005; VENEZUELA: BT-2289, 2292).

*O. funebris* Lamarck, 1811 (P.I.: BT-7218 to 7224). This is really a nomen nudum (see GREIFENER, DUCHAMPS & TURSCH, 1995). No replacement name yet selected. Name used here in its common, current acceptance.

*O. hilli* Petuch & Sargent, 1986 (TONGA: BT-5505, 5506, 5507, 5508, 6206).

*O. hirasei* Kira, 1959 (P.I.: BT-5021, 5022, 6202, 6194, 6196).

*O. incrassata* (Lightfoot in Solander, 1786) (W. MEXICO: BT-370, 371, 1664, 3235, 4135; W. PANAMA: BT-1018).

*O. irisans* Lamarck, 1811 (for this controversial name see GREIFENER, DUCHAMPS & TURSCH, 1995) (P.I.: BT-7203 to BT-7217).

*O. julieta* Duclos, 1840 (COSTA RICA: BT-735; W. MEXICO: BT-1663, 4129; W. PANAMA: BT-4130).

*O. kaleontina* Duclos, 1835 (GALAPAGOS: BT-4225; W. PANAMA: BT-3751, 3752, 3753, 3756).

- O. lenhilli* Petuch & Sargent, 1986 (P.I.: BT-7101, 7102).
- O. leonardhilli* Petuch & Sargent, 1986 (MADAGASCAR: BT-5515, 5516, 5706, 5707, 5708, 5709, 5710).
- O. lignaria* Marrat, 1868 (AUSTRALIA: BT-3206, 3207, 3208, 4831, 4832).
- O. mantichora* Duclos, 1840 (P.I.: BT-4534, 4540, 4544, 4545, 4546).
- O. miniacea* (Röding, 1798) (FIJI: BT-5184; MARSHALL: BT-2783, 2791; P.N.G.: BT-2783; TONGA: BT-026).
- O. mucronata* Marrat, 1871 (P.N.G.: BT-6510, 6512, 6515, 6516, 6522).
- O. multiplicata* Reeve, 1850 (TAIWAN: BT-660, 4257, 4629, 4260, 5463, 5466).
- O. mustelina* Lamarck, 1811 (HONG KONG: BT-6721; JAPAN: BT-4620; TAIWAN BT-4264; THAILAND: BT-2921, 2925).
- O. neostina* Duclos, 1840 (P.N.G.: BT-5016, 5017, 5018, 5019, 5020).
- O. nigrata* (Karsten, 1789) (Generally known as *O. vidua* (Röding, 1798), see TURSCH, DUCHAMPS & GREIFENEDER, 1994) (INDONESIA: BT-601; VANUATU: BT-610, 3312, 3313, 3314).
- O. oblonga* Marrat, 1870 (VENEZUELA: BT-970, 984, 2323, 6351, 6976).
- O. oliva* (Linné, 1758) (THAILAND: BT-1293, 1294, 1295, 1298).
- O. olivacea* (Karsten, 1789) (Generally known as *O. tessellata* Lamarck, 1811, see TURSCH, DUCHAMPS & GREIFENEDER, 1994)(P.I.: BT-4508, 4509, 4510, 4512, 4922).
- O. panniculata* Duclos, 1835 (JAPAN: BT-7172, 7173, 7174, 7275, 7176, 7177).
- O. parkinsoni* Prior, 1975 (P.N.G.: BT-681; SOLOMONS: BT-2480, 2481, 2483, 2485).
- O. paxillus* Reeve, 1850 (HAWAII: BT-1928, 1931, 4316, 4318; SOLOMONS: BT-665)
- O. peruviana* Lamarck, 1811 (PERU: BT-353, 2235, 2236, 2237, 3000, 4281, ).
- O. polita* Marrat, 1870 (MARQUESAS: BT-6051, 6054, 6055, 6056, 6057, 6058).
- O. polpasta* Duclos, 1840 (W. PANAMA: BT-3777, 3778, 3780, 3781, 3782).
- O. ponderosa* Duclos, 1840 (MALDIVES: BT-1199, 1200, 1954, 1955, 2326).
- O. porphyria* (Linné, 1758) (W. PANAMA: BT-3779, 3780, 3781, 3782, 3726).
- O. reclusa* Marrat, 1871 (ARUBA: AM-20, 21, 22, 25, 29).
- O. reticularis* Lamarck, 1811 (U.S.A., FLORIDA: BT-5537, 5539, 5541; E. PANAMA: BT-5616, 5617, 5618, 5619, 5620).
- O. reticulata* (Röding, 1798) (INDONESIA: BT-6715; P.N.G.: BT-451, 459; P.I.: BT-4596, 7231, 7132).
- O. rubrolabiata* Fischer, 1902 (VANUATU: BT-3493, 3494, 3959, 5011, 6676).
- O. rufofulgurata* Schepman, 1911. (P.I.: BT-4939, 4940, 4941, 4942, 4943; SOLOMONS: BT-3925).
- O. rufula* Duclos, 1840 (P.N.G.: BT-4599, 4600, 4601, 4602, 4603).
- O. sayana* Ravenel, 1834 (U.S.A., FLORIDA: BT-2410, 2793, 3113, 4077, 4084, 4100).
- O. scripta* Lamarck, 1811 (U.S.A., FLORIDA: BT-2154; HAITI: BT-2379; HONDURAS: BT-2756, 2757, 2762).
- O. semmelinki* Schepman, 1891 (P.N.G.: BT-792, 794, 795, 796, 797).
- O. sericea* (Röding, 1798) (INDONESIA: BT-006; 2052, 2053; JAPAN: BT-4048; TAIWAN: BT-4047).
- O. sidelia* Duclos, 1840 (MOZAMBIQUE: BT-2723; SEYCHELLES: BT-2707, 2708, 2710, 2714).
- O. solomonensis* Petuch & Sargent, 1986 (FIJI: BT-5228; P.I.: BT-5365, 5366; SOLOMONS: BT-2486, 2488).
- O. spicata* (Röding, 1798) (W. MEXICO: BT-334, 337, 4290, 5479, 5480, 5482; W. PANAMA: BT-2859, 3217, 3765, 3766, 3767, 3768, 3769, 3770, 4169).
- O. splendidula* Sowerby, 1825 (W. PANAMA: BT-946, 3736, 3741, 3746, 3749, 3750, 4023, 4024).
- O. tigrina* Lamarck, 1811 (MADAGASCAR: BT-1023, 1215, 4711; MOZAMBIQUE: BT-169; TANZANIA: BT-1240).
- O. tricolor* Lamarck, 1811 (INDONESIA: BT-4915, 4916, 5015, JS-027; P.I.: BT-6329).
- O. undatella* Lamarck, 1811 (ECUADOR: BT-2681; W. MEXICO: BT-331, BT-332; W. PANAMA: BT-1665, BT-1666).
- "*O. vermiculata* Gray, 1858 " (auct.)(ARUBA: AM-48, 49, 51, 54, 56).
- O. vicweei* Recourt, 1989 (INDONESIA: BT-375, 2025).
- O. zombia* Petuch & Sargent, 1986 (HAITI: BT-5489, 5490, 5491, 5492, 5493).
- Genus *Olivancillaria* Orbigny, 1840.  
*Olivancillaria urceus* (Röding, 1798) (BRAZIL).
- Genus *Olivella* Swainson, 1831.  
*Olivella biplicata* Sowerby, 1825 (U.S.A., CALIFORNIA).  
*Olivella japonica* Pilsbry, 1895 (JAPAN).  
*Olivella volutella* Lamark, 1811 (W. PANAMA).
- Incertae sedis:***  
"*Oliva*" *lacaniensis* Greifeneder & Blöcher, 1985. (P.I.: BT-5045, BT-5046, BT-5047, BT-6025, BT-6026).

### 3. METHODS

#### 3.1. Shell sections.

##### 3.1.1. Cuts.

Shells were cut with a rotatory diamond blade along the 5 lines shown on Fig. 4, taking care to make the cuts as perpendicular to the surface as possible. The position of the cuts is approximative but the direction is not. The three longitudinal cuts follow the growth lines. The two transversal cuts are perpendicular to the lip. This yields the two fragments to be examined, a "*lip sample*" and a "*central sample*" (see Fig. 4).

##### 3.1.2. Preparation.

Most often the samples can not be utilised as such, due to prominent traces of the cutting tool. The samples were hand-polished along each section to be examined, using wet carborundum grinding paste (grade 600) on a flat glass plate. In most instances the crystal structure is better seen after mild acid etching of the polished surface. Dyes (Fast Green or Brilliant Blue G) were occasionally utilised, to increase contrast.

##### 3.1.3. Observation.

A binocular lens (WILD model M3 or 308700) was utilized at magnifications (10 x 40) or (10 x 80) to observe the arrangement of the layers and the orientation of the lamellae. Accurate drawings were made in each case with a WILD *camera lucida*.

#### 3.1.4. Representation.

Geometrical perfection of the crystal arrangements is seldom observed. In addition to natural curving and torsion of the lamellae (evidenced by electron microscopy, see below), deviations from ideality can also result from even small angular errors in the orientation of the cuts. Individual variations and age-related differences are also the rule, as fully expected. In spite of variation, many hundreds of observations have shown that the shell structures of *Olividae* fall into large, defined categories. This allows the use of schematic, idealised representations of these categories, instead of space-consuming, repetitive illustration of individual cases differing only in details. A few individual cases will be illustrated when needed.

Shell structures are complex, and easy comparisons can be made only if the samples are always orientated in the same way (see Fig. 4). "*lip samples*" seen slightly from above, looking from inside, with the edge of the lip vertical, at the right of the picture. We will always represent "*central samples*" looking towards the lip, with the direction of the apex at the right and with the external surface visible above. It can be seen that a 90° counterclockwise rotation of the "*central sample*" representation yields an image equivalent to a view of the hidden, vertical face of the "*lip sample*", seen from the left.

Only the orientation of the third order lamellae are sketched in the schematic representations.

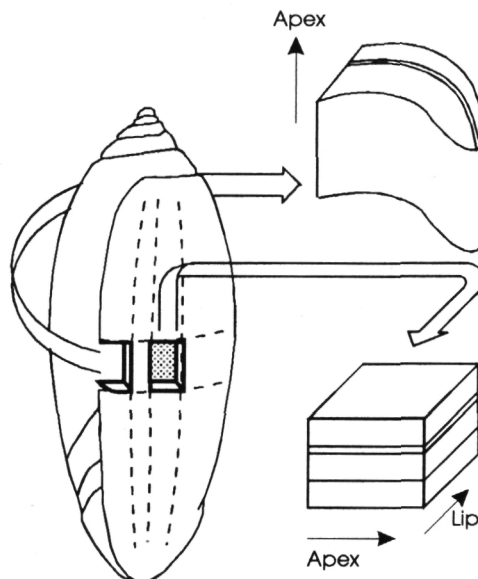
#### 3.2. Scanning Electron Microscopy (SEM).

For examination by scanning electron microscopy, shells were broken rather than cut. A thin (3-4 mm) slice of shell is first obtained by effecting two parallel cuts (longitudinal or transversal, according to the purpose), as described in § 3.1.1. This slice is then held in a vice and simply broken perpendicular to its length (by bending it with pliers). The sample is then coated with gold under vacuum, following the standard procedure.

#### 3.3. Surface observations.

##### 3.3.1. Difficulties.

The surface lamellae lie under a very thin, shining, translucent external pellicle (see below) and are most often not noticed on cursory examination. For most *Oliva* species, a tangent beam of light, directed along the direction of the crystals, makes them appear very clearly (a surprise for most students of *Oliva*). In many cases, and with some practice, the surface lamellae can easily be seen with a strong,



**Figure 4.** Shell sections. Upper right: "*lip sample*". Lower right: "*central sample*". Saw cuts indicated by dashed lines.

ordinary magnifying lens. Some species (such as *Oliva amethystina*) have a thicker external pellicle, impeding easy direct observation. Mild etching then solves the problem, the external pellicle being very sensitive to acid treatment. The surface lamellae at the internal face and at the edge of the lip are generally very easy to observe.

### 3.3.2. Observation.

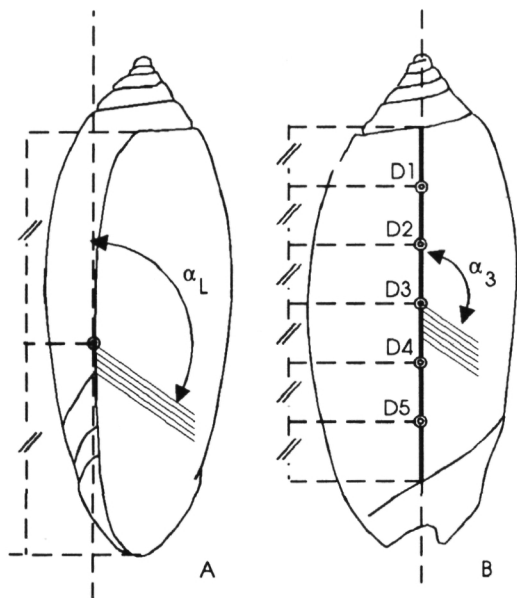
A binocular lens (WILD model M3 or 308700) equipped with optic fiber lighting was utilized at magnifications (10 x 40) or (10 x 80) to observe the orientation of the lamellae at the surface of the external layer. The thickness  $W$  of the surface lamellae was estimated with a binocular lens (WILD 308700) at magnification (10 x 180), using a precalibrated ocular reticulum at right angle from the direction of the lamellae. One then counts the number of lamellae crossed by a predetermined 0.5 mm segment on the reticulum. The measurement is repeated 5 times and the mean value reported. Values differ very little from reading to reading; measurement  $W$  is highly reproducible. Measurements effected on photomicrographs of known scale give essentially the same results. It should be stressed that  $W$ , as defined here, is really the thickness of the surface lamellae plus the thickness of the organic layer separating the lamellae.

### 3.3.3. Position.

In order to obtain reproducible angular observations, one must examine the direction of the surface lamellae at specified positions. The midpoint of the lip (where the external pellicle is thinner) is often the easiest place for observing the surface lamellae. An accurate drawing of the lip edge and of the direction of the surface lamellae is made with the *camera lucida*. A tangent to the lip is then drawn and angle  $\alpha_L$  is measured on the drawing as shown on Fig. 5A. In some species (for instance *O. rufula*) thickened longitudinal cords are present near the lip of mature specimens; in such cases  $\alpha_L$  is measured just behind the cord, as close to the lip as possible.

Other angular measurements have also been effected at selected points of the dorsal side. The shell is laid on its ventral side, in its equilibrium position, immobilised with modelling clay. Under proper magnification and following a guideline in the ocular reticulum, a longitudinal reference line is then carefully drawn with a fine felt pen on the body whorl, as shown in Fig. 5B. Five points D1 to D5 are obtained by dividing in six equal segments the portion of the line joining the filament channel to the fasciole. For each point, an accurate drawing of both the longitudinal reference line and the direction of the surface lamellae is made with the *camera lucida*. At each point  $D_i$  the corresponding angle  $\alpha_i$  is determined as shown in the figure.

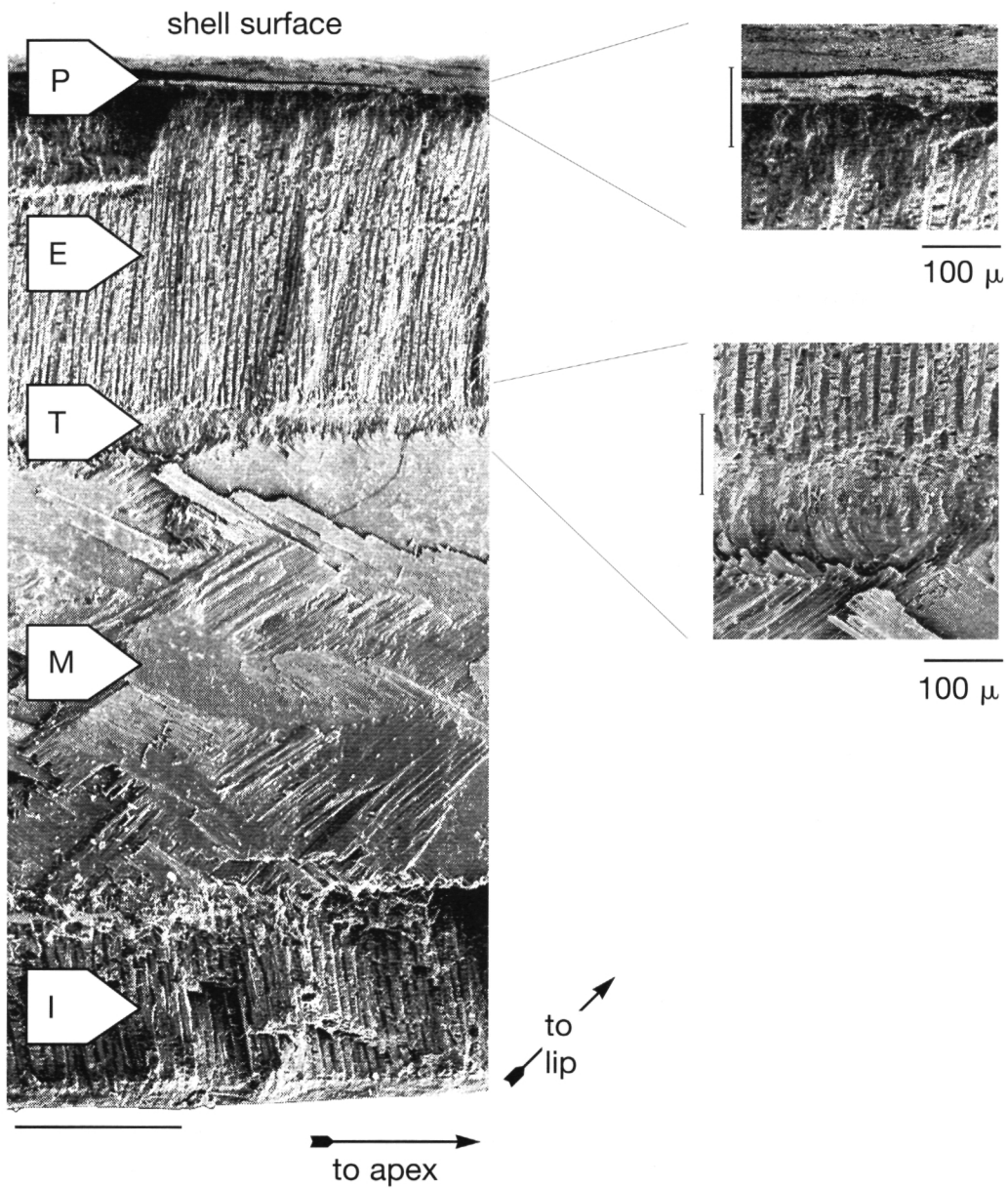
Angular measurements are reasonably fast (less than 10 minutes per specimen for all six measurements, much less for  $\alpha_L$  and  $\alpha_3$  only). They are highly reproducible, as demonstrated in Table 1.



**Figure 5.** Surface lamellae. Angle measurements at mid-lip (A) and on dorsal region (B).

angle	mean	SD	CV
$\alpha_1$	76.00°	2.00	2.63
$\alpha_2$	78.83°	1.47	1.87
$\alpha_3$	92.83°	1.17	1.26
$\alpha_4$	119.33°	0.52	0.43
$\alpha_5$	116.83°	2.64	2.26
$\alpha_L$	95.17°	1.72	1.81

**Table 1.** Direction of the surface lamellae. Experimental error. Six independent series of measurements on the same shell (*O. sayana* BT-4077, H=63.17 mm). SD = standard deviation. CV = coefficient of variability (see text).



**Plate 1.** *Oliva reticulata*. Scanning electron micrography. Longitudinal section, seen towards the lip (apex at the right of the observer).

**P:** external pellicle.

**T:** transition zone.

**I:** internal XLM layer.

**E:** external XLM layer.

**M:** middle XLM layer.



## 4. RESULTS

### 4.1. The genus *Oliva*.

#### 4.1.1. Observations on shell sections.

##### 4.1.1.1. The components of the shell.

*Oliva* are devoid of periostracum. The structure of the shell is clearly evidenced by scanning electron microscopy (SEM). As an example, Plate 1 is a view of a longitudinal section of *O. reticulata*, seen looking towards the lip, with the apex of the shell at the right of the observer (the view sketched in Fig. 7B).

The shell of all the examined *Oliva* species consists of three XLM layers: the **external, middle and internal XLM layers** (respectively layers E, M and I, Plate 1). It can be seen that the layers have different directions.

Between the external and the middle XLM layers one always finds a thinner, intermediate zone, where the structure of the crystals is ill-defined (considerable twisting, torsion and disorientation, see § 1.2). This will be called the "**transition zone**" (Plate 1, T). No such transition zone has been observed between the middle (Plate 1, M) and the internal (Plate 1, I) XLM layers, that are in direct contact.

Above the external layer there is a thin, shiny, translucent **external pellicle** (Plate 1, P). For *O. sayana* this structure has been clearly depicted in a scanning electron micrograph by WILMOT *et al.* (1992: 26, Fig. 6a). In most cases, the external pellicle is very thin (roughly 5 to 10  $\mu$ , as in most species) and the lamellae at the surface of the external XLM layer can be easily seen by transparency. In some species (such as *O. amethystina*) the external pellicle can be much thicker (up to 80-100  $\mu$ ); this may then conceal the lamellae at the surface.

Below the internal layer, an additional layer with no clearly defined crystal structure (this will be called the **internal lining**) is occasionally observed for some species. This layer is mostly thin but can become important, especially in aged specimens. When present, it thins down towards the lip and ends before reaching the edge.

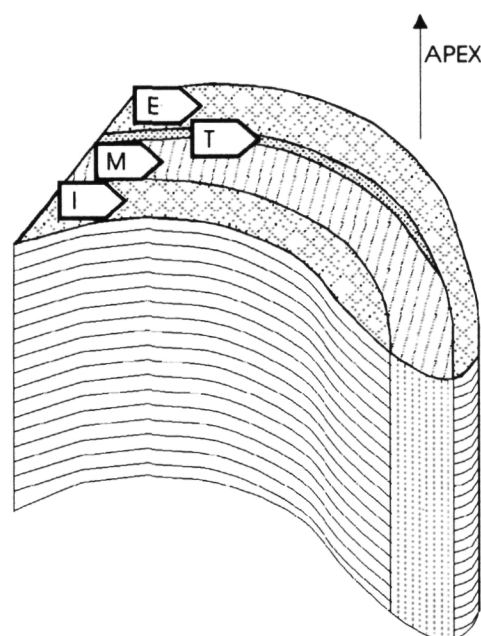
##### 4.1.1.2. General observations.

Observation of a large series of shells (see section 2, Material) has shown that the above description is general. Variations have been observed both in the direction and the tilt of the lamellae. Noticeable variations of tilt have often been evidenced within the same species (and even within short distance on the same specimen). Measurements of tilt seem most

unpromising for taxonomic applications. On the contrary, the direction of lamellae is remarkably constant within a given species, while exhibiting considerable differences between certain species (see Plate 2 for examples). These are precisely the qualities required for an operational taxonomic character.

Variations have also been observed in the relative thickness of the various XLM layers. These differences have a high intraspecific variability, often seem to be age-related and are also unpromising for taxonomic applications.

Most of the Indo-Pacific *Oliva* species fall into two groups of microstructure, exemplified by *Oliva reticulata* and *O. amethystina*.

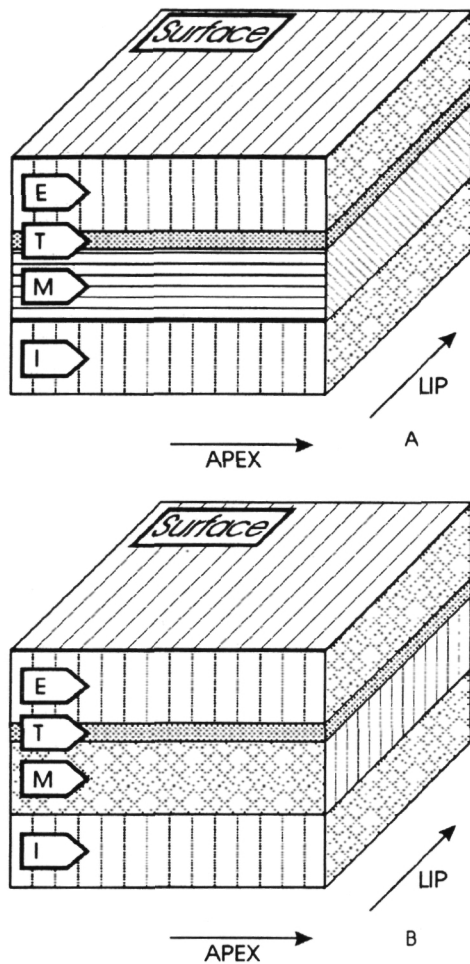


**Figure 6.** *Oliva reticulata*. Lip sample. Shell without internal lining. **P**: external pellicle. **E**: external XLM layer. **T**: transition zone. **M**: middle XLM layer. **I**: internal XLM layer.

##### 4.1.1.3. Shell sections. *Oliva reticulata*.

Sections of the shell of this species are schematised in Figures 6 and 7. One can see that the direction of the lamellae of each of the three XLM layers is perpendicular to that of the lamellae of the neighbouring layer:

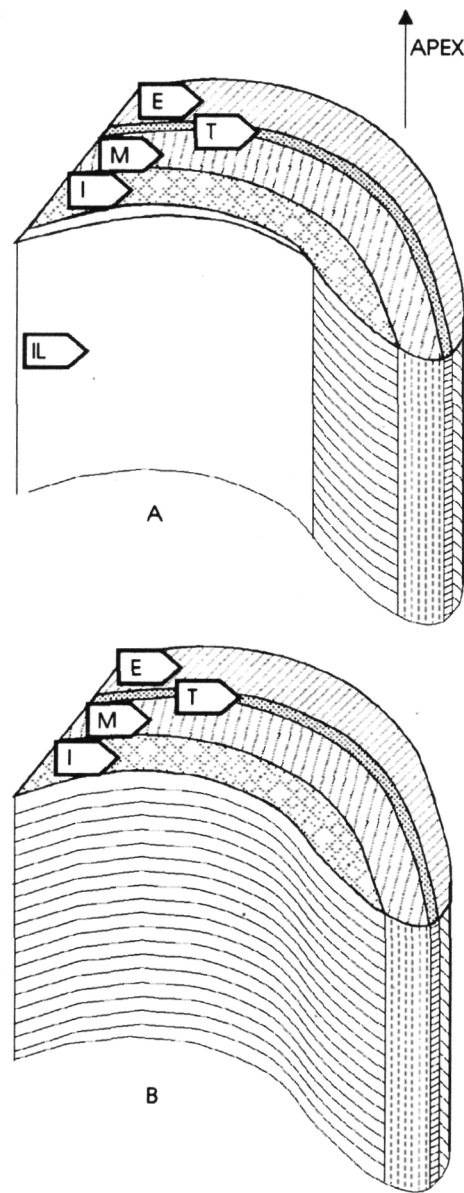
- The direction of the lamellae of the internal XLM layer (I) is nearly perpendicular to the lip.
  - The direction of the lamellae of the middle XLM layer (M) is nearly parallel to the lip.
- Small variations of tilt make it appear either as in Fig. 7A or as in Fig. 7B (see § 1.2 and Fig. 3).



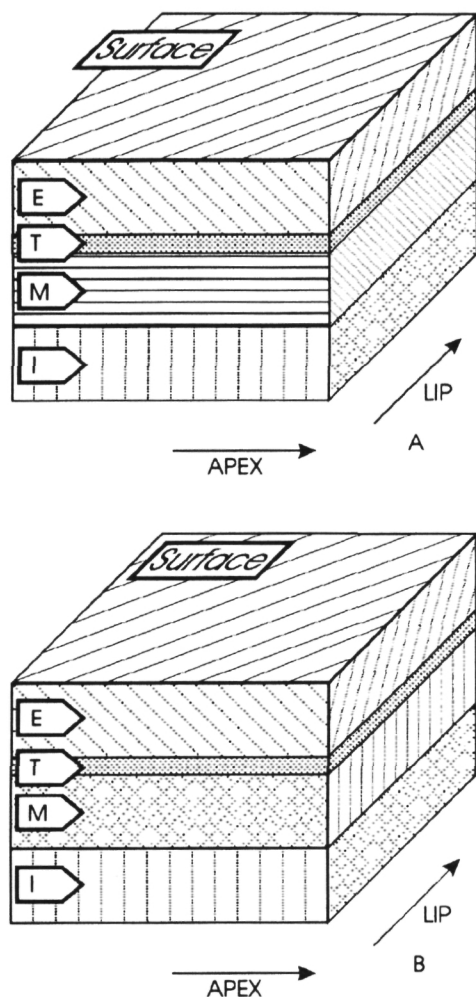
**Figure 7.** *Oliva reticulata*. Central sample. 7A and 7B differ only by the tilt of the middle XLM layer. P: external pellicle. E: external XLM layer. T: transition zone. M: middle XLM layer. I: internal XLM layer.

- The direction of the lamellae of the external XLM layer (E) is very nearly perpendicular to the lip.
- In aged specimens with a very thick lip, the transition zone (T) generally thins down and ends before the lip, so that the middle (M) and the external (E) XLM layers come into direct contact at the peristome. This can be seen (see Fig. 6) by direct observation of the edge of the lip. In younger specimens, the transition zone (T) mostly continues all the way to the lip, as shown for *O. amethystina* on Figs. 8A and 8B).
- The presence of an internal lining (not represented in Fig. 6, but appearing as for *O. amethystina* in Fig. 8A) is occasionally seen at some distance from the lip, especially in aged specimens.

A majority of Indo-Pacific *Oliva* species (see § 5.2) have this characteristic arrangement of XLM layers and form what will be referred to as the "horizontal group". This structure is also found in a few American taxa.



**Figure 8.** *Oliva amethystina*. Lip sample. A: shell with internal lining. B: shell without internal lining. P: external pellicle. E: external XLM layer. T: transition zone. M: middle XLM layer. I: internal XLM layer. IL: internal lining.



**Figure 9.** *Oliva amethystina*. Central sample. A and B differ only by the tilt of the middle XLM layer. P: external pellicle. E: external XLM layer. T: transition zone. M: middle XLM layer. I: internal XLM layer.

#### 4.1.1.4. Shell sections. *Oliva amethystina*.

Sections of the shell of this species are schematised in Figures 8 and 9. (Figures 8A and 8B differ only by the presence of the internal lining, shown in Fig. 8A). One can see that the direction of the lamellae of only the internal and the middle XLM layers is perpendicular to each other:

- The direction of the lamellae of the internal XLM layer (I) is very nearly perpendicular to the lip (like in *O. reticulata*).
- The direction of the lamellae of the middle XLM layer (M) is very nearly parallel to the lip (like in *O. reticulata*). Small variations of tilt

make it appear either as in Fig. 9A or as in Fig. 9B (see § 1.2 and Fig. 3).

- In contrast to *O. reticulata*, the direction of the lamellae of the external XLM layer (E) is markedly oblique to the lip.
- The extent of the transition zone (T) varies. In most specimens, it continues all the way to the lip, and can be directly observed of the edge of the lip (see Figs. 8A and 8B). This feature does not constitute a reliable taxonomic character: in aged specimens (with a very thick lip) the transition zone often ends before the edge of the lip (like in *O. reticulata*, see § 4.1.1.3. and Fig. 6). The presence of an internal lining (Fig. 8) is occasionally seen at some distance from the lip, especially in aged specimens.

A number of Indo-Pacific *Oliva* species (see § 5.2) have this characteristic arrangement of XLM layers and form what will be referred to as the "oblique group". This structure is also found in a few American taxa.

#### 4.1.1.5. Exceptions.

Remarkable discontinuities in the enamel of the body whorl occur in the shell of two *Oliva* species: *O. undatella* Lamarck, 1811 (the type species of the subgenus *Strephonella* Dall, 1909) and *O. paxillus* Reeve, 1850 (the type species of the subgenus *Omogymna* von Martens, 1897). In these species the body whorl shows a discontinuity: it is divided by an oblique line into two sections of different structure. Examination of shell sections shows that in both cases, the external layer (E) and the transition zone (T) are present on the anterior (abapical) portion of the shell. The external layer (E) of both species belongs to the "oblique group" (see § 4.1.1.4).

- In *O. paxillus* (Fig. 10B) both the external layer (E) and the transition zone (T) become gradually thinner (as if planed down) and generally terminate flush with the surface of the body whorl. The discontinuity line observed on the body whorl is the trace of the transition zone (T).
- In *O. undatella* (Fig. 10C) both the external layer (E) and the transition zone (T) terminate abruptly. The observed discontinuity line corresponds to a sharp difference of levels on the body whorl.
- Another special case is that of the deep water "*Oliva*" *lacanientai* Greifeneder & Blöcher, 1985. In contrast to all other *Oliva* species, the shell (even when examined by electron scanning microscopy) has only two XLM layers (see discussion in section 4.4.).

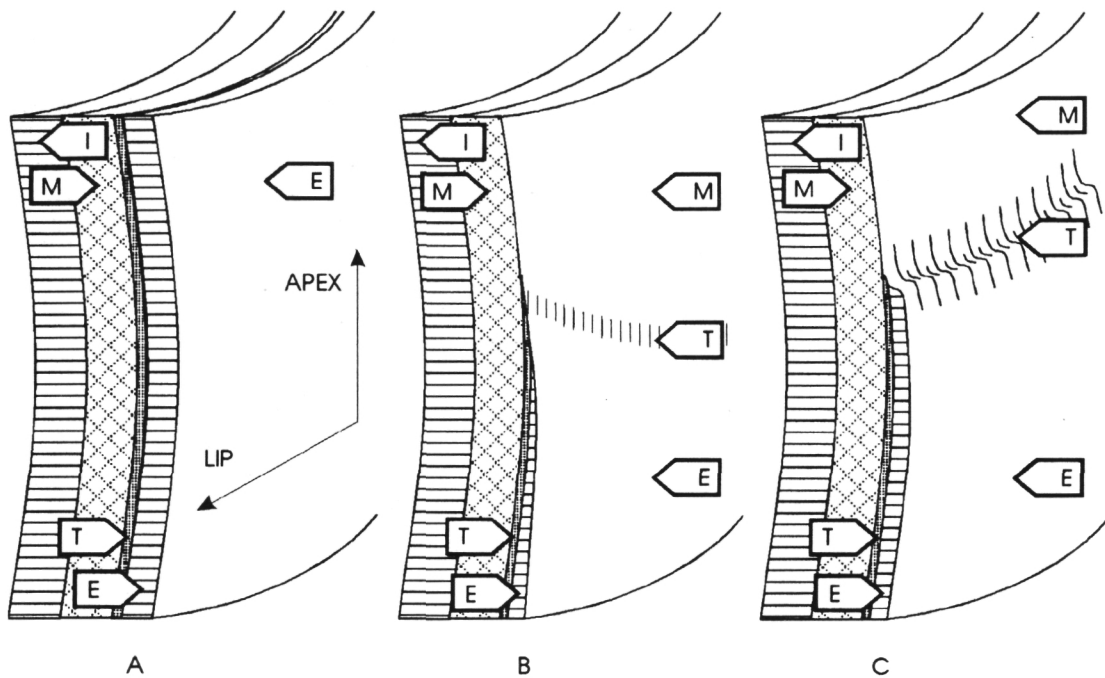


Figure 10. Particular cases. A: usual *Oliva* shell. B: *O. paxillus*. C: *O. undatella*.

4.1.1.6. Shell sections: Conclusions.

All the *Oliva* species examined so far share the same arrangement of the lamellae of the internal and the middle XLM layers (I and M). When species differ, it is mainly in the direction of the lamellae of the external XLM layer (E), which can be observed externally. So, in nearly all cases, the most relevant taxonomic information can be obtained without damaging the specimens.

4.1.2. Observation of shell surfaces.

The lamellae at the surface (see Plate 2) could be characterised by their shape, their length, their width and their direction.

4.1.2.1. Shape and length.

The shape and length of the lamellae varies from species to species. These might be useful indicative characters (despite of much intra-specific variability), but are quite difficult to quantify in a practical way. In addition, some "scrambled zones" with higher crystal disorder are occasionally seen in some shells of a few species.

4.1.2.2. Thickness.

The thickness (W) of the surface lamellae is easily measured, as described in § 3.3.2. Within a same species, W (measured at point D3, see § 3.3.3) has been shown to be correlated to the size of the shell (as shown for two species in Fig. 11). Large shells have wider lamellae (they could have had more lamellae).

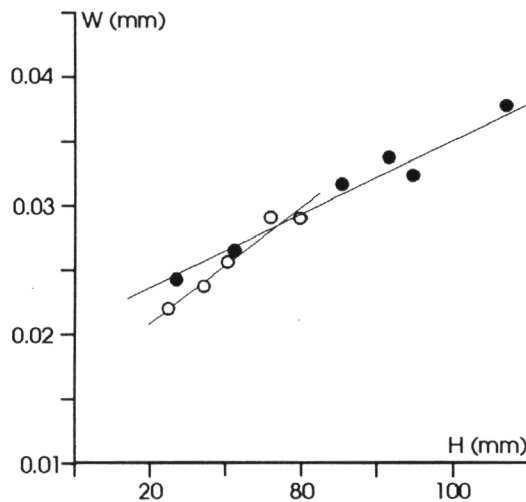
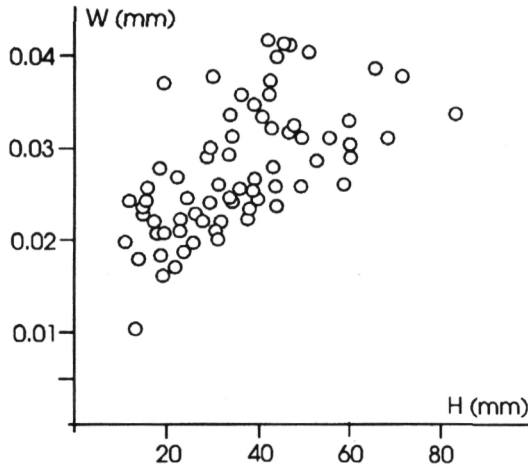
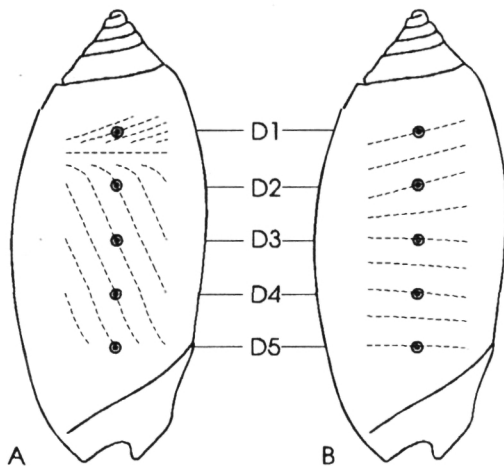


Figure 11. Thickness of surface lamellae (W, at point D3) vs. shell size (H). Black circles: *Oliva porphyria*. White circles: *Oliva lignaria*.



**Figure 12.** Thickness of surface lamellae (W, at point D3) vs. shell size (H). 73 *Oliva* taxa (see section 2, Material).



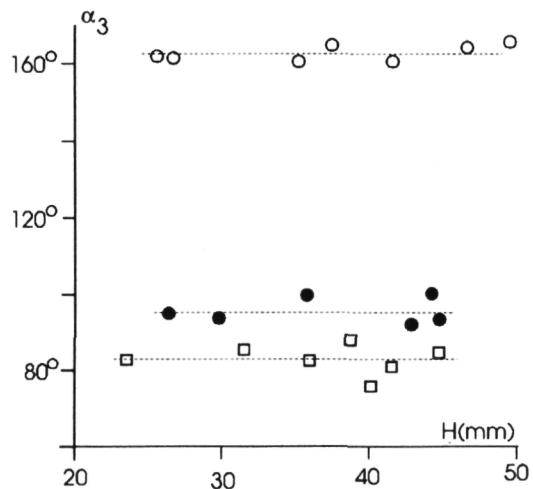
**Figure 13.** Examples of orientation of the surface lamellae. **A:** *Oliva splendidula*. **B:** *O. elegans*.

A scatter diagram of the thickness of the surface lamellae (W measured at point D3, see § 3.3.3) of 73 taxa of *Oliva* versus the length of the shell (H) is shown on Fig. 12. It can be seen that there is a general tendency for larger species to have thicker surface lamellae. There is much overlap and no clear cut groups emerge from the picture. In addition, the measurement W, even corrected for shell size, is quite variable in several species. In conclusion, W does not seem to constitute a promising taxonomic character.

**4.1.2.3. Direction.**

**4.1.2.3.1. Generalities.** The direction of the surface lamellae is very easily measured, as described in § 3.3.3. It can be seen (Fig. 13) that on the same shell, the direction of the surface lamellae varies regularly from point to point, hence the necessity of performing measurements at carefully determined points (see § 3.3.3 and Fig. 5). It can also be seen (Fig. 13) that the arrangement of the surface lamellae can differ very much from species to species.

For specimens of a same species, the direction of the surface lamellae (measured at the same point of the shell) displays (as expected) some individual variability but does not vary with shell size. An example on three species is given in Fig. 14 for the angle  $\alpha_3$ , measured at point D3 (see § 3.3.3 and Fig. 5B).



**Figure 14.** Direction of surface lamellae ( $\alpha_3$ ) vs. shell size (H). White circles: *Oliva splendidula*. Black circles: *O. peruviana*. White squares: *O. funebris*.

**4.1.2.3.2. Reliability of measurements.**

Both differences from species to species and independence from shell size suggest the potential of direction measurements as a taxonomic character for *Oliva* species.

The coefficient of variability (CV, the standard deviation expressed as a percentage of the mean) affords a comparison of the degree of variability in different species (MAYR, 1969). For seven of the nine species tested, the measurement  $\alpha_3$  has a CV lower than 4.5 %. This is comparable to the CV of many of the linear distance measurements utilised in *Oliva* taxonomy (see TURSCH & GERMAIN, 1985). For six out of the nine species tested, the measurement  $\alpha_3$  has a smaller CV than any



other dorsal angular measurement (see Table 2). The measurement  $\alpha_L$  is slightly more variable than  $\alpha_3$  for seven out of the nine species tested. It presents the advantage of being very easy to determine.

The experimental error being quite small (see Table 1), the high CV values found for the two American species *O. sayana* and *O. reticularis* must reflect the specially high individual variability of these taxa.

The values of  $\alpha_L$ ,  $\alpha_D$  and their coefficients of variability for 75 taxa in the genus *Oliva* are reported in Table 3.

#### 4.2. Other genera in Olividae.

A preliminary inspection indicated that more variation in shell structure occurs in other molluscs of the family Olividae. Only the two inner XLM layers present in *Oliva* were seen in *Agaronia acuminata* Lamark, 1811 and *Olivella japonica* Pilsbry, 1895. *Olivancillaria urceus* (Röding, 1798), *Olivella volutella* Lamark, 1811 and *Olivella biplicata* Sowerby, 1825 had the three layers typical of *Oliva* but in contrast *Ancilla lienardi* Bernardi, 1858 has four layers, plus a well marked transition zone. A great number of species has to be examined and a separate, detailed investigation is clearly called for.

## 5. DISCUSSION.

### 5.1. Results.

The purpose of this study was to see if the structure of the shell could provide additional (and much needed) taxonomic characters for shells of the genus *Oliva*. The answer is positive: many *Oliva* taxa are separable on the basis of the direction of their surface lamellae.

The non-destructive measurements  $\alpha_L$  and  $\alpha_3$  proposed here are fast (a few minutes) and reproducible (to less than 2%). Individual variation compares favourably with that of other measurements utilized in the genus: 71% of the taxa have a coefficient of variability smaller than 5% on  $\alpha_L$  and 67% of the taxa have a coefficient of variability smaller than 5% on  $\alpha_3$ . Rough estimations of  $\alpha_L$  and  $\alpha_3$  can often be made even with a small hand lens.

The present study was limited to the central part of the body whorl, where the arrangement of the internal layers seems constant for all *Oliva* species. Other parts of the shell (the fasciole, the columella, the spire) have more complex structural arrangements and have not been described here. The shell structure of the body whorl of other genera in Olividae appears to be more varied than in *Oliva* and requires a separate investigation.

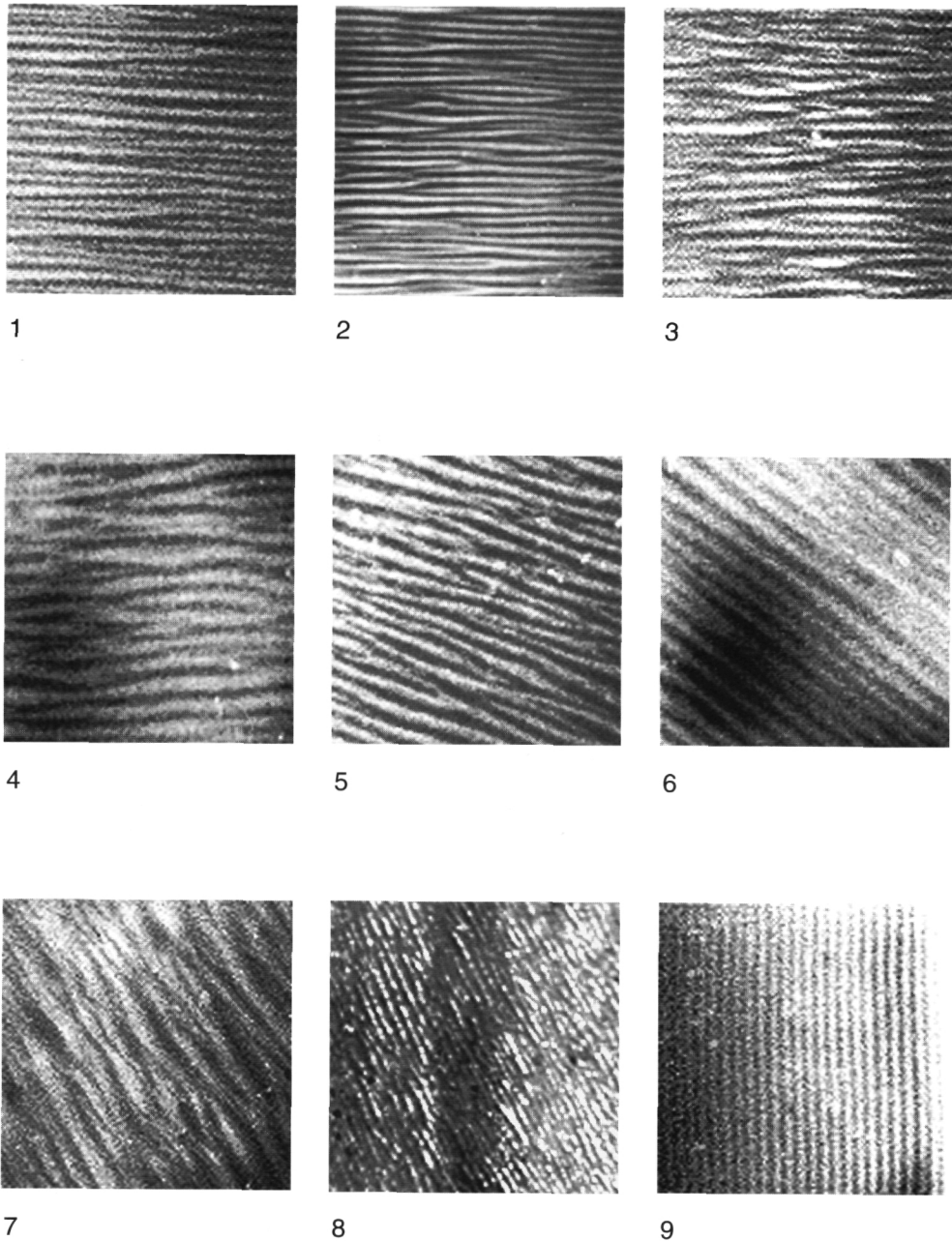
species	n		$\alpha_1$	$\alpha_2$	$\alpha_3$	$\alpha_4$	$\alpha_5$	$\alpha_L$
<i>O. elegans</i>	6	mean	75.5°	78.2°	89°	99.8°	98.8°	89.4°
		CV	3.48	4.55	3.63	7.19	12	3.87
<i>O. funebris</i>	7	mean	78°	80.2°	83.9°	103°	103°	92.3°
		CV	8.13	5.44	4.45	9.64	6.18	3.11
<i>O. irisans</i>	15	mean	82.4°	80.2°	86.5°	95.2°	99.3°	88.9°
		CV	3.33	4.92	1.62	4.84	9.15	2.95
<i>O. peruviana</i>	6	mean	92.4°	86.5°	95.8°	103°	104°	105°
		CV	11.6	5	3.52	7.46	10.4	4.04
<i>O. reticularis</i>	12	mean	87°	87.6°	102°	116°	111°	133.5°
		CV	7.92	8.7	12.5	9.87	6.22	17.33
<i>O. reticulata</i>	6	mean	76.5°	76.8°	82.6°	95.6°	108°	89.7°
		CV	7.57	8.83	3.92	4.52	7.52	3.79
<i>O. sayana</i>	6	mean	74.6°	79.9°	92.8°	116°	116°	94.6°
		CV	6.99	7.62	10	9.38	7.49	11.69
<i>O. splendidula</i>	7	mean	89.8°	159°	163°	156°	140°	178.2°
		CV	17.4	4.05	1.34	3.53	10.1	4.2
<i>O. tricolor</i>	6	mean	76.9°	83.5°	86.9°	98.3°	102°	89.1°
		CV	5.05	5.23	3.69	1.94	11.6	5.19

**Table 2.** Direction of the surface lamellae. Individual variability. Measurements and their dispersion for nine *Oliva* species. SD = standard deviation. CV = coefficient of variability (see text).

species	loc	n	$\alpha_L$ (in °)		$\alpha_D$ (in °)	
			mean	CV	mean	CV
<i>amethystina</i>	IP	5	171.6	2.69	ns	x
<i>arctata</i>	IP	5	91	1.1	89.6	1.27
<i>australis</i>	IP	5	88	2.45	89.6	2.18
<i>baileyi</i>	IP	2	127	x	122.5	x
<i>buelowi</i>	IP	5	170.8	0.87	ns	x
<i>bulbiformis</i>	IP	5	86	3.39	82.4	4.08
<i>bulbosa</i>	IP	5	89.8	0.93	94	3.77
<i>caerulea</i>	IP	5	83	1.21	80.2	2.23
<i>caldania</i>	IP	5	82.8	2.32	83.2	3.93
<i>carneola</i>	IP	5	87	1.41	80.4	2.43
<i>carnicolor</i>	IP	5	165.6	2.16	ns	x
<i>carolinensis</i> (†)	WA	5	158	16.14	119	20.53
<i>caroliniana</i>	IP	5	88	2.27	88.8	2.44
<i>ceramensis</i>	IP	6	87.5	2.14	84.7	4.99
<i>chrysoplecta</i>	IP	4	164.8	2.29	161.5	2.6
<i>circinata</i> ( )	WA	5	114	8.84	99.6	7.19
<i>concovospira</i> ( )	IP	4	93.6	1.22	86.4	4.45
<i>concinna</i>	IP	5	89.6	1.27	85.6	3.17
<i>dubia</i>	IP	5	159.4	6.98	138.4	7.7
<i>elegans</i>	IP	6	89.4	3.87	89	3.63
<i>esiodina</i>	IP	5	181.2	1.58	164	3.57
<i>faba</i>	IP	4	90	0.91	84.25	4.48
<i>flammeacolor</i>	IP	5	92.2	2.7	89	1.12
<i>flammulata</i>	EA	5	90.8	0.49	88.8	1.67
<i>foxi</i>	EP	2	167	x	143.5	x
<i>fulgurator</i>	WA	5	132	2.89	119.4	5.82
<i>funnebralis</i>	IP	7	92.3	3.11	83.9	4.45
<i>hilli</i>	IP	5	89.8	6.65	84.4	6.84
<i>hirasei</i>	IP	5	88	2.27	83.2	2.74
<i>incrassata</i>	EP	6	117	6.42	96.3	5.56
<i>irisans</i>	IP	15	88.9	2.95	86.5	1.62
<i>julieta</i>	EP	4	133.8	2.47	96.5	1.04
<i>kaleontina</i>	EP	5	82.2	4.5	74.8	4.91
<i>lenhilli</i>	IP	2	114.5	x	108.5	x
<i>leonardhilli</i>	IP	7	139	15.2	112	15.2
<i>lignaria</i>	IP	5	89.4	1	86	5.93
<i>mantichora</i>	IP	5	168.2	7.44	135.7	4.74

species	loc	n	$\alpha_L$ (in °)		$\alpha_D$ (in °)	
			mean	CV	mean	CV
<i>miniacea</i>	IP	5	93.2	2.98	89.6	3.01
<i>mucronata</i>	IP	5	101.6	6.01	85.8	4.62
<i>multiplicata</i>	IP	6	145	15.5	109	13.2
<i>mustelina</i> ( )	IP	5	90.8	1.44	86.4	2.67
<i>neostina</i>	IP	5	91.2	2.94	86	0.82
<i>nigrita</i>	IP	5	92	3.84	89.8	2.66
<i>oblonga</i>	WA	5	136	11.27	121.2	6.58
<i>oliva</i>	IP	4	84.75	3.78	82.25	0.61
<i>olivacea</i>	IP	5	89	2.1	83.6	4.36
<i>panniculata</i>	IP	6	174	4.5	95.3	4.43
<i>parkinsoni</i>	IP	5	166.6	6.52	ns	x
<i>pacillus</i>	IP	5	159.8	4.67	155	7.51
<i>peruviana</i>	EP	6	105	4.04	95.8	3.52
<i>polita</i>	IP	6	177.5	2.25	165	3.04
<i>polpasta</i>	EP	5	75.8	9.25	82.6	5.59
<i>ponderosa</i>	IP	5	92.4	2.82	89.4	3.76
<i>porphyria</i> ( )	EP	5	114.2	3.68	108.2	3.83
<i>reclusa</i>	WA	5	103.6	3.25	102.6	4.17
<i>reticularis</i>	WA	5	136	5.12	114.2	6.3
<i>reticulata</i>	IP	6	89.7	3.79	82.6	3.92
<i>rubrolabiata</i> ( )	IP	5	95.6	1.75	87.8	1.25
<i>rufofulgurata</i> ( )	IP	5	178	2.33	142.5	3.91
<i>rufula</i> ( )	IP	5	91.6	1.25	81.6	7.28
<i>sayana</i>	WA	6	94.6	11.69	92.8	10
<i>scripta</i> ( )	WA	5	98.4	4.8	87	4.3
<i>semmelinki</i>	IP	5	162.2	3.09	160	3.67
<i>sericea</i>	IP	5	92.8	2.99	85.2	4.27
<i>sidelia</i>	IP	5	90.6	0.99	84.4	2.73
<i>solomonensis</i>	IP	5	89.4	1.27	84.8	2.11
<i>spicata</i>	EP	15	146	10.39	118	12.8
<i>splendidula</i>	EP	8	178.2	4.2	163	1.34
<i>tigrina</i> ( )	IP	5	93	2.28	88.6	3.71
<i>tricolor</i>	IP	6	89.1	5.19	86.9	3.69
<i>vermiculata</i>	WA	5	132.4	11.51	106	5.62
<i>vicweeei</i>	IP	2	87	x	80	x
<i>zombia</i>	WA	5	138.6	5.29	109	5.98

**Table 3.** Direction of the surface lamellae of *Oliva* taxa. Measurements  $\alpha_L$ ,  $\alpha_D$  and their coefficient of variability (CV). EA: East Atlantic; EP: East Pacific; IP: Indo-Pacific; WA: West Atlantic. Symbols: (|): cords at lip, see text § 3.3.3. (†): fossil species. ns: not seen.



**Plate 2.** Surface lamellae at mid-body whorl (x 64). Axis of shell: vertical. 1: *O. concavospira* (H: 36.03 mm). 2: *O. funebris* (H: 26.23 mm). 3: *O. rufula* (H: 30.02 mm). 4: *O. kaleontina* (H: 30.40 mm). 5: *O. peruviana* (H: 43.27 mm). 6: *O. polpasta* (H: 36.17 mm). 7: *O. amethystina* (H: 42.21 mm). 8: *O. multiplicata* (H: 42.94 mm). 9: *O. semmelinki* (H: 15.75 mm).

	<i>n</i>	$\alpha_L$	$\alpha_3$
<i>O. spicata</i> (W. Mexico)	6	132.2 (CV=6.82)	106.7 (CV=6.54)
<i>O. spicata</i> (W. Panama)	9	156.3 (CV=7.18)	126.3 (CV=11.15)

**Table 4.** Geographic variation in the direction of the surface lamellae. *O. spicata* from W. Mexico and from W. Panama. Measurements  $\alpha_L$ ,  $\alpha_3$  and coefficient of variability (CV).

In many cases, the direction of the surface crystals of *Oliva* species seems to reflect taxonomic affinities. For instance, all the examined Indo-Pacific species that have been placed in the subgenus *Annulatoliva* Petuch & Sargent, 1986 (*O. amethystina*, *O. buelowi*, *O. carnicolor*, *O. parkinsoni*) have  $\alpha_L$  values in the range 165-172°. In contrast, all the examined species that have been grouped in the subgenus *Miniaceoliva* Petuch & Sargent, 1986 (*O. flammeacolor*, *O. hirasei*, *O. lignaria*, *O. miniacea*, *O. ponderosa*, *O. sericea*) have  $\alpha_L$  values in the very distinct range 83-94°. But in some other Indo-Pacific groups, this character does not appear to reflect phylogeny and the direction of surface crystals differs greatly between very closely related taxa. This is the case for *O. australis* ( $\alpha_L = 88$ ) and *O. leonardhilli* ( $\alpha_L = 139$ ). In the case of *O. panniculata* ( $\alpha_L = 174$ ,  $\alpha_3 = 95.3$ ) and *O. polita* ( $\alpha_L = 177.5$ ,  $\alpha_3 = 165$ ), the values are in close agreement for  $\alpha_L$  but are widely divergent for  $\alpha_3$ .

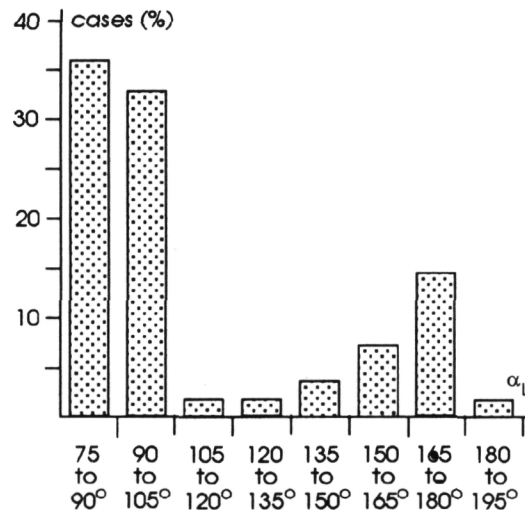
Small differences in crystal direction should be interpreted with great caution. Individual variation is quite large (CV over 10%) in a few species and in addition, geographic variation has been detected in some cases, for instance in *O. spicata* (see Table 4).

### 5.2. Trends.

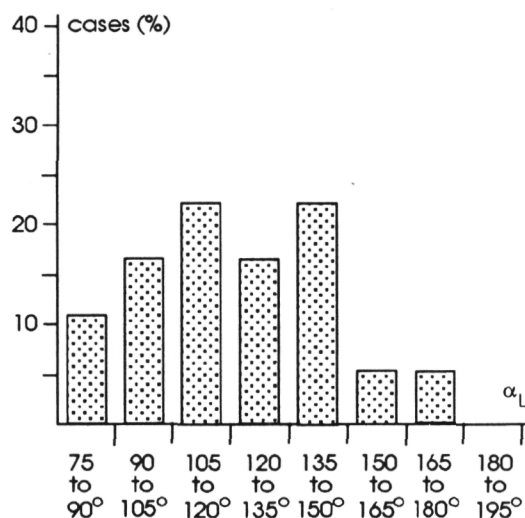
The frequency distribution of the easiest measurement,  $\alpha_L$ , is quite peculiar. Analysis of the data of Table 3 show (Fig. 15) that the Indo-Pacific *Oliva* taxa have a distinctly bimodal  $\alpha_L$  distribution: the great majority unmistakably belong either to the "horizontal" or to the "oblique" group. Only 4 taxa (of rather peculiar lineages) occupy intermediate values. These are *O. lenhilli* ( $\alpha_L = 114.5$ ), *O. baileyi* ( $\alpha_L = 127$ ), *O. leonardhilli* ( $\alpha_L = 139$ ) and *O. multiplicata* ( $\alpha_L = 145$ ).

In contrast, the American taxa (Fig. 16) (the closely related Western Atlantic and Eastern Pacific *Oliva* faunas are here considered together) have a regular, monotonous distribution that is centered on the intermediate values of  $\alpha_L$  rarely observed for Indo-Pacific taxa).

Indeed 61% of the American taxa are in the 105-150° range, where only 8% of the Indo-Pacific taxa do occur.



**Figure 15.** 53 Indo-Pacific *Oliva* taxa. Direction of surface lamellae. Histogram: distribution of  $\alpha_L$ .



**Figure 16.** 19 American *Oliva* taxa. Direction of surface lamellae. Histogram: distribution of  $\alpha_L$ .

### 5.3. Interpretation.

The "oblique" structure found in some American species certainly constitutes an old character, probably antedating the closing of the Panama isthmus and the separation of the Western Atlantic and the Eastern Pacific faunas, as this feature is already strongly marked ( $\alpha_L = 158$ ) in the fossil *O. carolinensis* (from the Caloosahatchee Formation). At first sight, the comparison of figures 15 and 16 (two separate groups opposed to one very variable group) evokes a case of evolution by disruptive selection (see for instance FUTUYMA, 1986: 154), suggesting that the Indo-Pacific *Oliva* species could derive from an ancestral American stock.

Such an interpretation should still be considered with much circumspection, as the data could as well (and possibly better) be interpreted in terms of adaptation. The direction of the surface crystals probably influences the mechanical resistance of the shell (as shown by CURREY, 1990 cited in VERMEIJ, 1993). Mollusc-eating crustaceans are larger, more powerful and better armed in the Indo-Pacific region than in the Western Atlantic (VERMEIJ, 1978), resulting in the general development of more efficient shell armour in the Indo-Pacific (VERMEIJ, 1993). It is thus plausible that the Indo-Pacific *Oliva* would be selected for the shell structures offering maximal resistance, while the American taxa (with the exception of *O. porphyria*, *O. kaleontina* and *O. splendidula*, all are very closely related and grouped in the genus *Strophona* Mörch, 1852) could afford to display a wide range of variation. But we have no experimental data so far on such a correlation between shell microstructure and mechanical resistance in *Oliva* (this should ideally be demonstrated on shells differing *only* in the orientation of surface lamellae).

The difference in frequency distribution reported here is not the only character differentiating the American and the Indo-Pacific *Oliva* faunas. A rather similar (but inverted) situation has already been reported (TURSCH, 1988) for protoconch characters: here the American taxa display a very large range of variation while the Indo-Pacific taxa are concentrated in a narrow, central range. Extreme variability in several shell characters and conservatism in colour patterns seem to be the hallmark of many American *Oliva* species.

### 5.4. The case of "*Oliva*" *lacanientai*.

It has been mentioned (in section 4.1.1.5.) that the deep water "*Oliva*" *lacanientai* Greifeneder & Blöcher, 1985 has only two

XLM layers, in contrast to the three layers present in all other *Oliva* species that we have examined. In the original description, the authors have underlined that its "subgeneric status is doubtful" and concluded that this species "is not closely related to any species of Olividae known so far". This additional evidence reinforces their doubts. In our opinion, it constitutes a strong evidence that the species does not belong to the genus *Oliva* and should be classified in a separate genus. Such a step should preferably be taken only after the soft parts of the animal could be studied.

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