

Non-isometric growth and problems of species delimitation in the genus *Oliva*¹

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ABSTRACT. The shape of the shell of some *Oliva* species undergoes abrupt changes during growth. If undetected, this often overlooked phenomenon can cause serious errors in the delimitation of morphospecies. Examples of non-isometric growth are reported and discussed.

RESUME. La forme de la coquille de quelques espèces d'*Oliva* subit des changements abrupts durant la croissance. La non-détection de ce phénomène, souvent négligé, peut entraîner des erreurs sérieuses dans la délimitation des morpho-espèces. Des exemples de croissance non-isométrique sont rapportés et discutés.

1. INTRODUCTION

All species of *Oliva*—like nearly all species of marine molluscs— have been described solely on the basis of morphological characters (mostly features of the shell). Other approaches, such as molecular genetics, might be preferable in theory but in practice the taxonomist deals nearly exclusively with morphospecies, resting upon the demonstration of morphological gaps. Such a demonstration is, of course, more objective if it rests upon quantitative characters.

Difficulties in taxonomic interpretation may arise for a variety of causes. For instance, species undergo morphological modifications over the course of time (this case, the *chronospecies* of the palaeontologist, will not be considered here). The delimitation of living species is fraught with other problems. Examples abound of animal species in which adults and juveniles, males and females and even different populations of a same species have very different morphological characteristics. So, it is important to keep in mind that morphological gaps do unambiguously demonstrate the existence of separate species only if three conditions (at least) are met:

a. The samples to be compared must be strictly sympatric. It is fully expected (see MAYR 1969 and FUTUYMA 1986) that different populations of a same species could be separated by a suitable combination of

characters. This is very much the case in the genus *Oliva*, in which populations of a same species - even when separated by very short geographical distances - are often fully separable. Sympatry should then be reduced to syntopy (see TURSCH 1994, 1995).

In these conditions, what should one do with allopatric populations? The set of local populations of every *Oliva* species studied so far appears to form a morphological continuum, in which no population can be separated from *all* the others (for an example, see TURSCH & GREIFENEDER 1996). The solution is then to test the presence of morphological gaps not between populations but between sets of populations covering the whole distribution ranges (TURSCH 1995).

b.- The discriminating characters should not be sex-related. In the case of *Oliva*, no significant sexual dimorphism could be evidenced (HUART, unpublished observations) in the shells of dissected series of the rather unrelated species *O. tigrina* Lamarck, 1811 (from Madagascar), *O. amethystina* (Röding, 1798) and *O. oliva* (Linnaeus, 1758) (both from the Philippines). The only case of sexual dimorphism reported so far is a slightly differential growth for male and female Indian specimens of *O. oliva* and is restricted to very large specimens of over 39.5 mm (KASINATHAN, MARUTHAMUTHU & TAGORE, 1987). Recent work (KANTOR & TURSCH, unpublished) could not evidence any sexual dimorphism in the population

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of *O. oliva* (from Sisimangum Beach Hansa Bay, Papua New Guinea) that will be discussed here under.

c.- Separations should rest upon unbiased samples. In practice, it is often difficult to check if this obvious requirement is met. The field collector, especially when dealing with abundant species, is often inclined to collect only the most 'interesting' specimens (extremes in the distribution of some attribute), neglecting the 'uninteresting' intermediates. Such biased samples are a frequent cause of taxonomic errors, because shells are generally not described by the same people who have collected them in the field. Authors are therefore often unaware of the collecting bias affecting the samples they study. For instance, a sample of *Oliva miniacea* (Röding, 1798) from Kwajalein Atoll, strongly biased for extremes in size, led to the description of the small specimens as a separate species, *O. berti* Terzer, 1986 (see TURSCH & GREIFENEDER 1996).

There is still an additional, often overlooked risk of errors: the growth pattern of many species undergoes rather abrupt changes. If this phenomenon is undetected, there is an obvious danger of splitting conspecific young and old specimens into separate, artificial "species" reflecting different, successive patterns of growth.

The present paper draws attention to the problems raised by some *Oliva* species in which the shape of the shell is greatly modified during growth. It only aims at illustrating the existence of complex cases, not at their rigorous statistical analysis.

2. OBSERVATIONS and INTERPRETATION

2.1. The general case: isometric growth.

Massive experimental evidence (see, amongst others, TURSCH & GERMAIN 1985; VAN OSSELAER & TURSCH 1993a; VAN OSSELAER & TURSCH 1993b) has shown that most linear measurements on *Oliva* shells can be approximated as being in isometric relation. The relationship between any two teleoconch linear measurements X and Y can be generally approximated as being linear. A few examples, selected amongst many others, are given here. Fig. 1 illustrates the relation of D (the maximum diameter) and H (the total length) with the length of the lip, L (for a definition of these measurements, see TURSCH & GERMAIN 1985). Fig. 2 depicts the relation of DN , a measure of the width of the anterior notch (for definition, see VAN OSSELAER & TURSCH 1993a) with L . Fig. 3 shows the variation of the fasciolar zone measurements PLI , UF and BW (for definitions, see VAN OSSELAER & TURSCH 1993b) with H .

It can also be seen that, in all these examples, the intercept with the Y axis is negligible, the regression lines passing practically through the origin of the axes. This means that, in most cases, one can consider the

ratios Y/X as constant for a given phenon. These ratios can therefore constitute reliable taxonomic discriminants.

It is important to be aware that the samples used for establishing the regression lines of Figs. 1, 2, 3 are strongly biased in order to represent all size classes. So, the frequency of sizes within the growth series is very different from that of natural populations.

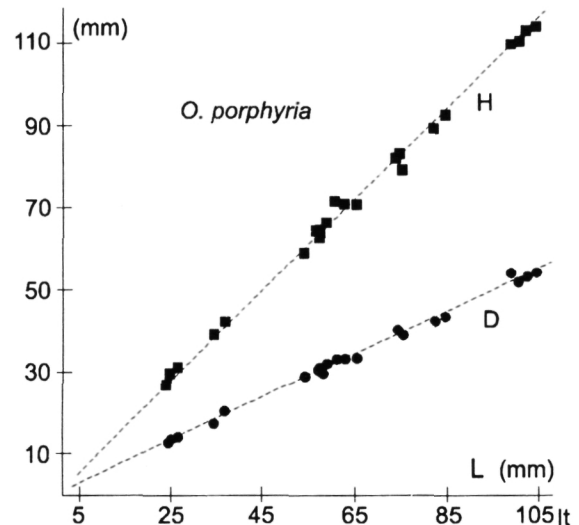


Fig. 1. Example of isometric growth. *Oliva porphyria*. Scatter diagram of teleoconch measurements H and D vs. shell size, expressed as the length of the shell, L .

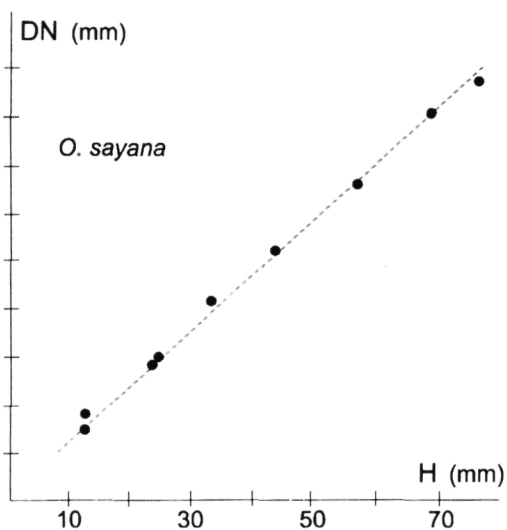


Fig. 2. Example of isometric growth. *Oliva sayana*. Scatter diagram of anterior notch measurement DN vs. shell size, expressed as the length of the shell, H .

Instead of reducing extensive variables to ratios of linear measurement (as in Figs. 1, 2, 3) to yield descriptors of shape, one could also use as internal

reference PNW (the number of postnuclear whorls) to yield *descriptors of growth*. Due to the helico-spiral growth of the shell, one cannot expect a linear teleoconch measurement *Y* to vary in a linear relation with PNW. As an example, specimens of a population of *O. rufula* Duclos, 1840 from Hansa Bay show a regular variation of *D* and *H* with PNW (see Fig. 4). As for most *Oliva* shells, the observed curvature is rather weak. Although the curve in Fig. 4 has an exponential aspect, this is not a case of allometric growth (because one is not comparing two linear measurements). With the possible exception of the slight sexual dimorphism reported for very large specimens in an Indian population of *O. oliva* (see § 1b), no case of strict allometry has been yet reported in *Oliva* shells.

This does not mean that the growth of *Oliva* shells is always isometric. In several species, the shape of the shell obviously varies during growth. Two different cases will be reported and discussed here.

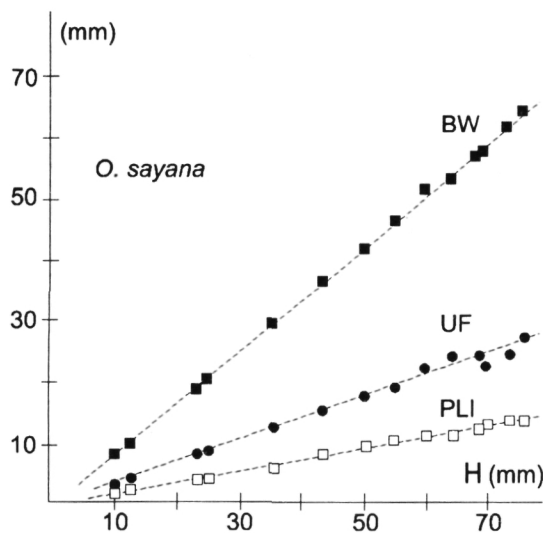


Fig. 3. Example of isometric growth. *Oliva sayana*. Scatter diagram of fasciolar zone measurements PLI, UF and BW vs. shell size, expressed as the length of the shell, *H*.

2.2. Non-isometry resulting from changes in lip angulation: *Oliva buelowi* Sowerby, 1889.

2.2.1. Data.

In the species *O. buelowi* Sowerby, 1889, the shapes of juvenile and "adult" shells are strikingly different. The shells undergo two consecutive shape transitions during their growth. A first modification in shape (and colour pattern) has been reported for very small shells (in the range 7.5-8.5 mm) by TURSCH, GERMAIN & GREIFENEDER (1986) and will not be re-discussed here.

The covariation of longitudinal measurements (all in the direction of the shell axis), such as *L*, *H* and *LW* (defined in TURSCH & GERMAIN 1985), is linear, just

like in the "normal" example of Fig. 1. The same, except for a greater dispersion of experimental points (see Fig. 5), goes for radial measurements (all perpendicular to the shell axis), such as *D*, *X* and *R* (defined in TURSCH & GERMAIN 1985).

In sharp contrast, if one plots radial against longitudinal measurements, then the experimental curves exhibit strong deviations from linearity (see Fig. 6). An important change of shape (*D* and *X* measurements quite suddenly increase more than expected) takes place when the shell reaches a length (*H*) of very roughly 18 mm (about 60% of the maximum size). A diffuse transition zone between the two growth patterns starts at shell length of about 15 mm.

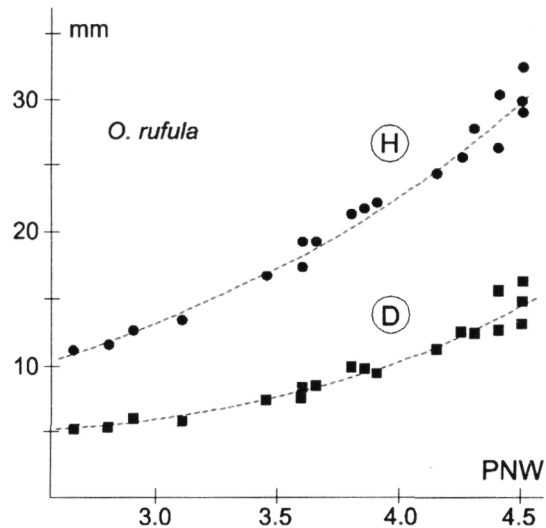


Fig. 4. *Oliva rufula*. Scatter diagram of *H* and *D* vs. PNW, the number of postnuclear whorls.

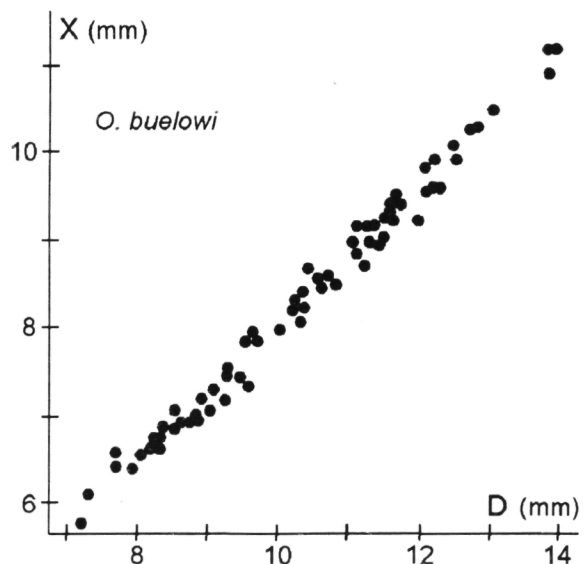


Fig. 5. *Oliva buelowi*. Scatter diagram of *R* vs. *D*.

3.2.2. Interpretation.

The curves of Fig. 6 cannot be explained by simple allometry, as this could not explain the peculiar, sigmoid-like aspect of the observed curves. The observed change in shape does not seem to be a case of abrupt change in the growth parameters of the generating spiral, as the spire of the shell appears to be quite regular. It is not an abnormality and it is not sex-related, as the phenomenon is observed for nearly all specimens of this population. It is also the norm in other populations (from the South coast of Papua New Guinea, from New Britain and from the Solomon Islands).

Large shells of *O. buelowi* (over 20 mm) have a very thick, angled, spiral thickening on the body whorl, whereas juveniles (under 15 mm) are completely regular, as sketched on Fig. 6. The change in shell shape does not always take place at *exactly* the same shell size. This explains why the points in the diagrams of Figs. 5 and 6 are much more scattered than usual (see Fig. 1).

What is the nature of the observed change in growth pattern? In the terms of the classical helico-spiral gastropod shell model (RAUP 1966) the observed facts can be explained by a delayed change in the shape of the generating curve (parameter *S*). Such cases of delayed development of a character in ontogeny are considered to be a special case of heterochrony: *hypermorphosis* (see e.g. GOULD 1977, SHELDON, 1993). Other examples of shape changes during the development of gastropod shells have been reported,

such as the case of fossil *Melanopsis* species (GEARY 1988).

3.3. Non-isometry resulting from changes in whorl expansion: *Oliva oliva* (Linnaeus, 1758).

3.3.1. Data.

Oliva oliva (Linnaeus, 1758) is one of the most protean species in the genus. The taxonomic problems raised by its extreme variability have been analysed by TURSCH, MISSA & BOUILLON (1992). The data reported here concern an intertidal population of *O. oliva* from Sisimangum Beach, Hansa Bay, Papua New Guinea. That particular population, probably the most intensively studied population in the whole genus, has previously been quantitatively monitored over nearly one year (TURSCH, QUIN & BOUILLON 1995).

The scatter diagram of diameter *D* vs. shell length *H* (see Fig. 7) has the usual, isometric appearance. In contrast, the scatter diagram of the lip length *L* vs *H* (see Fig. 7) shows a small, but definite deviation from linearity. The existence of an irregularity in the growth pattern becomes evident if one considers the scatter diagram of *D* and *L* vs the number of postnuclear whorls, PNW (see Fig. 8). One now clearly sees a discontinuity in the pattern of growth of *D* and especially of *H*. The corresponding changes in shell shape are sketched in Fig. 9.

Most individuals undergo a rather sudden increase of the length of the shell *H* (and of the maximum diameter *D*) at around 3.9 postnuclear whorls, corresponding to a shell length *H* of about 16-18 mm.

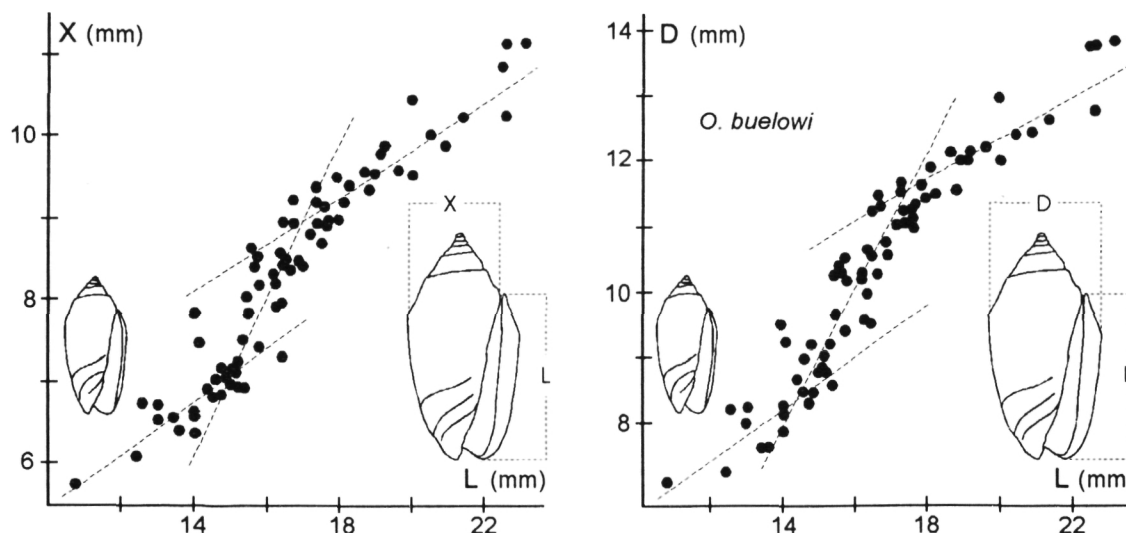


Fig. 6. *Oliva buelowi*. Scatter diagram of *X* (left) and *D* (right) vs. shell size, expressed as the length of the lip, *L*.

Some (much rarer) individuals continue along their initial growth trajectory for a while, the transition taking place before an observed maximum of 4.6 postnuclear volutions, corresponding to a shell length *H* of about 25-27 mm. Such individuals represent less than 1% in the well over 1000 specimens that were examined. Intermediate specimens, connecting the two successive growth patterns, are also very rare.

The change in growth pattern entails a change of *H* and *D*, as seen above. It also includes an abrupt change in the relative height of the spire, as evidenced by the scatter diagram of the spire height

(*H-L*) vs. *H* (see Fig.10): a rather sudden decrease of (*H-L*) is followed by an apparently normal development. This decrease in the relative height of the spire can be explained by the observation, on large specimens, of a change in the inclination of the spire whorls, relative to the axis of the shell, as illustrated in the sketch of Fig. 11A. This results in a decrease of the rate of growth of the spire. The change generally occurs quite abruptly (see Fig. 11A) on about 0.05 whorl. This is not a case of allometric growth, which would result in a progressive change in slope, as depicted in the hypothetical example of Fig. 11B.

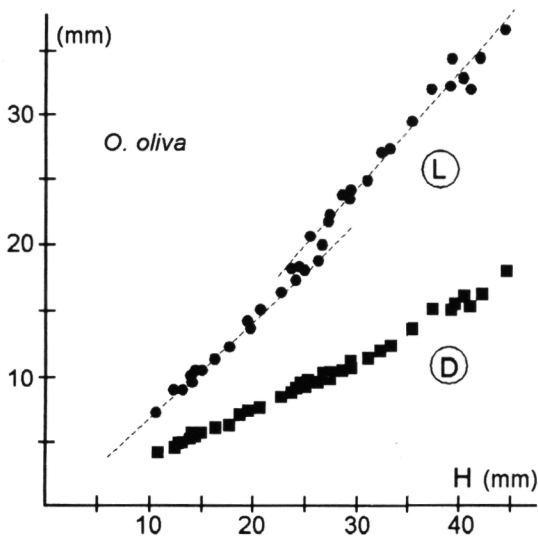


Fig. 7. *Oliva oliva* (growth series from Sisimangum Beach, Hansa Bay, PNG). Scatter diagram of *D* and *L* vs. *H*.

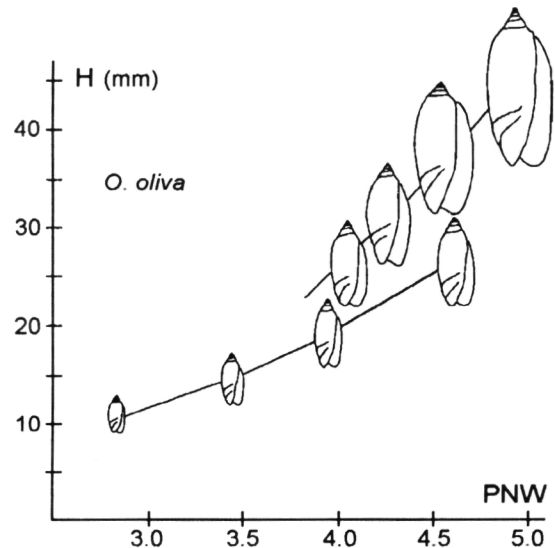


Fig. 9. *Oliva oliva* (growth series from Sisimangum Beach, Hansa Bay, PNG). Scatter diagram of *H* vs. PNW (shape of shells: note the variation of the position of the posterior notch).

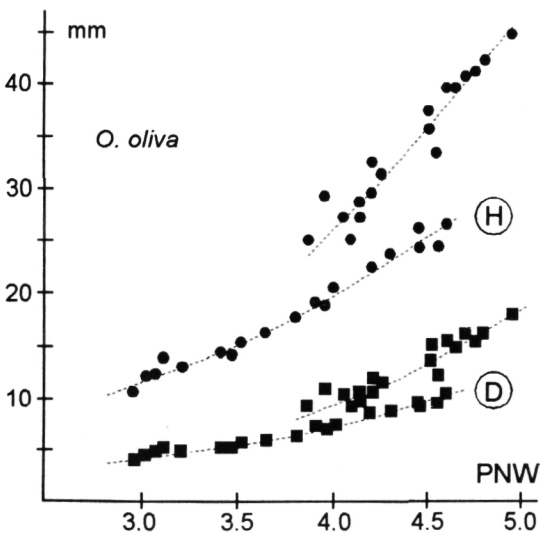


Fig. 8. *Oliva oliva* (growth series from Sisimangum Beach, Hansa Bay, PNG). Scatter diagram of *D* and *H* vs. PNW.

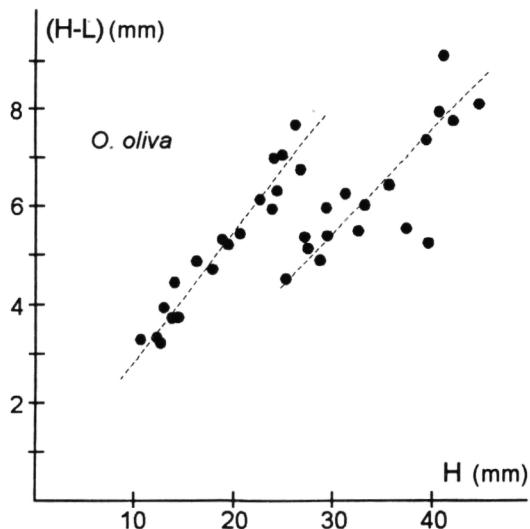


Fig. 10. *Oliva oliva* (growth series from Sisimangum Beach, Hansa Bay, PNG). Scatter diagram of the spire length (*H-L*) vs. *H* (see text).

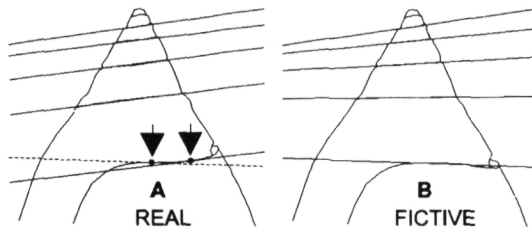


Fig. 11. *O. oliva*. **A:** Spire drawn to scale from actual specimen. The change in slope is abrupt and takes place over a small fraction of a whorl (indicated by arrows). **B:** Hypothetical example: change in slope due to allometric growth.

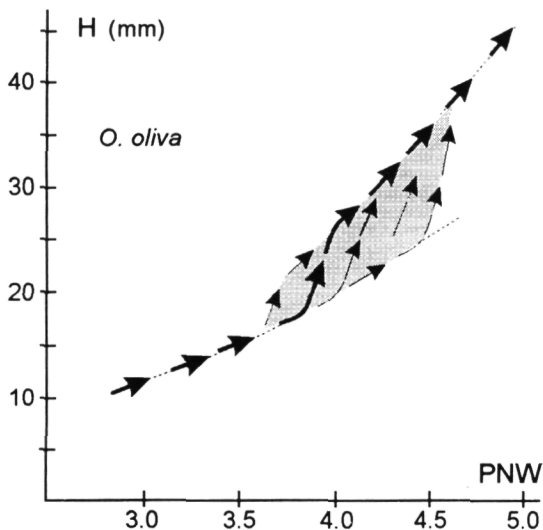


Fig. 12. *Oliva oliva* (Sisimangum Beach, Hansa Bay, PNG). Variation of H with PNW: inferred growth pattern of the population (see text).

3.3.2. Interpretation.

The general growth pattern of the population could be interpreted as in the sketch of Fig. 12. A change in shape does take place for all shells, but not *exactly* at the same time. Most specimens follow the path indicated by heavy arrows and only a few are found in the "transition zone" (shaded).

The rarity of intermediate specimens (connecting the two successive growth patterns) could be fully expected. For a shell reaching 5 postnuclear whorls, the chance of finding a particular specimen in a given 0.05 whorl range (corresponding to the transition zone) would be about one in a hundred, if shell growth is continuous (we have no reasons to doubt this). In the case of this population, the real odds are certainly much smaller because most individuals die before reaching the size at which the change in growth pattern takes place (see TURSCH, QUIN & BOUILLON 1995).

What is the nature of the observed change in growth pattern? The best explanation appears to be another case of hypermorphosis, this time entailing

a delayed, abrupt increase of W (the parameter of whorl expansion of RAUP 1966). This accounts for all the data, including the change in the inclination of the spire whorls.

4. DISCUSSION

Changes in lip outline. The phenomenon reported here above for *Oliva buelowi* has not caused taxonomic confusion, probably because the species was very rare in collections until recent years. In most other *Oliva* species in which adults have similar angulation at the lip [*O. incrassata* (Lightfoot in Solander, 1786), *O. parkinsoni* Prior, 1975; *O. mantichora* Duclos, 1840; *O. amethystina* (Röding, 1798), *O. peruviana* Lamarck, 1811], the phenomenon also had no taxonomic consequence, because lip angulation is already apparent in very small shells.

Changes in whorl expansion. Such cases are not rare. In several *Oliva* species, the rate of increase of the aperture becomes large enough to offset the effect of the rate of translation. Then the posterior tip of the outer lip as well as the parietal callus (on the columellar side) cease to move away from the apex during growth. In extreme cases, they can even raise above the channel of previous spire whorls, as for old specimens of *O. nigrita* (Karsten, 1789) (that case deals with a large number of nominal taxa and will be treated in a separate paper).

Such cases can lead to very serious errors in the taxonomic interpretation of morphological gaps. As an example, let us consider the sample of *O. oliva* (from Sisimangum Beach) considered here above in Fig. 10. A scatter diagram of $(H-L)/H$ vs. H/PNW (see Fig. 13) yields two very clearly separated groups.

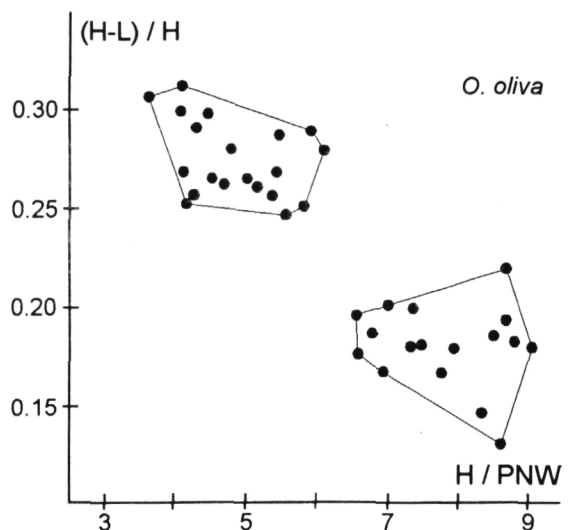


Fig. 13. *O. oliva*. (Sisimangum Beach, Hansa Bay, PNG, same specimens as Fig. 10). Scatter diagram of $(H-L)/H$ vs. H/PNW . This is an example of misleading separation (see text).

Such a separation is as good as one can expect. The sample being not only sympatric but strictly syntopic, one has logically to conclude to the presence of two different species (the possibility of sexual dimorphism having been excluded, see Section 1, § b). This case is not fictional: the group with large (H-L)/H corresponds to *Oliva longispira* Bridgman, 1906, considered as a valid species in the revision of PETUCH & SARGENT, 1986.

The observed separation is very real, but the interpretation is entirely wrong. In fact, one has just separated two consecutive stages in the development of *O. oliva*, assuming that they are not linked by intergrades. It so happens that individuals at an intermediate degree between these two stages are very rare (see § 3.3.2). The possibility of taxonomic errors due to differential growth is further amplified if the samples are biased for size (a common occurrence, see § 1.4).

Precautions in taxonomic interpretation. In theory, one could simply skip the problems of differential growth by restricting comparative studies to adult specimens only. But this raises the practical problem: when is an *Oliva* shell adult? "Adult" could mean that the animal is sexually functional, but we have yet no way of inferring this from the shell. Then does "adult" mean that the animal has reached its full size? The presence of a thickened lip is commonly considered as indicating the end of growth, but this assumption is most probably wrong. It is not supported by the study of shell sections of growth series, showing that specimens way below the maximum size can already possess a thick lip (see TURSCH & MACHBAETE 1995). So, one does not know if a given specimen of *Oliva* has stopped growing or not. When one says that a specimen of *Oliva* is "adult", one generally means that it does not present obvious juvenile characteristics (amongst others: a much thinner shell and a sharp lip).

The presence of changes in the slope of the spire of large *Oliva* specimens should be taken as a strong warning of possible taxonomic problems due to non-isometric growth. In such cases, one should exert special caution when the nature of morphological gaps is related to absolute size. Data on juvenile shells should be interpreted with great caution and all efforts should be directed at obtaining complete, uninterrupted growth series. Analysis of colour patterns often yields the first clue that objectively separated samples are in fact conspecific. Strong indications of conspecificity can also be derived from size-invariant characters (*intensive variables*) such as the protoconch measurements and the angular measurements utilised for describing the anterior notch (see VAN OSSELAER & TURSCH 1993a).

Biological significance. Hypermorphosis by increase of the rate of expansion of the aperture takes place quite late in shell ontogeny as if, at a certain moment, the shell had to rapidly make room for a sharp increase in the volume of the soft parts. It is tempting to speculate that this corresponds to sexual maturity (*Oliva* would not be the only case of getting a big mouth at puberty). Recent observations (Y. KANTOR, unpublished) established that the Sisimangum population of *Oliva oliva* does indeed reach sexual maturity at a size of about 18-20 mm. A problem remains: the gonads are not located near the aperture but are housed much higher in the shell.

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