Studies on Olividae. XVIII.
The distribution of *Oliva* species and the variation of their colour patterns in Hansa Bay (Papua New Guinea).

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ABSTRACT. Sediments of 64 stations where *Oliva* species have been collected in Hansa Bay (Papua New Guinea) have been analysed for carbonates, organic carbon and granulometry. Comparison between the classification of sediments and the distribution of 30 species shows that the latter fall into stenotopic and eurytopic species. Crypsis is generalised in both groups of species. The taxonomic consequences of crypsis are discussed.

RESUME. Les sédiments de 64 stations auxquelles des espèces d' *Oliva* ont été récoltées dans Hansa Bay (Papouasie Nouvelle-Guinée) ont été analysés pour leur teneur en carbonates, en carbone organique et leur granulométrie. La comparaison entre la classification des sédiments et la distribution de 30 espèces montre que ces dernières se divisent en espèces sténotopiques et eurytopiques. La crypsis est généralisée dans les deux groupes. Les conséquences taxonomiques de la crypsis sont discutées.

KEYWORDS. Mollusca, Gastropoda, *Oliva*, habitat, sediments, stenotopy, eurytopy, crypsis, polymorphism, taxonomy.

1. INTRODUCTION.

1.1. The problem.

One of the main biological causes of the old "*Oliva* problem" is the great variability of their colours and colour patterns. Colour variations said to be habitat-related have been observed by field collectors (such as HAMLYN-HARRIS, 1970) and the possibility that some described "species" could be ecovariants (GREIFENEDER, 1981) or colour morphs (PETUCH & SARGENT, 1986) has been raised. So the topic of habitat does not only concern ecology and ethology; it also has taxonomic implications.

1.2. Colour variation in molluscs.

A great number of studies (see ETTER, 1988) have been prompted by the obvious variations in the shell pigmentation of some molluscs. Much caution is necessary in the interpretation of such data. Many factors -such as the influence of environmental factors (COLTON, 1916; CREESE & UNDERWOOD, 1976; ETTER, 1988; MITTON, 1977), food (COLE, 1975; INO, 1949; LEIGHTON, 1961; MOORE,

1936), genetic determinism (ADAMKIEWICZ & CASTAGNA, 1988; INNES & HALEY, 1977; PALMER, 1985), selective predation (ELEK & ADAMKIEWICZ , 1990; REIMCHEN, 1979), behavioural polymorphism (GIESEL, 1970) and combinations of these can be (and have been) invoked to account for the observed facts.

The classical example of colour polymorphism in terrestrial molluscs populations is that of *Cepaea nemoralis* (CAIN & SHEPPARD, 1954; LAMOTTE, 1959; MURRAY, 1962; JONES *et al.* 1977) where the relative proportion of genetic morphs varies with habitat, even in localities separated by short distances and this has been correlated with the ability of a predator (thrushes, in that case) to detect their prey. Another visual predator, man, was shown to be responsible for the maintenance of colour polymorphism in an unidentified African Achatinid snail (OWEN & REID, 1986).

Conflicting interpretations have been proposed for some species. The degree of pale striping in the shell of the blue mussel *Mytilus edulis* was interpreted as having an adaptive significance, the morphs varying in the proportion of incident sunlight transformed into heath (MITTON, 1977). On the contrary, INNES & HALEY (1977) concluded that the coloration polymorphism of *Mytilus edulis* was determined by genetic rather than by environmental differences. Colour changes associated with a change of food were first reported for *Nucella lapillus* by MOORE (1936), after COLTON (1916) noted that the shell colour of this mollusc was influenced by the environment. It was later shown that the interpopulation variation in shell colour of *Nucella lapillus* is in part a response to a selective gradient in the physiological stress due to temperature and desiccation and that selection for crypsis by visually hunting predators does not appear to play a prominent role (ETTER, 1988).

In summary, the better studied cases in marine molluscs point at an *"intimate relationship between genotypic and environmental factors which influence prosobranch shell colour"* (COLE, 1975).

The enormous number and variety of colour forms in some natural populations could be an adaptation in itself, providing protection against visual predators. This hypothesis, known as reflective selection was proposed by MOMENT (1962) for extremely variable *Donax* species.

1.3. Purpose.

Any attempt at defining a potential correlation between the colour pattern of *Oliva* specimens and their habitat had to start with the accumulation of detailed habitat data. Very little detailed information on the habitat of *Oliva* species is available, excepted for a few qualitative reports (HEMMEN, 1981; WIDMER, 1981; WITTIG-SKINNER, 1981).

It was felt that useful information could be gained by a methodical study of the distribution of a number of *Oliva* species between different, well-characterised sediments within a restricted geographic range, followed by the analysis of a possible habitat-pattern relationship.

1.4. Location.

A most suitable location for such a study is provided by Hansa Bay, on the North coast of Papua New Guinea. It is a small semicircular bay (approximately 10 km in diameter) located in Madang Province, near the mouth of the Ramu River, about 110 nautical miles West of Madang. Laing Island (4°10'30"S -

144°52'47"E), lying roughly at the middle of the bay is a raised coral reef, covered with vegetation and separated from the mainland by depths of 45-50 m, muddy bottom. Climatic and hydrological data are described by BOUILLON *et al.* (1986) and CLAEREBOUDT *et al.* (1989). Detailed environmental data can be found in CLAEREBOUDT (1989). All the coast of Hansa Bay is lined with a long black sand beach, except for small Boro Beach that is formed of white, coarse coral sand.

2. MATERIAL AND METHODS.

2.1. The collection of *Oliva*.

The *Oliva* species of Hansa Bay have been under survey for nearly 20 years, since the establishment of King Leopold III Biological Station on Laing Island in 1974.

Oliva specimens have been obtained over the years by a variety of methods including dredging (using a small rectangular steel mesh dredge with an opening of 60 x 22 cm), trawling (with a small mesh 3 m rigid frame trawl), SCUBA diving (day and night dives), snorkelling in shallow waters, or beach collecting at the turn of the low tide. When diving, small rigid steel mesh hand "dredges" (in the shape of a dustpan, about 20 x 30 cm) have been especially productive. Baiting and trapping have been often used.

The 30 following species have been collected in Hansa Bay: *O. amethystina* (Röding, 1798), *O. athenia* Duclos, 1835, *O. buelowi* Sowerby, 1888, *O. bulbiformis* Duclos, 1835, *O. caerulea* (Röding, 1798), *O. carneola* (Gmelin, 1791), *O. ceramensis* Schepman, 1911, *O. concavospira* Sowerby, 1914, *O. concinna* Marrat, 1871, *O. sp. DHB* (abbreviation for species "D" of Hansa Bay), *O. dubia* Schepman, 1911, *O. elegans* Lamarck, 1811, *O. funebralis* Lamarck, 1811, *O. longispira* Bridgman, 1906, *O. mantichora* Duclos, 1835, *O. miniacea* (Röding, 1798), *O. mucronata* Marrat, 1871, *O. panniculata* Duclos, 1835, *O. parkinsoni* Prior, 1975, *O. paxillus* Reeve, 1850, *O. reticulata* (Röding, 1798), *O. rufula* Duclos, 1835, *O. semmelinki* Schepman, 1911, *O. sericea* (Röding, 1798), *O. smithi* Bridgman, 1906, *O. solomonensis* Petuch & Sargent, 1986, *O. tesselata* Lamarck, 1811, *O. vidua* (Röding, 1798), *O.* cfr. *volvaroides* Duclos, 1835, *O. sp. ZHB* (abbreviation for species "Z" of Hansa Bay).

As far as we know, this is by far the largest number of *Oliva* species ever recorded for a single locality, but this might only reflect an unusual collecting effort. Nearly all species have

been obtained in adequate numbers and most specimens have very accurate locality data. All species have been kept and observed in aquaria, some for several months.

The taxonomy of the genus *Oliva* being what it is (see ABBOTT, 1991), some of the above names will undoubtedly have to be corrected in the future. For the time being, the names *O. longispira* and *O. smithi* were selected only because of the existence of adequate type material. These two taxa are respectively the "*species L+X*" and "*species G*" of the "*Oliva oliva* complex" (see TURSCH & *al.*, 1992). *O. amethystina* and *O. mantichora* were formerly part of *O. annulata* Gmelin, 1791, a *nomen dubium* encompassing a mixture of species (TURSCH, GERMAIN & GREIFENEDER, 1986). *O. sp. ZHB* (the specific rank of which is still open to question) and *O. sp. DHB* have been collected in numbers but could not be positively identified. Decision on their taxonomic status depends upon future biometric comparison with all possibly related type material.

2.2. The analysis of sediments.

During 20 years of study, *Oliva* specimens have of course been collected at many more locations than we could analyse for sediment and representative stations had to be selected. Two maps (Figs. 1 and 2) show the points where samples were collected in the early months of 1992. Individual sampling stations can be identified in Table 1.

All sediments were collected by diving, about 800 g being taken in the first 6 cm of substrate, corresponding to the maximum observed burrowing depth observed for *Oliva* species (VAN OSSELAER & *al.*, 1993). The samples were homogenised, dried at 70-80°C in an oven at Laing Island, individually sealed and sent to Brussels for analysis. The colour of the dried sediments was determined with the Rock Colour Chart of the Geological Society of America. Each sample was separated (homogeneous fractionation by inquartor) into a fraction of about 10 g for carbon analysis and a fraction of about 100 g for granulometric analysis. All weightings were effected with a 0.01 g precision.

Granulometric analysis was effected by sieving, using the Udden scale modified by Wenthworth. Sieves were selected for the sand's range, as commonly used in studies of benthic fauna (see for instance JONES *et al.*, 1990). The samples were passed through a series of sieves (2000, 1000, 500, 250, 125 and 63 µm mesh) in a vibrating shaker (HAVER and BOEKER) for 20

minutes (15 minutes for calcareous sands that are subject to rapid mechanical wear).

For total carbon analysis, an aliquot of about 10 g of sample was finely ground in a FRITSCH apparatus (type WRR 731 1/4) for 5 min at 98 rpm. Analysis was effected by pyrogenation followed by measurement of the released carbon dioxide with a STRÖHLEIN carbon doser calibrated with Standard B.C.S. Steel 163/2. Temperature and atmospheric pressure corrections were accounted for (using the Ströhlein's "Umrechnungstabelle zum Kohlenstoffbestim-mungsapparat").

The same technique was used for organic carbon analysis, but after prior elimination of the carbonates by treating with 50% HCl until no more effervescence was observed, then drying on a hot plate. Carbonate content is calculated from the difference between the total carbon and the organic carbon.

Every sample was thus characterised (see VAN OSSELAER, 1992) by a reference number, a date and the 13 following parameters: locality, depth, colour, % total carbon, % organic carbon, % carbonates and the percentages of the seven textural classes (>2000 µm, 2000-1000 µm, 1000-500 µm, 500-250 µm, 250-125 µm, 125-63 µm and < 63 µm).

3. RESULTS.

3.1. The classification of sediments.

The data obtained on the sediment samples are given in Table 2. Multivariate analysis soon revealed that some order was hidden in that apparent chaos.

Application of the classical U.P.G.M.A. (Unweighted, Pair-group, Method using arithmetic Averages) clustering method (see SNEATH & SOKAL, 1973) using squared Eucliduan distances to the matrix containing six textural classes, the percentage of organic carbon, the percentage of carbonates and depth yields the dendrogram shown in Fig. 3. Taking all seven classes into account would introduce redundancy, as the sum of the classes is necessarily 100%. Sediments are characterised mainly by either fine or coarse particles, so we elected to eliminate one of the 3 intermediate textural classes. Amongst these, the class 250-125 µm has the smallest contribution to the total variation (in the analysis of principal components on raw data) and was therefore discarded.

It can be seen that the sediments fall into two clusters that are very clearly separated (over 50% of the maximal distance between groups).

One of these clusters corresponds to light-coloured coral sands, with coarse particles and a high carbonate content. Colours of dry samples of this group were: bluish white 5B 9/1, dusky yellow 5Y 6/4, grayish yellow 5Y 8/4, light olive gray 5Y 6/1, very pale orange 10YR 8/2, yellowish gray and yellowish gray 5T 7/2. The other cluster corresponds to dark terrigenous sediments with fine particles and low carbonate content. Colours of dry samples of this group were: dark greenish gray, dark greenish gray 5GY 4/1, grayish olive 10Y 4/2, greenish gray 5GY 6/1, light olive gray 5Y 5/2, olive gray, olive gray 5Y 3/2 and olive gray 5Y 4/1. For the sake of simplicity we shall not use the rich vocabulary available for sediments (see for instance COLLINSON & THOMPSON, 1989) and these groups will be here under referred to as "black substrate" and "white substrate".

U.P.G.M.A. clustering works on distances in the attribute hyperspace and gives no information on the relative importance of the different factors under consideration. This was obtained by the equally classical F.A.C. (Factorial Analysis of Correspondences) method, first effected on all the factors considered in the analysis here above. The same analysis, performed with all textural classes (this hardly brings any modification in this case) is illustrated in figure 4. It fully confirms not only the existence of the two groups "black" and "white" obtained by U.P.G.M.A. but also the correctness of their interpretation. The principal axis (52.7 % of the total inertia) corresponds to the textural classes, ordered by size. The least important factors are depth and organic carbon.

The same analysis, effected without considering depth hardly shows any modification. This might appear surprising at first sight but is quite logical because organic matter is related to depth, the role of which depends upon the nature of the sediment. This is confirmed by the observation that when F.A.C. are performed separately on each group of sediments (not illustrated here), the contributions of depth and organic carbon become apparent, especially in the case of black sediments.

Very similar results were obtained by A.P.C. (Analysis of Principal Factors, not illustrated here).

The clustering of sediments into two groups can even be evidenced in a much simplified representation (Fig. 5) in which all stations are reported on a scatter diagram of the carbonate content *vs.* depth.

It must be stressed that this classification into two clear-cut, compact groups does not encompass all the sediments of Hansa Bay but only those in which *Oliva* specimens have been found. The two groups of sediments are most probably bridged by intermediate, deep water points, where *Oliva* have not been met with.

3.2. The distribution of species.

The occurrence of the various *Oliva* species at the different stations, together with a brief description of their common habitat, is given in Table 3.

3.2.1. Correlation with depth.

The distribution of the *Oliva* species in Hansa Bay is obviously related to depth, as can be seen on the graph of figure 6. Some species are restricted to deep water and some others to shallows. One will notice that the observed depth range of some species is rather extensive. Specimens of *O. amethystina, O. panniculata* and *O. paxillus* have exceptionally been collected at much greater depths than normal. These rare findings occurred only on very steep reef slopes and have not been reported in the graph, as they are most probably accidental (on such slopes, an unsuccessful attack by a predator could result in a considerable fall). With the exception of the widespread *O. carneola,* wide depth ranges seem to be a feature of deep water species.

The graph of figure 7 gives the number of species as a function of depth. The curve sharply culminates at 5m (where two thirds of the Hansa Bay species can be found) then shows a rapid, regular decrease.

The distribution of *Oliva* species is certainly not a function of depth alone. If this would be the case, all shallow water species would be expected to coexist, which is not at all the observed situation. One should be aware that the correlation between depth and distribution is most probably indirect: Olives are not known to possess any pressure-sensitive anatomical structure and specimens can be rapidly brought to the surface from -70 m, then kept for extended periods in aquaria without any apparent disability.

3.2.2. Correlation with nature of the sediment.

The distribution of each species was established by drawing contour lines around its points of presence both in the F.A.C. diagram and in the depth vs. carbonate scatter diagram. For the sake of space economy, only two species, *Oliva parkinsoni* and *O. reticulata* will

be given as examples. It can be seen (Figs. 4 and 5) that these two species have different distributions (this is also apparent on the UPGMA, Fig. 3). *O. parkinsoni* is found only in a very restricted zone of "white" sediments, while *O. reticulata* occupies disjunct portions of both "black" and "white" sediments. The following groups of species are observed:

Species found on "white" substrate only: *O. amethystina* (°), *O. buelowi*, *O. caerulea* (°), *O. concinna*, *O. mantichora*, *O. miniacea*, *O. panniculata*, *O. parkinsoni*, *O. paxillus*, *O. semmelinki*, *O. sericea* (°), *O. tesselata*. The species marked (°) are found also in small patches of somewhat darker "white" coral sand (coloured with terrigenous sediments) formed around World War 2 wrecks lying in "black" sediment.

Species found on "black" substrate only: *O. athenia*, *O. ceramensis*, *O. concavospira*, *O. sp. DHB*, *O. dubia*, *O. funebralis*, *O. mucronata*, *O. rufula*, *O. sp. ZHB*.

Species found on both "black" and "white" substrates: *O. bulbiformis*, *O. carneola*, *O. elegans*, *O. longispira*, *O. reticulata*, *O. smithi*, *O. solomonensis*, *O. vidua*, *O.* cfr. *volvaroides*.

The species restricted to only one type of sediment will be here under referred to as *stenotopic* and the species occupying different types of substrate as *eurytopic*. Experiments in aquaria (VAN OSSELAER & *al.*, 1993) have shown that it is highly unlikely that restriction of habitat is caused by a choice of substrate by adult specimens.

3.3. Observations on colour patterns and crypsis.

Oliva species are famous for the variability of the colour pattern of their shells, but this variability is not entirely haphazard. Our observations fully confirm the previous impressions that the colour pattern can vary with the substrate. Of the 30 *Oliva* species collected in Hansa Bay 28 are cryptic (coloration and markings of the shell and the soft parts resemble the surroundings and aid in concealment). For instance *O. amethystina* and *O. mantichora* that live exclusively in coral sand in proximity to live reefs, are easily mistaken for fragments of dead *Acropora* coral. The crypsis of more colourful species like *O. semmelincki*, *O. parkinsoni* and the brightly coloured *O. buelowi* is not evident when specimens are seen in a drawer but quite convincing in the field: these species live in much deeper water, where the colours red and orange are seen dark brown and brown. One must also remember that the sediment is

generally not uniform but contains debris and rubble of various sizes. On such a substrate, the reticulated or variegated pattern of many olive shells constitutes a most effective camouflage.

One should note that in eurytopic species both the mantle and the shell are cryptic. The general aspect can vary strikingly within the same species (see Pl. 1, Figs. 6 and 7).

The two non cryptic species are *O. carneola* and *O. rufula*, which will be discussed later.

There is an obvious (and probably continuous) variation in the "*colour strategy*" of the *Oliva* species in Hansa Bay. On the one hand, for most species every local micropopulation is cryptic and quite homogeneous in colour pattern. An experienced local collector can often guess the exact origin of a given specimen because the colour pattern is often characteristic of a given locality.

On the other hand, local populations of a species can be extremely heterogeneous. Of 35 specimens of *O. concinna* (found exclusively on white sand off Boro Beach) 25 (71%) were white, 9 were all black and 1 was orange. Of nearly one thousand *O. longispira* specimens observed on the black beach at Sisimangum 76% were "black", 15 % were "white" and 9 % did not fit into these categories. In these populations, it is only the large majority of the specimens that is cryptic. These are clear cases of population polymorphism. It is interesting to note that the "colour strategy" of a given species can differ from one locality to another. We have just seen that *O. longispira* is polymorphic on the black sand of Sisimangum beach but it is not so on the white sand of Boro Beach where all of the 42 collected specimens of this species were "white". This can also be observed for *O. carneola*, some populations of which are very homogeneous while others are highly heterogeneous. Some of the homogeneous populations of this species are cryptic, others not.

Intermediate strategies do occur. For instance, the colour pattern of the *O. vidua* populations is always cryptic but very variable within a given micropopulation.

4. DISCUSSION.

The *Oliva* species habitats reported here are based only upon observations in Hansa Bay. It is conceivable that the same species might occupy different habitats in other localities. The present data so far agree with the habitats we have observed in other localities in Papua New Guinea (Boesa I., Legoarant Is., Bogia,

Madang, New Ireland) and in other regions of the Indo-Pacific (Indonesia, Seychelles, Sri Lanka, Thailand, Vietnam).

4.1. Crypsis.

One might wonder what olives that are burrowing and nocturnal could gain from crypsis, a strategy obviously directed at diurnal predators endowed with good vision. But olives do come in full light when they detect prey at the sediment surface (they burrow back immediately after the capture of prey). As they do not bury deep (only a few centimetres, see VAN OSSELAER & al., 1993) they could also easily be exposed by any of the many digging or rummaging predators present in their biotope. Crypsis is then very efficient, especially when compounded with very fast burrowing (many a diving collector will recall a coveted *Oliva* specimen literally vanishing under his eyes). A strong argument for crypsis being due to predator pressure stems from the observation (see Plate 1) that crypsis is more convincing on the dorsal face and the mantle (the parts a predator is more likely to see) than it is on the ventral face.

In Hansa Bay, there are two exceptions to the generalised crypsis of *Oliva* species. The first is arguably *O. rufula* (Fig. 8), restricted to deep, dark, very soft sediments. Although its background colour blends with its surroundings, its strikingly disruptive colour pattern could be interpreted as an aposematic (warning, protective) signal, indeed the very contrary of crypsis. The pattern is indeed seen as very contrasting nearly black-and-white if on a colour picture of *O. rufula* one filters off the colours red and yellow (that do not reach the depth where the animal lives). This interpretation is tenable because we have often observed captive, stressed specimens of this species to produce a deep-green, highly toxic exudate.

The second, quite obvious exception is the abundant *O. carneola* (nearly ubiquitous from 0 to -30m). The populations of this very variable species are not homogeneous in coloration: those living on "black" sediment consist mostly of brownish (cryptic) specimens while populations from "white", shallow substrates consist very predominantly in bright orange individuals, sharply contrasting with their surroundings. We still lack data on the possible defences of this form (which produces a bright yellow exudate of unknown toxicity) and have no interpretation to propound for this puzzling case.

The Hansa Bay *Oliva* species display a large spectrum of "colour strategies" and strict analogy with any of the previous studies on shell colour variation (see Introduction) is not obvious. In our case the problem is even more complex because the colour pattern of *Oliva* specimens can vary during the lifetime of an individual, as attested by the abrupt colour pattern changes often observed on the shells of many species. Synchronism of such colour pattern transitions in a population of the East African *O. bulbosa*, has led GREIFENEDER (1984) to suggest that colour pattern changes could be used as a "chronicle of the habitat".

The possibility that the shell colour of *Oliva* specimens depends upon food cannot be rejected at this point. The colour of the small bivalves that seem to constitute an important part of the diet of *Oliva* species is also often matched to the colour of the sediment.

Oliva species could constitute an ideal experimental material for the study of shell colour variation, if one could solve the problem of raising their veliger larvae. These are very easy to obtain but our first, crude attempts at raising them have so far been unsuccessful.

In summary, crypsis in *Oliva* species is still far from being understood, but whatever its interpretation, the phenomenon is the rule rather than the exception in Hansa Bay.

4.2. Taxonomic consequences.

The colour pattern of *Oliva* shells is a character that has been of paramount taxonomic importance and still constitutes a large part of contemporary species descriptions. Our observations call for some comments on the use (and possible abuse) of this character, as many authors working on the genus *Oliva* seem completely unaware of the vast literature available on shell colour variation.

In Hansa Bay, most species of *Oliva* are cryptic and many are eurytopic. On the one hand, within the same eurytopic species, specimens imitating very dissimilar habitats will acquire greatly different aspects. On the other hand, syntopic populations of different species will mimic the same substrate and will thus tend to resemble each other (see Plate 1), forming local assemblages at first sight reminiscent of Müllerian groups of mimics (but this concept should be restricted to aposematic and not to cryptic colorations). So crypsis has two consequences: divergence within eurytopic species and convergence between syntopic species. This can obviously cause much taxonomic confusion and crypsis is thus likely

to have been a major contributor to the old "*Oliva* problem".

The taxonomic value of gross colour features should be considered with great caution. In Hansa Bay, the overall colour pattern of an *Oliva* specimen (especially with depth correction for colours) often gives more information on the underwater aspect of its habitat than it does on its taxonomic status. This remark does not apply to features of the ventral face (not seen by the predator) or to small details (the patterns of the spire, the fasciolar band, the subsutural zone, etc.) that hardly affect concealment. Such features, being less adaptive, are more likely to constitute reliable identification characters.

We see no reason why this situation should be restricted to the genus *Oliva* and one can expect crypsis to occur in other controversial groups of molluscs, with similar taxonomic consequences.

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Station (diving)	Map coord.	Depth (m)	Station (diving)	Map coord.	Depth (m)	Station (diving)	Map coord.	Depth (m)
A1	H5/b	0.7	A25	Z7/b	0.5	A49	X4/d	45
A2	J4/b	3	A26	J8/c	30	A50	Y2/b	15
A3	J4/b	2.5	A27	J7/d	17	A51	U2/a	15
A4	J4/b	4	A28	J4/d	3	A52	U2/a	15
A5	J4/b	6.5	A29	U2/c	18	A53	U2/a	15
A6	J4/b	6.5	A30	H7/d	17	A54	B7/b	40
A7	J4/b	4.5	A31	V2/b	31	A55	U2/a	15
A8	J4/b	2.5	A32	E3/a	25	A56	U1/b	10
A9	U1/b	0	A33	Z4/a	11	A57	Z9/c	0.5
A10	T2/c	10	A34	Z4/a	8	A58	U1/b	10
A11	K3/a	16	A35	Z7/b	6	A59	U1/b	0.5
A12	Z7/b	9	A36	W2/c	9	A61	Y7/d	22
A13	Z7/b	8	A37	W1/d	5	A62	Y7/d	17
A14	Z7/b	5	A38	U5/c	30	A63	J4/d	1
A15	F3/b	20	A39	V5/a	41	A64	J5/a	1
A16	S2/d	3	A40	T2/d	17	A70	U1/b	3
A17	N3/d	25	A41	J6/c	0.5	A71	V1/b	10
A18	N4/a	12	A42	U1/b	6	A72	S3/d	0
A19	H5/d	0.5	A43	Z9/d	10	A75	L8/c	30
A20	T2/a-c	4	A44	Y8/c	9	A76	H5/c	0
A21	T1/d	4.5	A45	Z6/b	4	A77	H5/c	0
A22	V1/b	7	A46	Z5/b	7	A78	H5/c	0
A23	T1/b	0.5	A47	S3/d	3	A79	V1/a	0
A24	Z5/b	0.5	A48	Y4/abcd	21	S1	W4/a	40

Station (Dredging)	Map coord.	Depth (m)	Station (Dredging)	Map coord.	Depth (m)
D1	Z7	6	D13	V1	5
D2	Z4	5	D14	W1	5
D3	U1	3	D15	W1	3
D4	T1	3	D16	W2	3
D5	T1	3	D17	V1	10
D6	U1	3	D18	W2	10
D7	U1	5	D19	W2	10
D8	U1	10	D20	U1	10
D9	U2	15	D21	U1	3
D10	Y2	10	D23	U1	5
D11	Y2	5	D24	U1	15
D12	V1	3	A69	Z9	10

Table 1. Identification of sampling stations. Coordinates refer to maps figures 1 and 2, where each surface unit was subdivided into *a* (upper left), *b* (upper right), *c* (lower left) and *d* (lower right).

Station	Granulometry (µm)							Carbon analysis		Substrate group
	>2000	2000> >1000	1000> >500	500> >250	250> >125	125> >63	<63	Org. C.	CaCO3	
	%	%	%	%	%	%	%	%	%	
A.1	9.02	13.63	46.60	26.19	4.23	0.33	0.01	0.11	86.07	White
A.2	10.69	31.28	38.47	10.50	6.16	2.05	0.85	0.17	90.93	White
A.3	12.60	42.50	38.42	3.02	1.60	1.25	0.62	0.12	87.46	White
A.4	2.87	14.94	28.09	25.85	16.33	9.39	2.53	0.27	83.50	White
A.5	1.57	12.36	27.25	24.76	21.90	9.29	2.86	0.26	82.96	White
A.6	8.13	13.33	21.65	23.71	23.58	6.36	3.24	0.23	88.56	White
A.8	22.95	25.98	25.31	14.30	8.98	1.85	0.63	0.14	91.03	White
A.9	0.00	0.00	0.17	4.57	56.04	38.67	0.55	0.09	1.05	Black
A10	0.08	0.37	0.82	0.79	6.71	86.96	4.25	0.21	0.33	Black
A11	1.21	4.67	24.70	31.07	25.27	10.89	2.21	0.15	88.13	White
A12	0.03	0.08	1.56	7.62	60.70	29.03	0.98	0.16	82.40	White
A13	0.13	0.24	1.64	5.91	60.72	30.39	0.97	0.16	91.04	White
A14	0.00	0.13	2.76	28.09	65.54	3.42	0.05	0.12	93.18	White
A15	0.19	0.86	5.76	8.74	28.82	34.04	21.59	0.41	82.17	White
A16	0.07	0.31	1.42	12.10	64.11	21.64	0.34	0.10	0.01	Black
A17	1.05	1.21	6.78	13.35	39.84	28.43	9.35	0.24	84.70	White
A18	0.20	3.64	13.55	20.19	41.80	18.62	1.99	0.13	86.67	White
A20	0.05	0.11	0.76	6.45	53.00	38.96	0.66	0.11	0.00	Black
A21	0.20	0.44	0.92	3.12	49.33	44.01	1.99	0.12	0.89	Black
A22	0.03	0.33	1.00	4.40	21.77	64.36	8.11	0.27	1.54	Black
A23	0.03	0.25	1.14	6.90	51.38	39.49	0.81	0.01	1.70	Black
A24	1.35	0.19	0.54	0.98	34.91	61.23	0.80	0.02	2.90	Black
A25	0.47	0.97	5.04	29.37	63.31	0.85	0.00	0.11	92.93	White
A26	4.75	6.93	14.82	12.10	27.61	28.06	5.74	0.25	56.25	White
A27	16.96	15.65	23.24	15.70	17.38	8.88	2.19	0.29	87.79	White
A28	42.94	36.08	18.66	1.12	0.41	0.48	0.31	0.16	96.04	White
A29	0.05	0.45	2.82	3.37	9.52	59.06	24.73	0.29	5.68	Black
A30	9.23	10.19	16.94	16.21	30.72	14.44	2.26	0.28	87.13	White
A31	0.03	0.89	7.80	11.18	24.93	45.20	9.98	0.10	14.28	Black
A32	14.49	15.09	21.84	15.84	19.91	10.56	2.27	0.16	80.30	White
A33	0.51	0.45	1.35	2.76	40.17	51.16	3.59	0.08	3.52	Black
A34	0.65	0.12	0.61	0.95	14.25	74.04	9.37	0.14	3.42	Black
A35	.0.17	0.32	10.31	52.71	35.20	1.29	0.00	0.16	91.40	White
A36	1.22	0.28	0.56	2.85	22.80	65.57	6.72	0.27	3.03	Black
A37	0.20	0.31	1.03	2.17	26.33	64.49	5.48	0.36	1.53	Black
A38	14.65	12.05	20.10	20.28	25.37	6.16	1.38	0.27	86.96	White
A39	16.80	16.85	22.85	20.09	20.37	2.47	0.58	0.07	84.62	White
A40	0.30	0.67	2.33	1.86	10.17	76.16	8.51	0.19	2.73	Black
A41	23.90	8.77	10.92	11.72	38.94	5.73	0.01	0.20	91.53	White
A43	0.03	3.29	19.07	25.45	37.22	12.94	2.00	0.22	92.35	White
A44	2.52	2.02	2.62	70.82	21.22	0.80	0.00	0.22	89.56	White
A45	0.00	0.02	0.07	0.18	4.36	87.43	7.94	0.07	4.13	Black
A46	0.09	0.15	0.76	2.54	7.75	57.03	31.67	0.09	1.67	Black
A47	0.09	0.08	0.34	3.41	55.83	38.83	1.41	0.15	0.81	Black
A48	0.02	0.08	0.20	0.43	19.12	31.90	48.26	1.77	5.68	Black
A49	0.31	1.28	4.42	7.64	29.58	32.50	24.27	0.31	25.15	Black
A50	0.00	0.04	0.09	0.41	43.10	52.28	4.08	0.14	1.09	Black
A55	0.18	0.26	1.87	3.15	23.38	55.10	16.07	0.17	4.72	Black
A57	0.25	0.68	5.38	15.34	53.02	24.95	0.38	0.17	89.29	White
A58	0.00	0.12	1.35	3.35	35.08	52.70	7.40	0.11	0.94	Black
A61	0.00	0.04	0.28	4.91	17.42	48.10	29.26	0.43	37.67	Black
A62	0.00	0.02	0.43	1.61	23.23	48.26	26.45	0.35	58.19	Black
A63	28.99	24.27	41.90	2.63	1.50	0.67	0.04	0.14	86.28	White
A64	28.07	19.68	47.63	2.68	1.16	0.68	0.10	0.18	83.00	White
A70	0.31	0.16	0.31	1.83	39.00	55.78	2.60	0.06	0.87	Black
A71	0.00	0.11	0.36	0.38	3.76	68.91	26.47	0.55	2.85	Black
A72	0.00	0.02	0.14	0.48	50.31	49.02	0.03	0.06	0.66	Black
A75	22.26	17.30	28.74	19.43	10.28	1.79	0.20	0.19	91.86	White
A76	49.87	20.94	20.11	3.76	3.56	1.69	0.05	0.17	81.93	White
A77	37.07	7.10	7.98	5.82	25.94	16.08	0.00	0.16	91.91	White
A78	29.60	13.84	22.11	17.48	13.32	3.64	0.01	0.15	93.06	White
D12	0.02	0.38	0.98	15.45	61.05	21.22	0.89	0.12	0.58	Black
D13	0.05	0.12	0.75	23.38	69.21	5.96	0.54	0.14	1.25	Black
S1	0.11	0.31	1.97	3.27	17.45	28.62	48.28	0.56	42.31	Black

Table 2. Characteristics of sediment samples.

| SPECIES	HABITAT	EXAMPLES
amethystina	coral sand near living coral, mostly 1-10m. Also around wrecks.	A2, A3, A4, A8, A28, A30, A60.
athenia	"black" sediment, 5-10m.	D13, D14.
buelowi	coral sand, bottom of reefs, 20-50m.	A32.
bulbiformis	"white" or "black" sediment, 1-8m (shallow only in quiet waters).	A14, A24, A35, A42, D3.
carneola	"black" or "white" sediment, 0.5-30m (not in very agitated shallow waters).	A2 to A8, A10, A15 to A19, A21, A22, A 26 to A28, A36, A40, A42 to A45, A47, A51 to A53, A55 to A58, A60, A63, A64, A70, D7 to D9, D14, D16, D20.
ceramensis	"black" sediment, 10-31 m (generally 18-25m).	A10, A29, A31, A40, A51 to A53, A55, A56, A58, A61, D8 to D10, D19, D20, D24.
caerulea	coral sand, 0.5-3 m in Laing I. lagoon, 6m on Durangit Reef.	A1, A19, A63, A64, A76, A77, A78.
concavospira	"black" sediment, 8-22 m (generally 12-18m).	A34, A50, A51, A52, A53, A55, A56, A58, A62.
concinna	"white" sediment, 5-10 m (off Boro Beach only).	A14, A35.
DHB	"black" sediment, 3-12 m.	A13, A16, A20, A33, A45, A56, A58, A70, D12 to D15, D21, D23.
dubia	very fine "black" sediment, 40-60 m.	
elegans	"black" sediment, 0.5-7 m near Sakula and Awar Rivers; "white" sediment (0.5-1 m) at Mandi Beach.	A57, D15.
funebralis	"black" sediment; 3-7 m.	A70.
longispira	"black" or "white" sediment, surf-exposed beaches only.	A9, A23, A24, A25, A59, A79.
mantichora	coral sand near living coral, mostly 20-40 m.	A54.
miniacea	coral sand, 10-18 m. Rare in Hansa Bay.	A43.
mucronata	"black" sediment, 5-8 m, mostly near Sakula River.	A45.
panniculata	coral sand, 6-20 m, agitated water (top of Durangit Reef).	A44.
parkinsoni	coral sand near reef, 12-42 m.	A11, A26, A27, A30, A32, A38, A39, A54, A75.
paxillus	coral sand, 6 m, agitated water.	top of Durangit Reef.
reticulata	"black" or "white" sediment, 0.5-12 m.	A13, A19, A37, A41, A44, A45, A57, A63, A64, A76, A77, A78, D1.
rufula	"black" sediment, 18-35 m (mostly 25-35m).	A29, A31.
sericea	coral sand, mostly 1-10 m. Also around wrecks.	A35, A63, A64.
semmelincki	coral sand, bottom of reefs, 35-70 m.	A39.
smithi	"black" or "white" sediment, 0.5-12 m.	A1, A12, A13, A14, A35, A45, A46, A57, A70, D1 to D6, D11, D12, D15, D21.
solomonensis	"black" or "white" sediment, 5-10 m.	A14, A35, A43, D13, D14.
tesselata	coral sand near reef, 3-7 m, only in lagoon.	A5.
vidua	"black" or "white" sediment, 0.5-12 m.	A1, A12, A13, A34, A45, A70, D3, D13, D14, D16, D17, D18, D20.
cfr. *volvaroides*	"black" or "white" sediment, 6 m. Very rare in Hansa Bay.	A22, A35.
ZHB	only found at one locality, 6 m.	Awar wreck.

Table 3. Brief notes on habitat of *Oliva* species, with collecting stations in February-March 1992.

Plate 1. (opposite)
1. *Oliva bulbiformis*. Laing Island lagoon. 1 m, "white" substrate.
2. *Oliva. solomonensis*. Off Boro Beach. 5 m, "white" substrate.
3. *Oliva caerulea*. Laing Island lagoon. 0.5 m, "white" substrate.
4. *Oliva concinna*. Off Boro Beach. 6 m, "white" substrate.
5. *Oliva elegans*. Mandi Beach. 0.5 m, "white" substrate.
6. *Oliva reticulata*. Laing Island lagoon. 1 m, "white" substrate.
7. *Oliva. reticulata*. Off Sisimangum. 5 m, "black" substrate.
8. *Oliva vidua*. NE of mouth of Sakula River. 5-7 m, "black" substrate.
9. *Oliva* sp. *DHB* (see text, section 2.1). NE of mouth of Sakula River. 5-7 m, "black" substrate.
10. *Oliva athenia*. NE of mouth of Sakula River. 5-7 m. "black" substrate.
11. *Oliva elegans*. NE of mouth of Sakula River. 5-7 m, "black" substrate.
12. *Oliva reticulata*. NE of mouth of Sakula River. 5-7 m, "black" substrate.
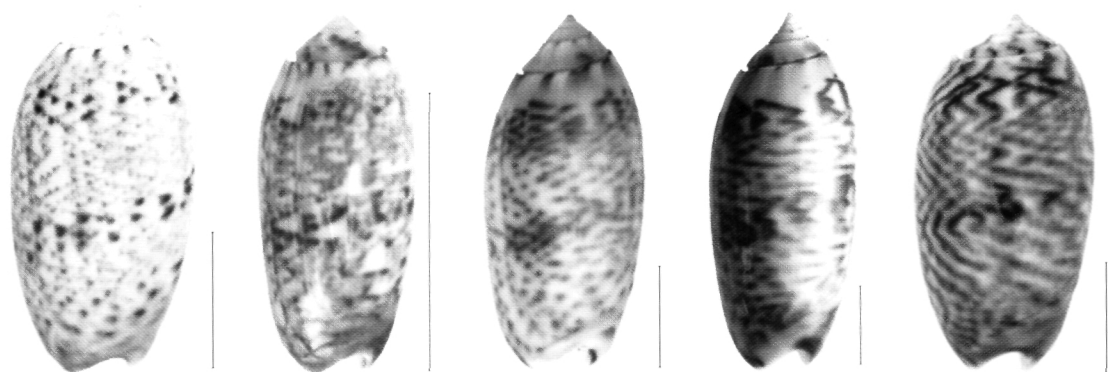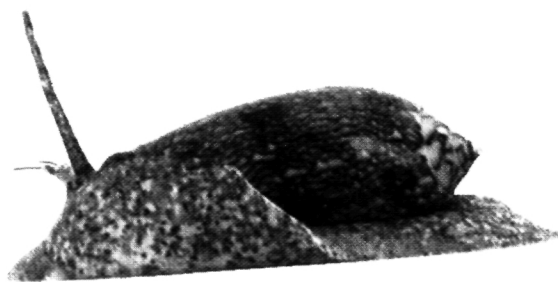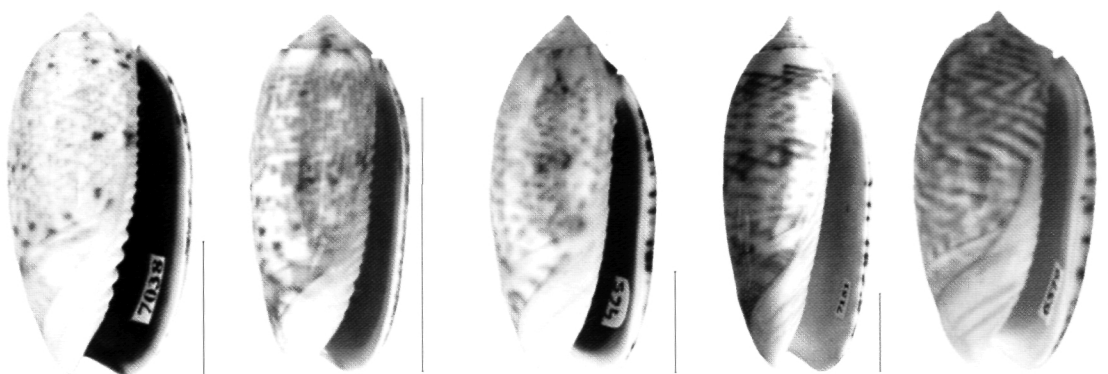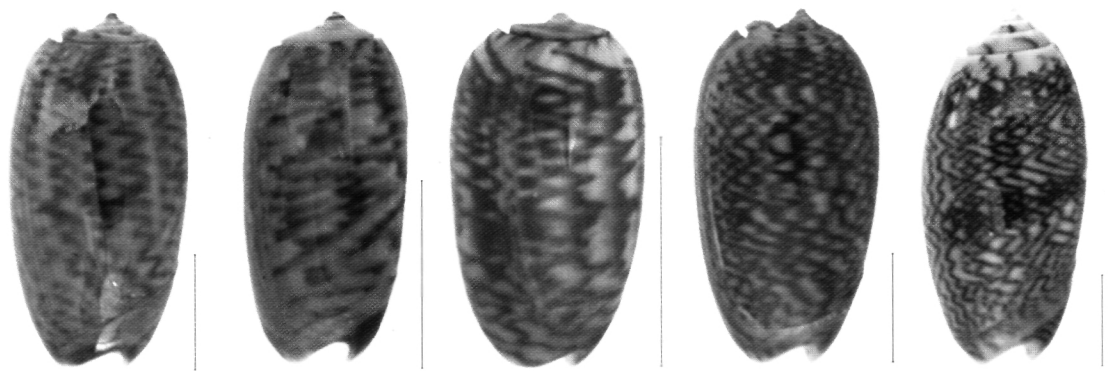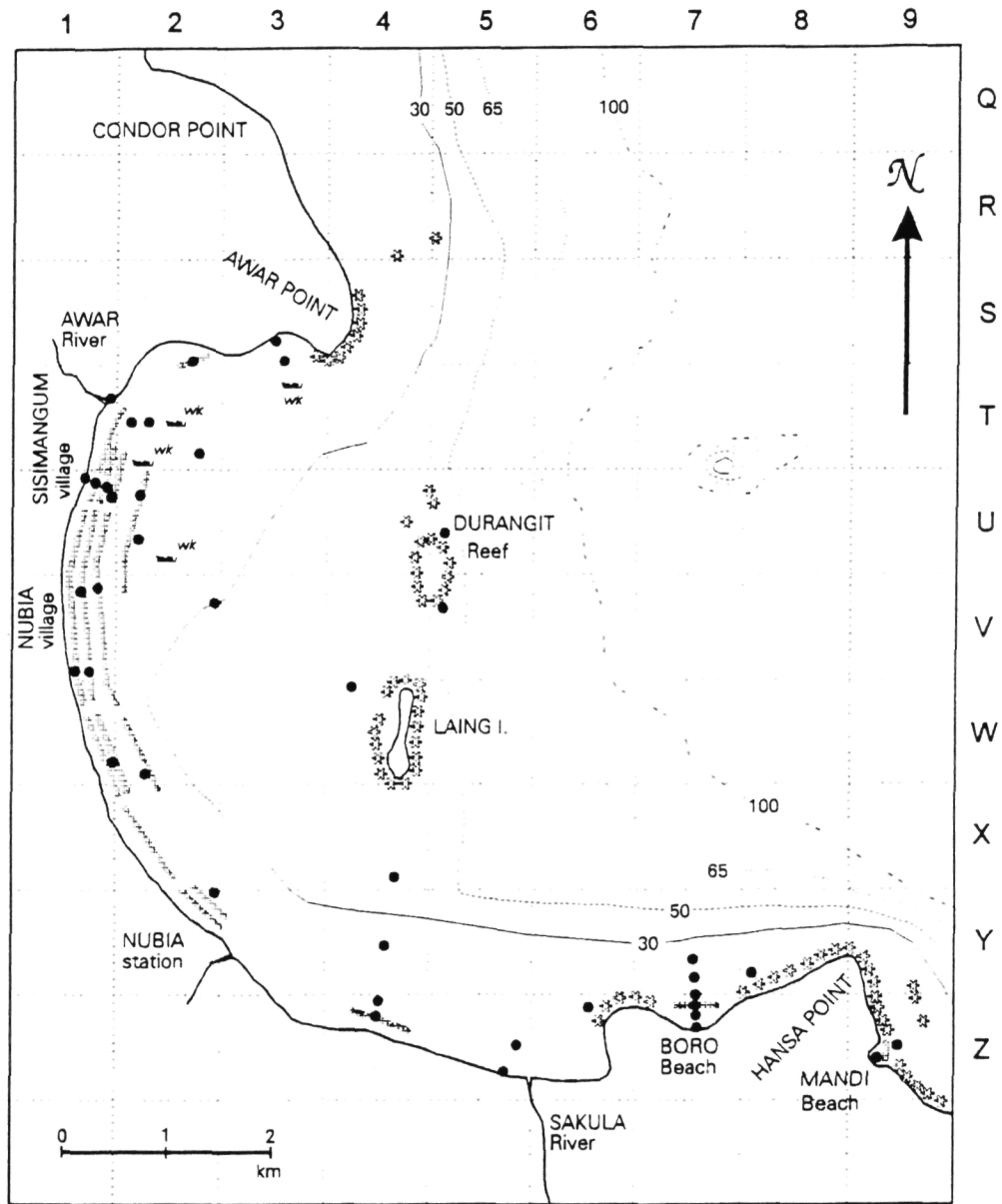
Fig. 1. Hansa Bay. Black circles represent locations of sediment samplings at sites where *Oliva* species have been collected during February-March 1992. Dredgings are represented by thick gray lines. Stars represent coral reefs.
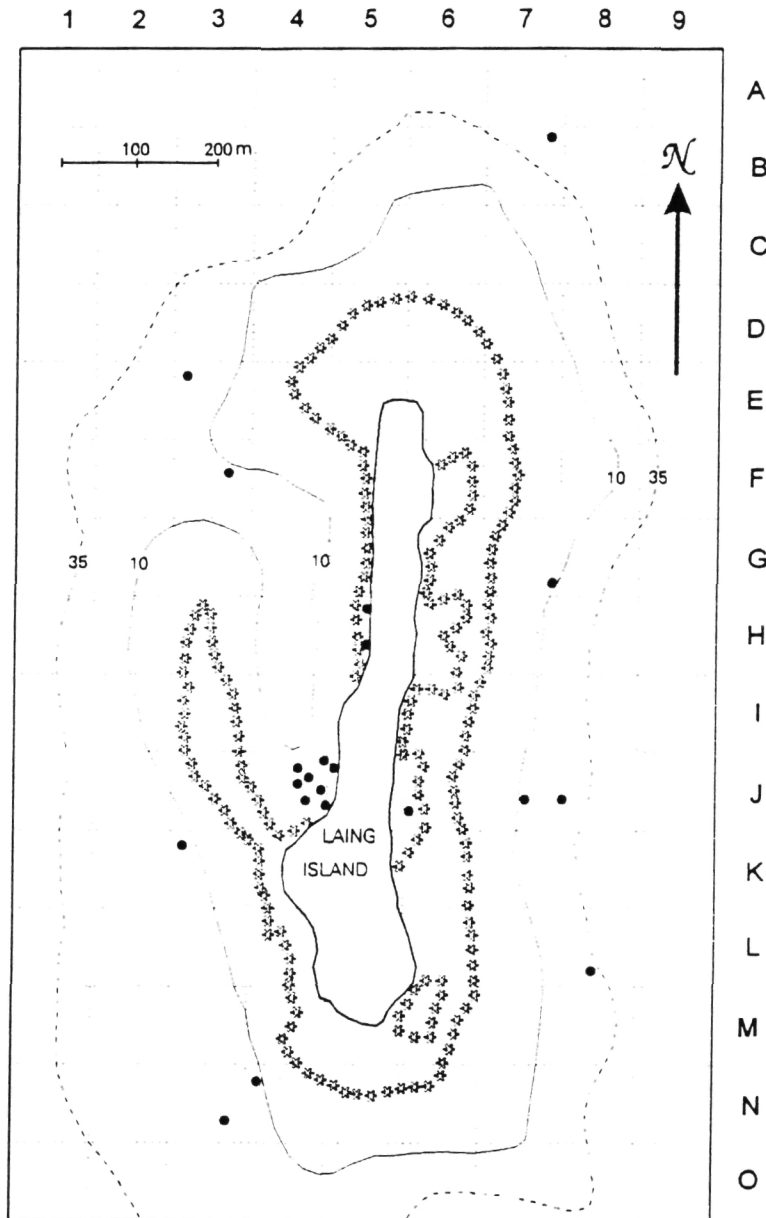
Fig. 2. Laing Island. Black circles represent locations of sediment samplings at sites where *Oliva* species have been collected during February-March 1992. Stars represent the limit of coral reefs emerging at low tide.
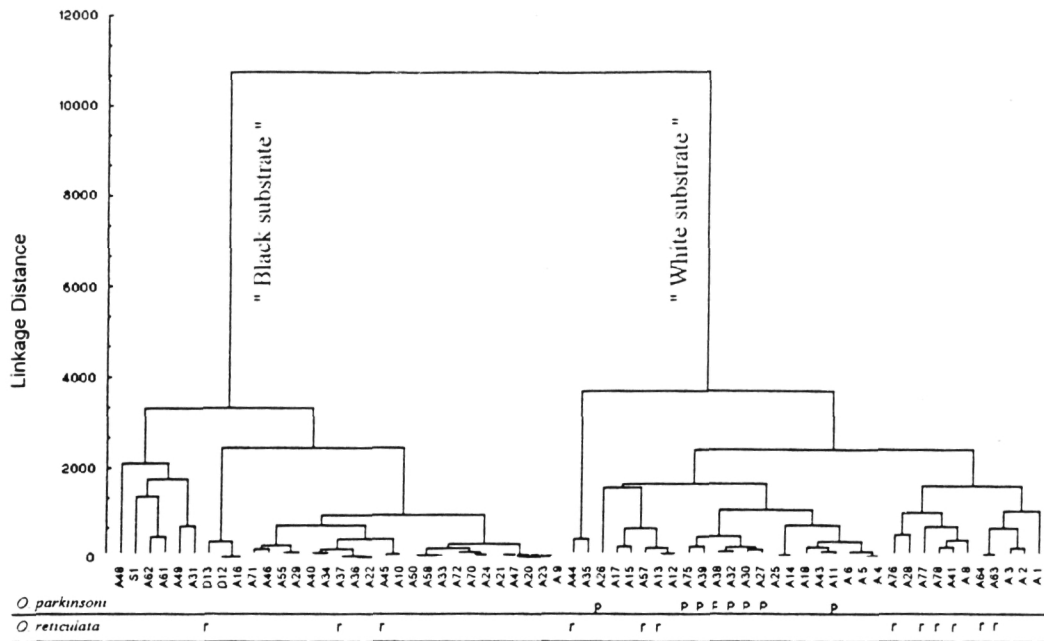
Fig. 3. U.P.G.M.A clustering (squared euclidian distances) of sediment samples. Variables: six textural classes (>2000 μm, 2000-1000 μm, 1000-500 μm, 500-250 μm, 125-63 μm and < 63 μm), percentage of organic carbon, percentage of carbonates and depth. The disjunct distributions of *Oliva reticulata* (r) and *O. parkinsoni* (p) are shown below the dendrogram, as an example.
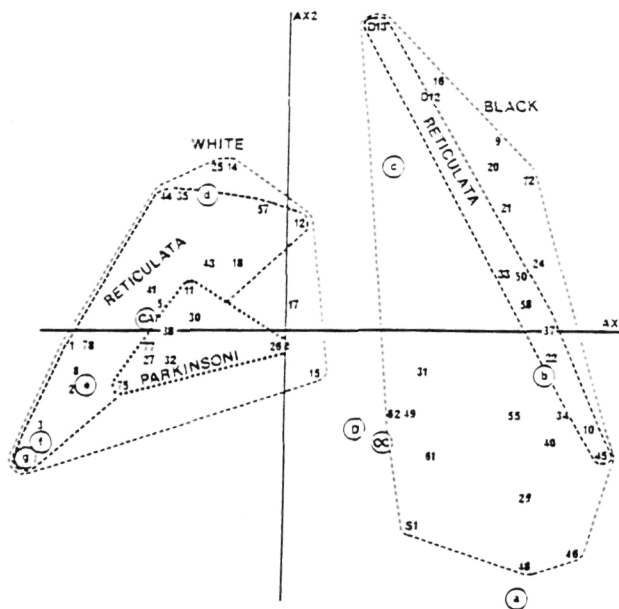

Fig. 4. F.A.C. (Factorial Analysis of Correspondences) analysis of sediment samples. Variables: seven textural classes [>2000 μm (g), 2000-1000 μm (f), 1000-500 μm (e), 500-250 μm (d), 250-125 μm (c) 125-63 μm (b) and < 63 μm (a)], percentage of organic carbon (OC), percentage of carbonates (CA) and depth (D). The disjunct distributions of *Oliva reticulata* and *O. parkinsoni* are shown as an example.

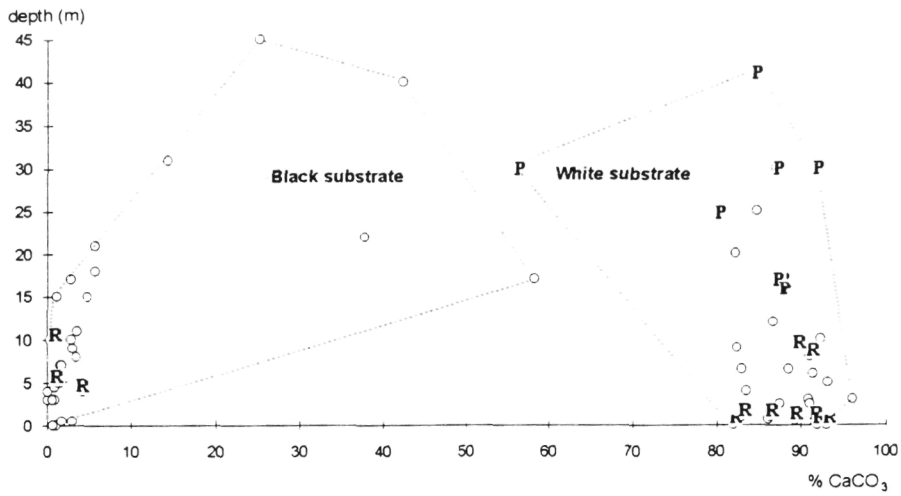| point seen	point hidden	point seen	point hidden	point seen	point hidden
CA	4	g	28	3	63, 64
5	6	22	36	24	70
12	13	32	39	46	71
20	23	20	47	f	76

Fig. 5. Scatter diagram of % carbonates vs. depth. The two groups of sediments are again separated on this simplified representation. The disjunct distributions of *Oliva reticulata* (R) and *O. parkinsoni* (P) are shown as an example.
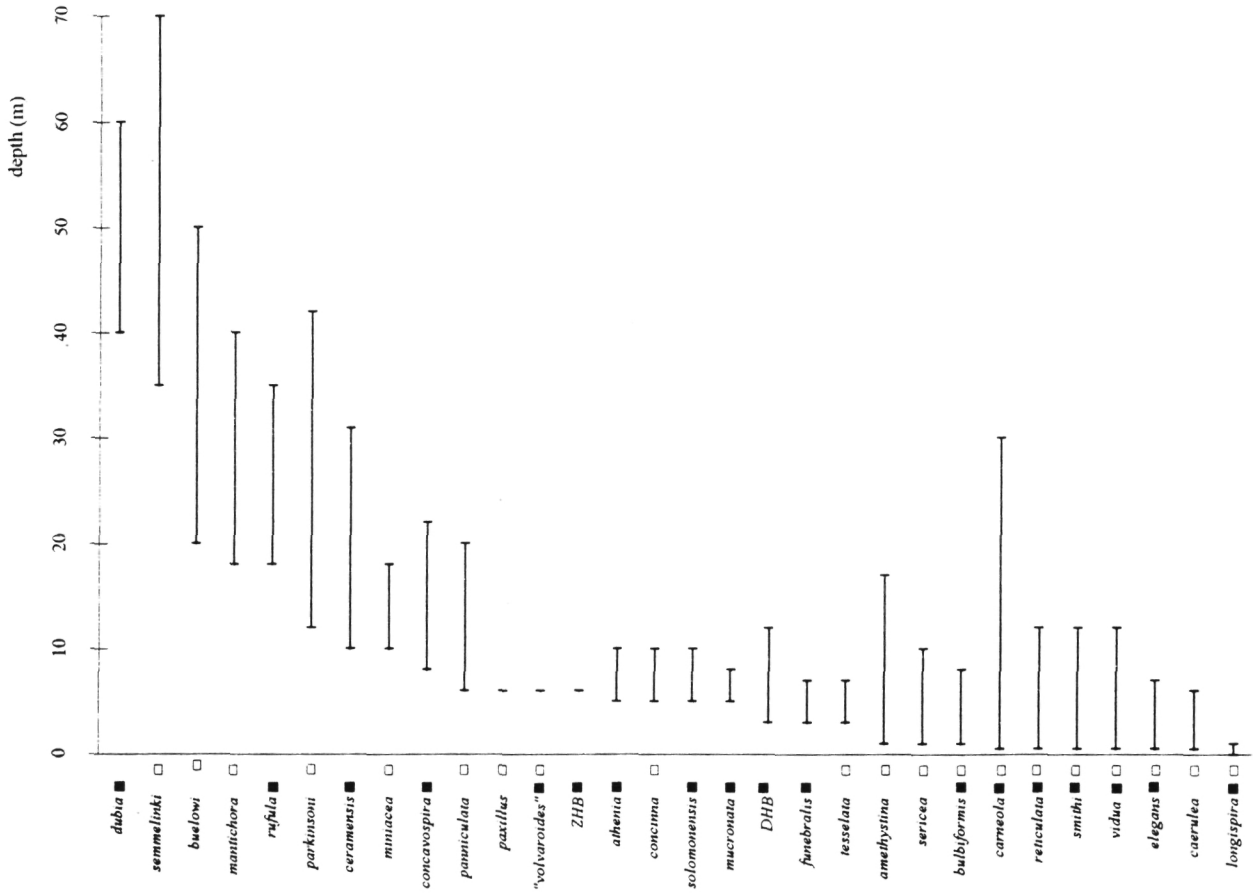
Fig. 6. Observed bathymetric range of *Oliva* species in Hansa Bay. Data from 1974 to 1993 (see text section 3.2.1). Black and white squares indicate occurence in "black" and "white" sediments, respectively.
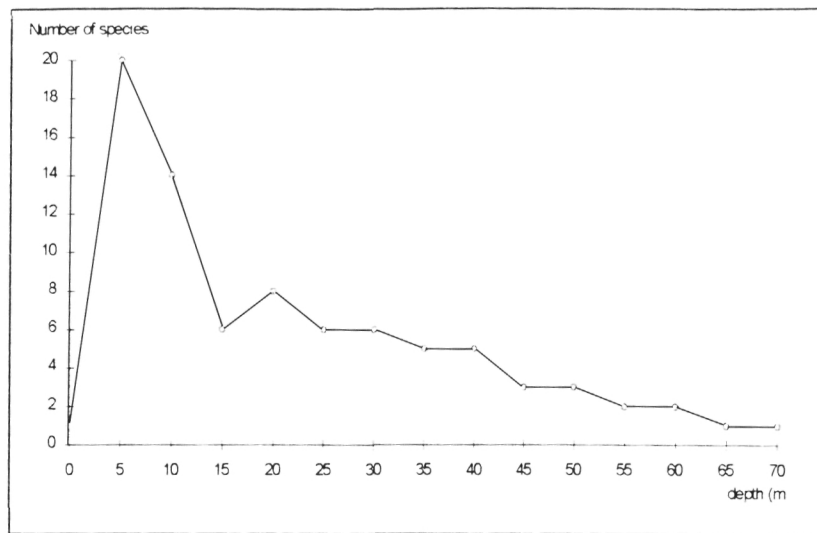
Fig. 7. Number of *Oliva* species in Hansa Bay as a function of depth.

Fig. 8. Aposematic pattern of the toxic species *Oliva rufula* (trapped NW of Laing I., 35 m, "black" substrate). Scale bar: 10 mm.