The Muricidae (Gastropoda) from Madeira with the description of a new species of *Ocenebra* (*Ocinebrina*) (Muricidae: Ocenebrinae).

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KEYWORDS: Gastropoda, Muricidae, review, new species, Madeira.

ABSTRACT. Nine species of Muricidae are reported here from the Archipelago of Madeira (*Hexaplex trunculus, Ocenebra erinaceus, O. edwardsi, O. aciculata, O. inordinata* n.sp., *Bedeva paivae, Muricopsis aradasii, Cytharomorula grayi, and Stramonita haemastoma*). Two of these species, *Hexaplex trunculus* and *Bedeva paivae*, are new records for the Archipelago. Three species listed by previous authors remain doubtful records for the region and have not been confirmed [*Muricopsis cristatus, Orania fusulus*, and *Trophonopsis richardi* (= *T. droueti* or *T. muricatus*)]. The presence of *Typhis fistulatus* (= *Typhis sowerbyi*), once recorded from the Archipelago, is probably based on a misidentification, and is not accepted here. A new species, *Ocenebra (Ocinebrina) inordinata*, is described from the Island of Madeira.

RESUME. Neuf espèces de Muricidae sont signalées dans l'Archipel de Madère (*Hexaplex trunculus, Ocenebra erinaceus, O. edwardsi, O. aciculata, O. inordinata* n.sp., *Bedeva paivae, Muricopsis aradasii, Cytharomorula grayi*, et *Stramonita haemastoma*). Deux de ces espèces, *H. trunculus* et *B. paivae* sont signalées pour la première fois dans la région. Trois espèces listées par des auteurs précédents n'ont pas été retrouvées, leur présence dans l'Archipel reste douteuse [*Muricopsis cristatus, Orania fusulus*, et *Trophonopsis richardi* (= *T. droueti* ou *T. muricatus*)]. La présence de *Typhis fistulatus* (= *T. sowerbyi*), signalée précédemment dans l'Archipel est probablement basée sur mauvaise identification de l'espèce et n'est pas acceptée ici. Une nouvelle espèce, *Ocenebra (Ocinebrina) inordinata* est décrite de l'Ile de Madère.

INTRODUCTION

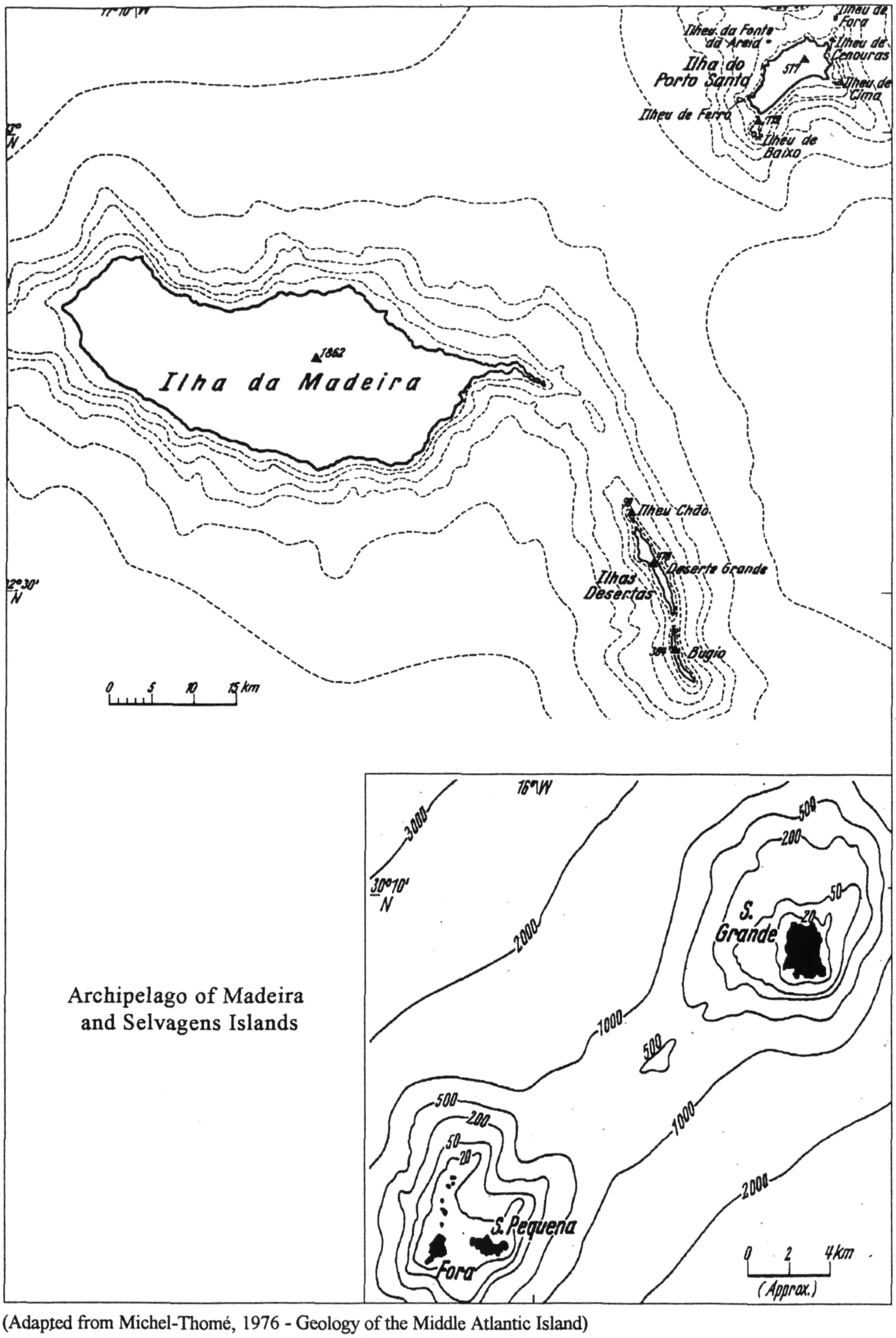
The Archipelago of Madeira is situated between 35°05' - 32°25' N and 17°15' - 16°15' W. It includes Madeira, Porto Santo, the Desertas and a group of islets around these islands. Administratively, the Selvagens Islands, situated 160 miles south of Madeira, between 30°12' - 30°02' N and 16°05' - 15°50' W, also belong to the madeiran archipelago.

The largest island of the archipelago is Madeira, which comprises an area of 737 km^2 and is situated 700 km off the coast of Morocco. Porto Santo is situated 20 miles NE of Madeira and its area is approximately 41 km^2 including the islets. The Desertas are composed of the Ilhéu Chão, Deserta Grande and the Bugio, which are situated 10 miles SE off Madeira and have an area of approximately 14 km^2. The Selvagens have an area of 4 km^2 (Text Fig. 1).

Despite small local and seasonal variations, the Archipelago of Madeira is strongly influenced by a current which flows from NE and is formed by a terminal branch of the Gulf Stream.

The mean temperature at the surface of the water in Madeira is 19.5° C. The lowest is 17.0° C (February and March) and the highest is 22.5° C in September. In the Selvagens the mean values are 0.3° C higher.

Faunal elements of several provinces are represented in the composition of the marine Mollusca of Madeira. There are species from North Africa, Western Mediterranean, NW and NE Atlantic, but also several dozen endemic species. From the biogeographic point of view, the Archipelago of Madeira is a part of Macaronesia which also includes the Azores, the Canary Islands and the Cape Verde Archipelago.



(Adapted from Michel-Thomé, 1976 - Geology of the Middle Atlantic Island)

The actual known total of the marine molluscan fauna of Madeira is about 500 species. The first author giving a general view of this matter was WATSON (1897) with a list containing 382 species. Later, NOBRE (1937) added 13 species to Watson's list. Apart from these two authors, NORDSIECK & TALAVERA (1979) have made a general study which, however, was only devoted to the Gastropoda. More recently, MOOLENBEEK & FABER (1987 a-c) and MOOLENBEEK & HOENSELAAR (1989) have dedicated special attention to the Rissoidae, describing some new species.

The family Muricidae in Madeira is represented by several species, but not all the species reported by previous authors were rediscovered by us. Of course, it does not mean *ipso facto* that these do not occur in Madeira at all, and later reports perhaps will confirm the presence of these in the Archipelago.

Abbreviatons

BMNH: The Natural History Museum, London.
MMF: Museu Municipal do Funchal, Madeira.
RH: Roland Houart collection.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815
Subfamily Muricinae Rafinesque, 1815
Genus *Hexaplex* Perry, 1811

Hexaplex trunculus (Linné, 1758)
Figs 1-2

Murex trunculus Linné, 1758: 747.

Records: Madeira (Garajau); Porto Santo; Desertas Is, many live and dead taken specimens at a depth of approximately 70 m. (MMF).

Remarks: *Hexaplex trunculus* is a very common species occuring in the Mediterranean Sea. The species was not reported before from the Madeira Archipelago, despite the fact that it is very common in Madeira and the other islands.

There are at least 40 synonyms known for this variable species, most of them named to designate minor morphological differences in shell structure such as the length of spines, the dimensions, the colour, etc.

Subfamily MURICOPSINAE
Radwin & D'Attilio, 1971
Genus *Muricopsis*
Bucquoy & Dautzenberg, 1882

Subgenus *Muricopsis*

Muricopsis (Muricopsis) cristatus
(Brocchi, 1814)

Murex cristatus Brocchi, 1814: 394, pl.7, fig.15.

Records: NOBRE, 1937: Funchal.

Remarks: As noted above, Muricopsis cristatus was listed in NOBRE (1937), but it is not yet recorded by us from the Archipelago. Its presence in Madeira, even if doubtful, is possible. The species is common in the Mediterranean Sea.

Subgenus *Murexsul* Iredale, 1915

Muricopsis (Murexsul) aradasii
(Monterosato, 1883)
Figs 3-4

Murex aradasii Monterosato in Poirier, 1883: 123.

Murex (Ocinebra) medicago Watson, 1897: 242, pl. 19, fig. 11.
Murex medicago -NOBRE, 1937: 29
Muricopsis medicago -NORDSIECK & GARCIA-TALAVERA: 131.

Records: Only a few specimens from Madeira (Caniçal) and Porto Santo (MMF); WATSON, 1897 (as *M. medicago* n.sp.): Madeira, Punta de Lourenço to 50 fms. (91 m); Magdalena (dredged); Selvagem Grande, shore; NOBRE, 1937 (as *M. medicago*): same as above, and Funchal; NORDSIECK & GARCIA-TALAVERA, 1979 (as *M. medicago*): Madeira.

Remarks: No live specimens but only fresh dead specimens have been recorded until now by us. The species is apparently rare in the Archipelago (as it generally is elsewhere). There are only a few synonyms, amongst them *Murex medicago* Watson, 1897, described from Madeira.

Subfamily ERGALATAXINAE
Genus *Cytharomorula* Kuroda, 1953

Cytharomorula grayi (Dall, 1889)
Figs 5-6

Nassarina grayi Dall, 1889: 183, pl. 32, fig. 12a.

Trophon lowei Watson, 1897: 244, pl. 19, fig. 12.
Trophon lowei -NOBRE, 1937: 28.
Urosalpinx lowei -NORDSIECK & GARCIA-TALAVERA, 1979: 134.

Records: Some live and dead taken specimens from Madeira (with no precise locality data, and Funchal Bay) and from Porto Santo, up to 100 m. depth (MMF); WATSON, 1897 (as *Trophon lowei* n.sp.): Madeira, 50 fms (91 m) (Labra and Punta de São Lourenço); NOBRE, 1937 (as *T. lowei*): same as above; NORDSIECK & GARCIA-TALAVERA (as *Urosalpinx lowei*): Madeira.

Remarks: *Nassarina grayi* was described from Barbados (West Atlantic), *Trophon lowei* from Madeira and a third synonym, *Cantharus laevis* Smith, 1891, was described from St. Helena. The species is also known from the Canary Islands. It is now classified in the Muricidae, subfamily Ergalataxinae, due to morphological affinities of shell and radular characters with other species of the subfamily. The geographical distribution is probably worldwide because closely related specimens, probably belonging to the same species, have been recorded from the Indian and Pacific Oceans.

Genus *Orania* Pallary, 1900

Orania fusulus (Brocchi, 1814)

Murex fusulus Brocchi, 1814: 409, pl.8, fig.9.

Records: NOBRE, 1937: Funchal; Porto Santo; NORDSIECK & GARCIA-TALAVERA, 1979: Madeira.

Remarks: The species is not yet recorded by us, but its presence in Madeira is not doubted due to its presence from the Mediterranean Sea to Angola (West Africa).

Subfamily OCENEBRINAE
Cossmann, 1903
Genus *Ocenebra* Gray, 1847

Ocenebra erinaceus (Linné, 1758)
Fig. 7

Murex erinaceus Linné, 1758: 748.

Murex (Ocinebra) erinaceus -WATSON, 1897: 294.
Murex erinaceus -NOBRE, 1937: 28.
Ocenebra erinaceum -NORDSIECK & GARCIA-TALAVERA, 1979: 132.

Records: Madeira (many localities); Porto Santo; Desertas Is, many live and dead taken specimens (MMF); WATSON, 1897: from Funchal to East point and Porto Santo (abundant); NOBRE, 1937: same remarks as above; NORDSIECK & GARCIA-TALAVERA, 1979: Porto Santo.

Remarks: The species is common in the Archipelago. It is also common in the Eastern Atlantic and the Mediterranean sea, with a lot of synonyms, because of the many shell variations.

Subgenus *Ocinebrina* Jousseaume, 1880

Ocenebra (Ocinebrina) edwardsi (Payraudeau, 1826)
Figs 9-10

Purpura edwardsi Payraudeau, 1826: 155, pl. 7, fig. 19, 20.

Murex (Ocinebra) edwardsii -WATSON, 1897: 294.
Murex edwardsi -NOBRE, 1937: 28.
Ocinebrina edwardsi -NORDSIECK & GARCIA-TALAVERA: 133.

Records: Madeira (loc.inc.) (MMF); WATSON, 1897: from Funchal westwards. Very abundant; NOBRE, 1937: Funchal, Porto Santo; NORDSIECK & TALAVERA, 1979: Madeira.

Remarks: Numerous specimens are present in the collections of the Museum of Funchal, all from Madeira, but with no precise locality data. The species is widely dispersed in the Mediterranean and the East Atlantic Ocean, and many forms have been named. All specimens examined from Madeira are strongly spirally sculptured, with low, broad axial varices.

Ocenebra (Ocinebrina) aciculata (Lamarck, 1822)
Fig. 8

Murex aciculatus Lamarck, 1822: 176

Murex (Ocinebra) aciculatus -WATSON, 1897: 294.

Murex aciculatus -NOBRE, 1937: 29.

Ocinebrina aciculata -NORDSIECK & GARCIA-TALAVERA, 1979: 133.

Records: Madeira (Ponta Gorda), Porto Santo and the Desertas Is (common) (MMF); WATSON, 1897: from Madalena to island's East point and Porto Santo; NOBRE, 1937: from Madalena to East point; Porto Santo; Funchal, Pontinha; Porto Santo; NORDSIECK & TALAVERA, 1979: Madeira.

Remarks: A small species, reaching a maximum length of 15 mm. It is common in the Eastern Atlantic and the Mediterranean Sea. It is not variable morphologically, however some form names have been proposed for smaller, larger, or more colourful specimens.

Ocenebra (Ocinebrina) inordinata n.sp.
Figs 11-13

Type material: Madeira Is (no other locality data), **holotype** MMF 25429, 19.2 mm; 1 paratype coll. R. Houart, 14.2 mm; 1 paratype coll. J. Verstraeten, 21 mm.

Description: Shell medium sized for the subgenus, up to 21 mm in length at maturity, heavy, tuberculate. Spire high with 1.25-1.50 protoconch whorls and up to 6 shouldered, strongly nodose teleoconch whorls. Suture appressed. Protoconch whorls rounded, weakly elongate, smooth; terminal varix very shallow, nearly straight.

Axial sculpture consisting of ridges and varices: 12 low axial ridges on first teleoconch whorl; 11 on second whorl; 10 or 11 low to high ridges on third whorl; 9 high, strong ridges on 4th whorl; 7 high ridges, and varices on 5th whorl; last teleoconch whorl with 4 or 5 erratically placed varices, some with low, blunt open spines, and one or two high, strong axial node.

Spiral sculpture consisting of 2 nodose cords on first teleoconch whorl; 2 primary cords and 1 secondary cord on the shoulder on second whorl; third to fifth teleoconch whorls with 2 primary cords and narrow threads between them, some 2 or 3 additional threads on shoulder; last teleoconch whorl with 5 or 6 low, obsolete cords, forming short, rounded, broadly open spines on the varices, chiefly on apertural varix. Occasionally with 2 or 3 low, shallow threads between cords.

Aperture ovate, moderately large. Columellar lip smooth, margin partially weakly erect, adherent at adapical extremity. Anal notch broad. Outer lip erect, smooth, with 5 or 6 strong nodes within, adapical node strongest.

Siphonal canal short, narrow, straight, closed, smooth.

Shell entirely light brown; aperture glossy white.

Remarks: We are aware of the great diversity of forms existing in the *Ocenebra (Ocinebrina) edwardsi* group of shells, but *O. inordinata* does not fit any of these forms. A great number (more than 500 specimens) of *O. edwardsi* were observed from different localities, representing many varieties (both colour and morphological forms). Moreover, the varieties of *O. edwardsi* are generally mixed, and many forms live together in the same region. We also examined more than 200 specimens of *O. edwardsi* from Madeira, all are very similar morphologically.

Ocenebra inordinata constantly differs in its completely white aperture, in the few, strong nodes on its last whorl, and in the erratically placed varices with blunt, broad, open spines. One form of *O. edwardsi* (valid taxon?) from Vigo (Spain) has a completely white aperture, with a white shell, but it differs strongly morphologically from *O. inordinata*. That shell was illustrated by ROLAN (1983: 231) as *Ocinebrina* cf. *nicolai* (Monterosato, 1884).

From *O. miscowichi* (Pallary, 1920), a species occuring off the North-West African coast, *O. inordinata* differs in its white aperture, stronger and higher axial sculpture, in its erratically placed varices, and in its fewer, broader spiral cords.

Other species of European or West African Ocenebra or Ocinebrina are very different and need not to be compared.

Etymology: *inordinata* (Latin): not arranged, disorderly. Named for the erratically placed varices and axial ridges.

Genus *Bedeva* Iredale, 1924

Bedeva paivae (Crosse, 1864)
Figs 15-17

Trophon paivae Crosse, 1864: 278.

Records: Madeira, Funchal Harbour, 0-10 m, many specimens.

Remarks: *Bedeva paivae* was originally restricted to Australia, from South Queensland to Shark Bay, West Australia, and in Tasmania (WELLS & BRYCE, 1986). KILBURN & RIPPEY (1982: 91) recorded the species from the eastern Cape Province (South Africa) where it lives in colonies of up to 72 individuals per square meter. *Bedeva paivae* was also collected alive in the Canary Islands (GOMEZ, 1983). It is obvious that the species was introduced to South Africa, to the Canary Islands, and now to the Archipelago of Madeira in the hull of ships (oil tankers, merchant ships...), as already noted in KILBURN & RIPPEY (1982) and in GOMEZ (1983). The presence of *B. paivae* in the Archipelago of Madeira was never reported before. It is apparently very common but not outside of the harbour. The first known specimen was collected by Nicolas Vassart.

The classification of *Bedeva* in the Ocenebrinae is tentative and based on the observation of radular morphology (Vokes, pers. comm.).

Subfamily TROPHONINAE
Genus *Trophonopsis* Bucquoy & Dautzenberg, 1882

Trophonopsis richardi (Dautzenberg & Fischer, 1896)

Trophon richardi Dautzenberg & Fischer, 1896: 438, pl. 18, fig. 6.

Records: NORDSIECK & GARCIA-TALAVERA, 1979: Madeira.

Remarks: No recent record is known for this species. Moreover, the real identity of the recorded species in NORDSIECK & GARCIA-TALAVERA (1979: 132) is very doubtful because of the confusion existing between *Trophonopsis muricatus* (Montagu, 1803) and *Trophonopsis richardi* (Dautzenberg & Fischer, 1896) (= *Trophon droueti* Dautzenberg, 1889) (HOUART, 1981: 33). The presence of *T. droueti* or *T. muricatus* in the Archipelago thus remains doubtful.

Subfamily TYPHINAE
Genus *Typhis* Montfort, 1810
Subgenus *Typhinellus* Jousseaume, 1880

Typhis (Typhinellus) fistulatus (Risso, 1826)

Murex fistulatus Risso, 1826: 191 (not *Muricites fistulatus* Schlotheim, 1820 = *Lyrotyphis*).

Typhis sowerbii Broderip in Broderip & Sowerby 1833: 178.

Records: NORDSIECK & GARCIA-TALAVERA, 1979: Madeira (as *Typhis sowerbyi* Broderip, 1833).

Remarks: The record of this species in Madeira is probably based on a misidentification. The specimen in the possession of Garcia-Talavera (from the Canary Islands) is an example of *Typhis (Typhina) belcheri* Broderip, 1833. Moreover, Garcia-Talavera (pers. comm.) has no material from Madeira. The presence of *Typhis fistulatus* in the Archipelago of Madeira is rejected here.

Subfamily RAPANINAE (ex Thaidinae)
Genus *Stramonita* Schumacher, 1817

Stramonita haemastoma (Linné, 1767)
Fig. 14

Buccinum haemastoma Linné, 1767: 1202.

Purpura haemastoma -WATSON, 1897: 306.
Purpura haemastoma -NOBRE, 1937: 30.
Thais haemastoma -NORDSIECK & GARCIA-TALAVERA, 1979: 132.

Records: Many live and dead taken specimens from the Desertas Is and the Selvagens Is (MMF); WATSON, 1897: Everywhere, very common; NOBRE, 1937: Porto da Cruz, Funchal, Porto Santo, Zimbral; NORDSIECK & GARCIA-TALAVERA, 1979: Madeira.

Remarks: *Stramonita haemastoma* is variable and is recorded from both the eastern and western Atlantic. It also occurs all along the West African coast, as well as in the Mediterranean Sea. Many synonymous names and a few subspecies have been proposed for this species.

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Figures 1-8 (opposite page).

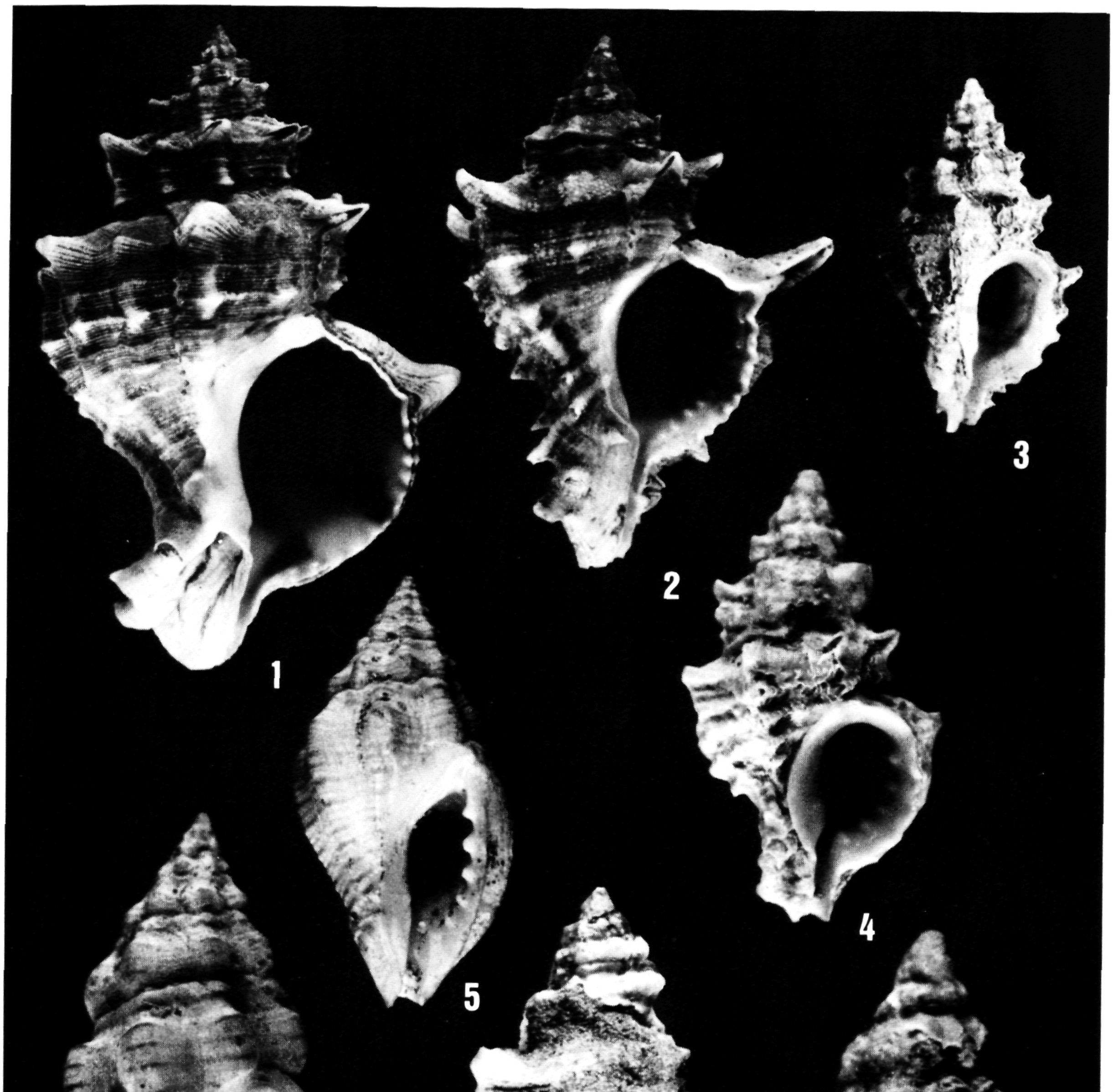
1-2. *Hexaplex trunculus* (Linné, 1758), Madeira, Garajau, 70, MMF.
  1. 83.3 mm.
  2. 41.2 mm.

3-4. *Muricopsis (Murexsul) aradasii* (Monterosato, 1883).
  3. *Murex medicago* Watson, 1897. Holotype BMNH 1911.7.17.3, 13.5 mm.
  4. Madeira, Caniçal, MMF JSL-3004, 13 mm.

5-6. *Cytharomorula grayi* (Dall, 1889).
  5. *Trophon lowei* Watson, 1897. Holotype BMNH 1911.7.17.2, 19 mm.
  6. Madeira (no other locality data), MMF, 19.5 mm.

7. *Ocenebra erinaceus* (Linné, 1758), Madeira (no other locality data), MMF 24702, 44.1 mm.

8. *Ocenebra (Ocinebrina) aciculata* (Lamarck, 1822), Madeira Arch., Desertas, MMF 25160, 10.8 mm.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Figures 9-14 (opposite page).

9-10. *Ocenebra (Ocinebrina) edwardsi* (Payraudeau, 1826), Madeira (No other locality data), MMF 24631. 9: 17 mm. 10: 14 mm.

11-13. *Ocenebra (Ocinebrina) inordinata* n.sp.

11. Holotype MMF 25429, 19.2 mm.

12-13. Paratype coll. J. Verstraeten, 21 mm.

14. *Stramonita haemastoma* (Linné, 1767), Madeira Arch., Selvagens, MMF 14332, 60.3 mm.

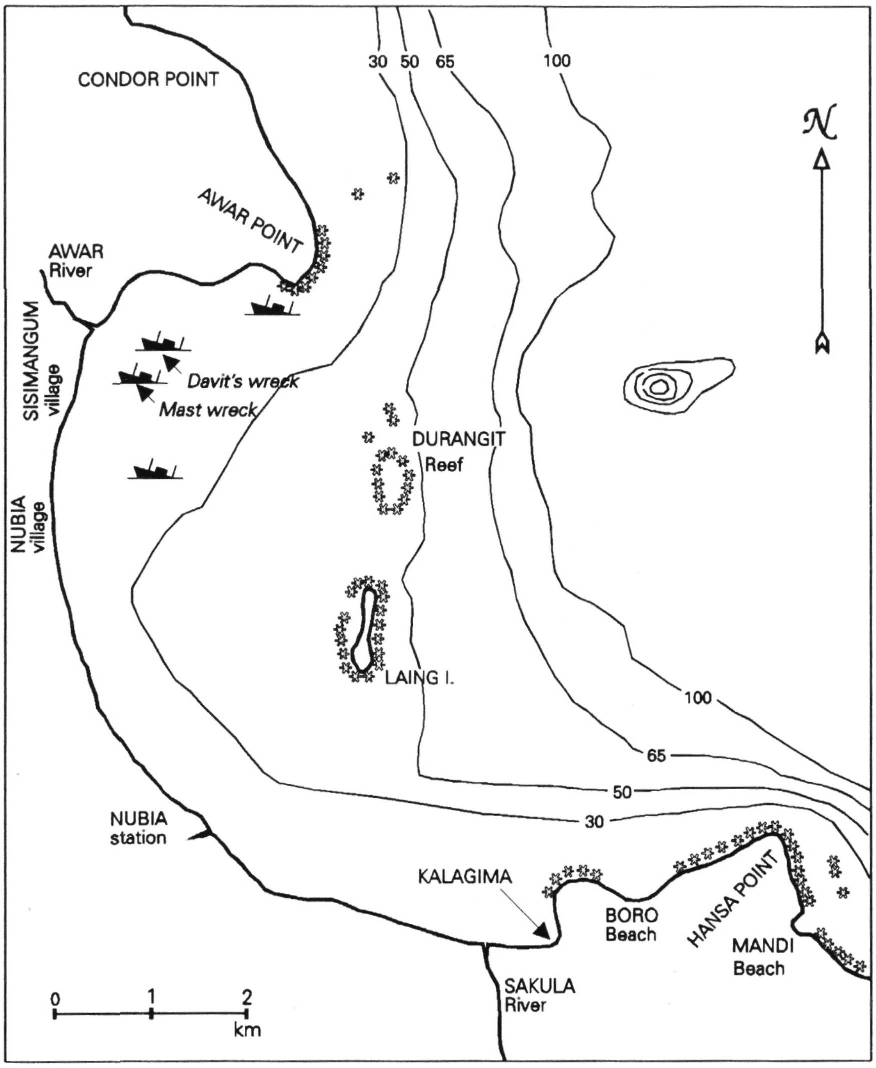

Fig. 1. Hansa Bay.

2.3. Material measured

BT-numbers refer to specimens in the author's collection, DG- numbers to the collection of Dr. Dietmar Greifeneder (Schwenningen) and JS- numbers to that of Dr. Jacques Senders (Brussels).

Oliva amethystina (Röding, 1798).

PAPUA NEW GUINEA, HANSA BAY: - DURANGIT REEF, 6m: specimens BT-7002, BT-7003, BT-7004, BT-7006 to BT-7001; - "DAVIT'S WRECK" (near Awar river), 6 m: specimens BT-6779 to BT-6786; - "MAST WRECK" (near Awar river), 5 m: specimens BT-7178 to BT-7182.

OTHER LOCALITIES: SOLOMON IS. : specimens BT-2454, BT-3512, BT-3516, DG-2521/5, DG-2521/8, DG-2523/6, DG-2524/3.

Oliva smithi Bridgmann, 1906.

PAPUA NEW GUINEA, HANSA BAY: - LAING ISLAND West coast (lagoon), 0.5-1 m: specimens BT-2174 to BT-2183. - OFF BORO BEACH, 6-8 m: specimens BT-2164 to BT-2173.

OTHER LOCALITIES: AUSTRALIA (North Queensland): specimens BT-5767, BT-5807, BT-5808, BT-6122 to BT-6126, BT-6128, BT-6130; INDONESIA (Ceram I.): specimens BT-167, BT-169, BT-296, BT-298; PHILIPPINES (Cebu): specimens BT-1312, BT-4999 to BT-5003, BT-5789, BT-5791 to BT-5793; PHILIPPINES (Pamilacan): specimens BT-6277 to BT-6279, BT-6281, BT-6284.

Oliva oliva (Linnaeus, 1758).

PAPUA NEW GUINEA, HANSA BAY: - BORO BEACH, low tide: specimens BT-2154 to BT-2163 (all of very light ground colour, hereunder designated as "white"). - SISIMANGUM BEACH, low tide: specimens BT-2154 to 2158 (all of very light ground colour, hereunder designated as "white") and specimens BT-2149 to BT-2153 (all of very dark ground colour, hereunder designated as "black").

OTHER LOCALITIES: PAPUA NEW GUINEA (Samarai, Milne Bay): specimens BT-5245 to BT-5247, BT-5251, BT-5254, BT-5259, BT-5263, BT-5269, BT-5272, BT-5273; PHILIPPINES (Zamboanga): specimens BT-4589 to BT-4593, BT-5700, BT-5779 to BT-5784; THAILAND (Patong Beach, Phuket): specimens BT-4768, BT-6142, BT-6149, BT-6154, JS-035, JS-037, JS-040, JS-176, JS-186.

In addition to the measured material, several hundred Hansa Bay specimens of the most common populations of these species have been visually checked, in order to verify the constancy of the discriminating characters described below.

2.4. Tests of conspecificity.

Special care was taken to verify that the populations presented here as conspecific do really belong to the same species. All are common, widely distributed *Oliva* species for which abundant comparison material is available. In each case it was established (by principal factor analysis and/or discriminant factor analysis) that these populations are parts of a much larger morphological continuum, covering the whole distribution area of the species. Within a species continuum, no population (or group of populations) could be distinguished from all the others by any of the many metric shell variables that were tested (alone or in combination). Examples of the applications of these methods to *Oliva* have already been reported (for instance in TURSCH *et al.,* 1992) and, for the sake of brevity, details of these lengthy procedures will not be reported here. For every case, it was demonstrated (by scatter diagrams) that the morphological gaps distinguishing the Hansa Bay populations are bridged in other, allopatric populations. For each species, only one scatter diagram will be illustrated here. One should note that the "bridging populations" do not necessarily occur in Hansa Bay.

2.5. Measurements

The following measurements have been used in this paper: H, L, D (Fig. 2) and R (Fig. 3) are teleoconch measurements defined in TURSCH & GERMAIN (1985). Pat15, pat16, pat17 and pat18 (Fig. 4) are protoconch measurements defined in TURSCH & GERMAIN (1987).

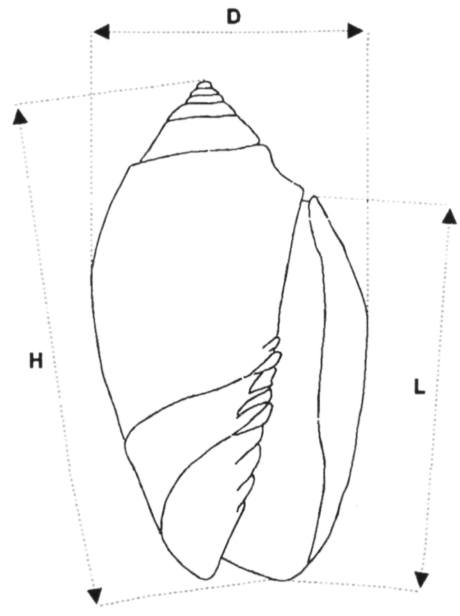

Fig. 2. Sketch of the measurements H, D and L.

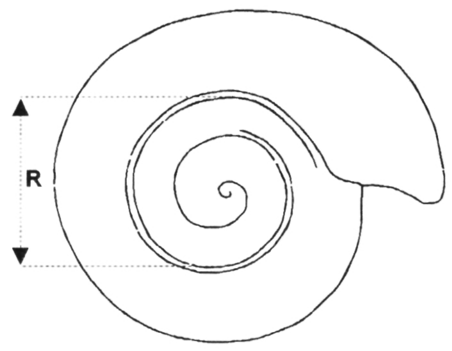

Fig. 3. Sketch of the measurement R.

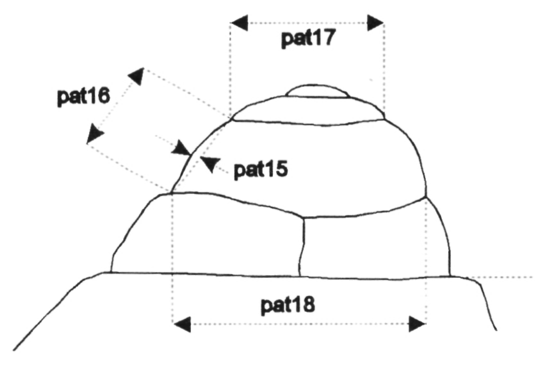

Fig. 4. Sketch of the protoconch measurements pat15, pat16, pat17 and pat18.

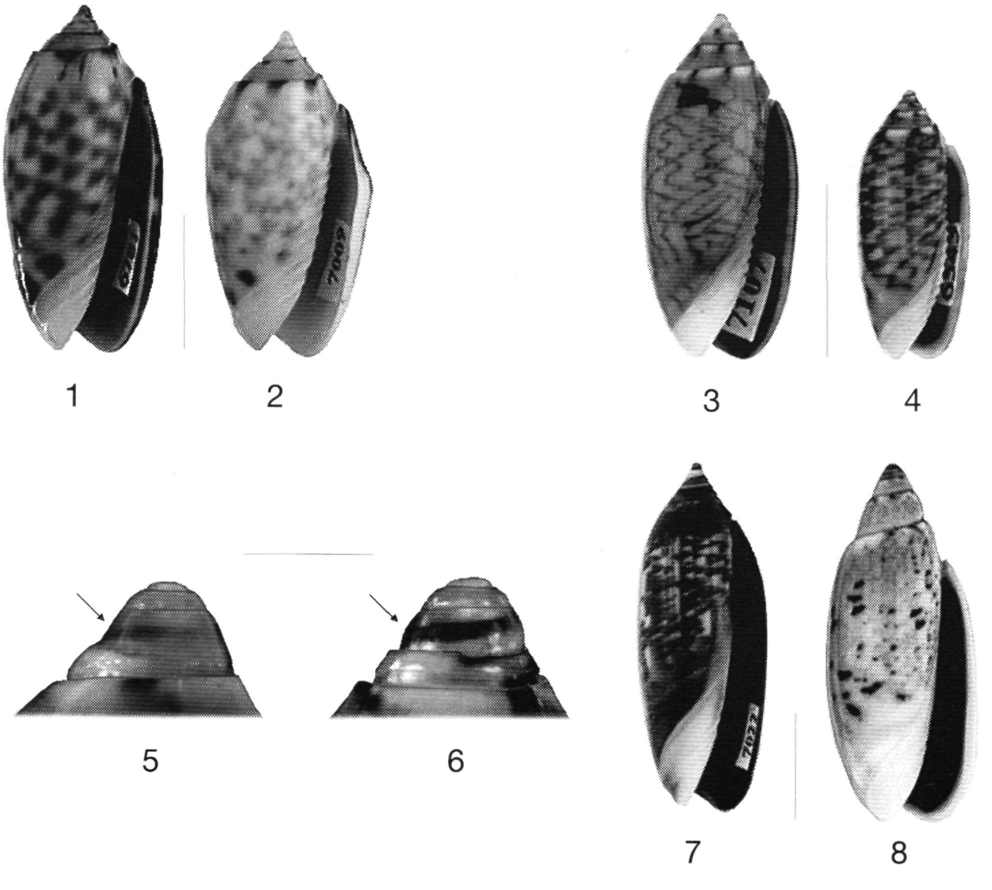

Plate 1.
Figs. 1-2: *Oliva amethystina* (Röding, 1798).
Fig. 1. Typical specimen (BT-6781) from "Davit's wreck", 6 m.
Fig. 2. Typical specimen (BT-7009) from Durangit Reef, 6 m.
Figs. 3-4: *Oliva smithi* Bridgman, 1906.
Fig. 3. Typical specimen (BT-7107) from Laing I. lagoon, 0.5-1 m.
Fig. 4. Typical specimen (BT-6543) from Boro Beach, 6-8 m.
Figs. 5-6: Protoconchs of *Oliva smithi.* Note the difference in convexity of the penultimate protoconch whorl (arrows) and the fusion of the two last protoconch whorls in specimen BT-7107 (fig. 5).
Fig. 5. Protoconch of specimen BT-6225 from Laing I. lagoon, 0.5-1 m.
Fig. 6. Protoconch of specimen BT-6543 from Boro Beach, 6-8 m.
Figs. 7-8: *Oliva oliva* (Linnaeus, 1758).
Fig. 7. Typical specimen (BT-7022) from Sisimangum Beach, low tide.
Fig. 8. Typical specimen (BT-6573) from Boro Beach, low tide.

3. OBSERVATIONS AND RESULTS

3.1. *Oliva amethystina* (Röding, 1798).

In Hansa Bay, this common species lives mostly between -1 and -10 m, exclusively in coral sand, in proximity to live coral (where it is easily mistaken for a dead *Acropora* coral fragment). Two populations (Plate 1, figs. 1-2) have been compared: one living on the top of Durangit Reef and another living around "Davit's wreck", two localities distant of only 2.8 km and separated by a bottom of very fine dark mud, in 40-48 m, extending over about 1 kmMany specimens have been collected at -6 m, in coarse, white coral sand, on the top of the large Durangit Reef. This biotope is often exposed to heavy water motion (high waves and swift current), so *Oliva* tracks are immediately erased and specimens have to be collected with a small hand dredge. Adult specimens are mostly found around the rocky ledges of the sand pockets, while juveniles are mostly found in the sand ripples. The population of *O. amethystina* at the top of Durangit Reef is very similar to (and could not be separated from) that of the Laing Island reef (excepted that the percentage of large, adult shells is much higher at Durangit).

A much smaller number of specimens were collected at -6 m, around a Japanese wreck called "Davit's wreck" because its davits could be seen above water until a few years ago. The specimens lived in a mixture of fine and coarse coral sand(including dark terrigeneous material). In this biotope where the water is mostly quiet, all our juvenile *amethystina* were found (by hand dredging) only in the white coral sand recently deposited just along the hull, whereas some adults were found by their tracks in the darker sand further away from the wreck. The wreck is quite small and we have been careful not to overcollect this little biotope. The shells are quite characteristic and no matching specimens have been found in or around Hansa Bay despite extensive exploration over 20 years, with the exception of a few rather similar specimens found around "Mast wreck", another sunken ship lying close to "Davit's wreck". The two wrecks are separated by about 200 m of hard, fine dark sediment, in 5-7 m depth.

All available specimens (8) from "Davit's wreck" were compared to an equivalent number of randomly selected specimens from Durangit. The two samples differ by protoconch as well as by teleoconch characters and are completely separable, as demonstrated (Fig. 5) by a scatter diagram of pat17/pat18 *vs.* D/L (pat17/pat18

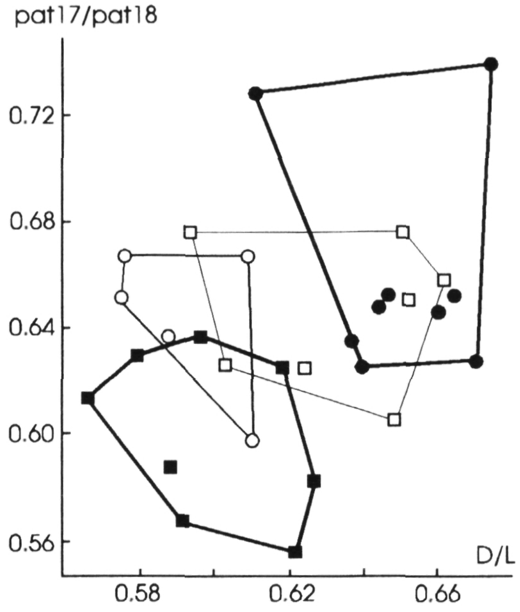

Fig. 5. Comparison of populations of *Oliva amethystina*. Scatter diagram of D/L *vs.* pat17/pat18. Minimum convex polygons. The populations from Hansa Bay (thick contour lines - black circles: shells from Durangit Reef - black squares: shells from "Davit's wreck") are separated by an obvious moprphological gap. This gap is bridged by other conspecific populations (thin contour lines - white circles: shells from "Mast wreck" - white squares: shells from Solomon Is.).

roughly reflects the conical angle of the penultimate protoconch whorl). All specimens collected at Durangit are squat, heavy, with a tendency to bulge on the body whorl (Plate 1, fig. 2); all have a light coloured background. All specimens from "Davit's wreck" are more slender, have a darker background (Plate 1, fig. 1) and the surface of their protoconch is mostly corroded. This is also the case for the "Mast wreck" specimens. Fig.5 also shows that the morphological gap separating the Durangit Reef and the "Davit's wreck" populations is bridged in other, allopatric populations of the same species.

It should be noted that "Davit's wreck" was sunk during World War II. Like the other wrecks in the bay, it is now overgrown with a luxuriant reef, the decay of which surrounds the hull with coral sand, the exclusive habitat of *O. amethystina*. This small pocket of white coral sand is isolated in a plain of fine black sediment. If one estimates the time required for the growth and the subsequent decay of the coral it is unlikely that the "Davit's wreck" population of *O. amethystina* is more than 30 years old.

3.2. *Oliva smithi* Bridgman, 1906.

Two distinct populations of this common species are found in Hansa Bay (Plate 1, figs. 3-4). One is widely spread along the coast, in depths of 2-14 m (generally 5-9 m), on sediments ranging from fine, dark terrigeneous material (off Awar, in usually quiet waters) to fine, white coral sand (off Boro Beach, where the sediment is in nearly constant motion, due to heavy swell). The colour pattern of the shells is very variable, mostly matching the colour of the sediment.

The other population has a very restricted distribution in the lagoon of Laing Island, in shallow water (0.5-1 m), coarse coral sand, occasional moderate wave action, and is quite constant in colour pattern. It is a recent (maybe accidental) introduction, not found before 1992 although the lagoon has been the object of regular, intensive search for 20 years. Furthermore, the lagoon population happens to live in the place where our native co-workers (all experienced *Oliva* watchers) daily wash their dishes, and it is unlikely that the shells would have escaped their trained eye for very long. The lagoon beach appears quite uniform, but during a thorough search in early 1993, *O. smithi* was found only on a stretch of about 50 meters. Only a few shells were gathered, in order not to upset this small population.

A sample of *O. smithi* from Laing Island lagoon was compared to a sample from off Boro Beach. These localities are roughly 3.8 km apart and are separated by a bottom of very fine dark mud, at 40-48 m, extending over about 1.5 km. The two samples are completely separated (Fig. 6) on a scatter diagram of D/L *vs.* pat15/pat16 (pat15/pat16 is an expression of the convexity of the penultimate nuclear whorl). Specimens from Laing Island reach a larger size than the Boro Beach shells (H_{max} 22.8 mm *vs.* 15.8 mm) and their body whorl is less cylindrical (see Plate 1, figs. 3-4). The protoconchs of the two samples, albeit similar, show constant differences (see Plate 1, figs. 5-6). In the Laing Island specimens, the two last whorls of the protoconch are fused (the suture is covered by a thin, transparent layer of enamel) and the profile of the penultimate nuclear whorl is quite flat. In the Boro Beach specimens, the two last whorls of the protoconch are distinct and the profile of the penultimate nuclear whorl is convex. Fig.6 also shows that the morphological gap separating the Laing Island and the Boro populations is bridged in other, allopatric populations of the same species.

3.3. *Oliva oliva* (Linnaeus, 1758).

In Hansa Bay, this abundant species is restricted to the low water level on sandy beaches exposed to frequent surf. It is polytopic and cryptic (VAN OSSELAER *et al.*, 1994), the background colour of the shells ranging from very pale to very dark (hereafter called "white" and "black" shells).

One small population lives on white, coarse coral sand at Boro Beach, where heavy swell is generally prevalent. Specimens from Boro (see Plate 1, fig. 8) reach a moderate size (H_{max} 33.15 mm). All 42 specimens collected are "white" and have an elongated spire. The aperture is short and consistently reddish brown. The protoconch of all specimens is severely eroded.

Another population (this one very large) extends all the way from the northern tip of the bay to the mouth of the Sakula river, on fine, black volcanic sand, with occasional, moderate swell. Specimens from Sisimangum (see Plate 1, fig. 7) reach a larger size (H_{max} 42.31 mm). On nearly one thousand specimens observed, 76% are "black", 15 % are "white" and 9 % do not fit into these categories. The spire is short, the aperture long and mostly dark purple. Most specimens have an intact protoconch.

A sample of 10 specimens (all "white") from Boro Beach was compared to a sample of 10 specimens (5 "white", 5 "black", all protoconchs intact) from Sisimangum. These localities are distant of roughly 12 km along the coast but the Sisimangum population reaches the Sakula river and the two populations actually come within 1.5 km of each other. The only physical obstacles separating these populations are a small rocky point between Boro and Kalagima and the mouth of the Sakula River. The two samples are entirely distinct, separated by a large morphological gap, as shown (Fig. 7) on a scatter diagram of H/L *vs.* R/D. Within the Sisimangum sample, "white" and "black" specimens are not separated; shell morphology seems unrelated to colour. Fig. 7 also shows that the morphological gap separating the Sisimangum Beach and the Boro Beach populations is bridged in other, allopatric populations of the same species.

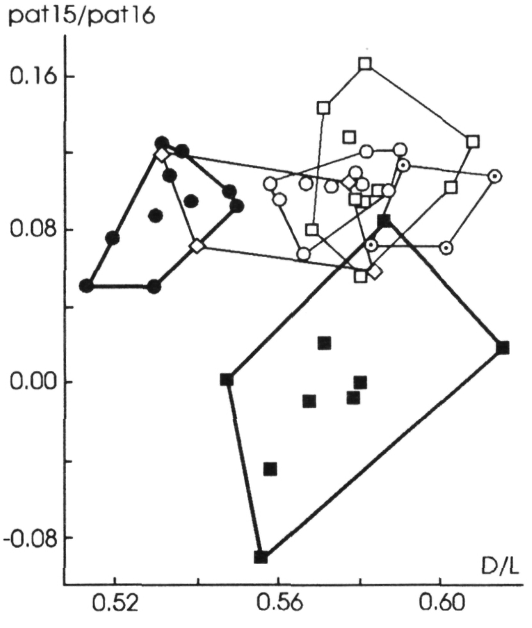

Fig. 6. Comparison of populations of *Oliva smithi*. Scatter diagram of D/L *vs*. pat15/pat16. Minimum convex polygons.

The populations from Hansa Bay (thick contour lines - black circles: shells from Boro - black squares: shells from Laing Island lagoon) are separated by an obvious moprphological gap. This gap is bridged by other conspecific populations (thin contour lines - white circles: shells from Australia, North Queensland - white squares: shells from Philippines, Cebu - white circles, centered: shells from Indonesia, Ceram - white lozenges: shells from Philippines, Pamilacan).

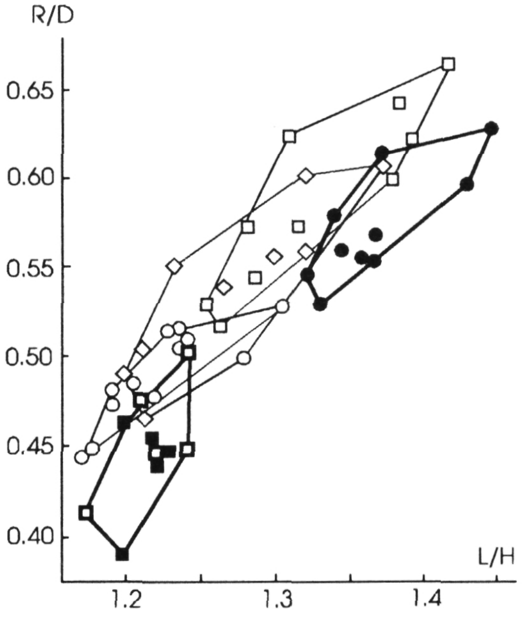

Fig. 7. Comparison of populations of *Oliva oliva*. Scatter diagram of D/L *vs*. pat15/pat16. Minimum convex polygons.

The populations from Hansa Bay (thick contour lines - black circles: shells from Boro Beach - black squares: black shells from Sisimangum Beach - thick white squares: white shells from Sisimangum Beach) are separated by an obvious moprphological gap. This gap is bridged by other conspecific populations (thin contour lines - white circles: shells from Philippines, Zamboanga - white squares: shells from Papua New Guinea, Samarai - white lozenges: shells from Thailand, Phuket).

It should be noted that the characters of these two populations have been stable for 20 years (judging from specimens in our collection) and probably for much longer a time, judging from specimens in ancient leg ornaments, still used in traditional *sing-sing* ceremonies by the local Dawar people.

4. INTERPRETATION

In short, it has been shown that:

a. Close neighbouring populations of the same *Oliva* species often present notable differences. These differences reach complete morphological separation in the examples presented here, but it should be stressed that this point is not essential. Some overlap in the distribution of population characters would not affect the conclusions here under. Many *Oliva* variants exhibit a remarkable fidelity to their locality, to the point that an experienced collector can often guess the precise origin of a given specimen.

b. The observed divergence of micropopulation characters can occur fast. It can be estimated to less than 30 years for *O. amethystina* (see section 3.1, last §) and to probably a few years for *O. smithi* (see section 3.2, § 2). In contrast, all the established populations regularly sampled for a long time have been stable in their characters at least over a period of 20 years and probably for much longer (see section 3.3, last §).

The observed differences in shell morphology could stem both from phenotypic plasticity and genetic isolation. On the one hand, environmental effects are probably an important contributor to colour variation, as illustrated by the fact that 24 of the 29 *Oliva* species encountered in Hansa Bay are cryptic to some degree, a phenomenon suggesting intense pressure from visual predator(s) (this is discussed in VAN OSSELAER *et al.*, 1994). Considerable predation has indeed been demonstrated in the case of *O. oliva,* where nearly every specimen of the Sisimangum population bears the scars of at least one unsuccessful attack (*study in progress*). No data for linking *Oliva* shell morphology to environmental effects are yet available.

On the other hand, genetic isolation is strongly suggested by the frequent observation of differences in the protoconch (*e.g.* in the case of *O. smithi*). The protoconch of *Oliva* species is produced inside the egg capsule (OLSSON & CROVO, 1968; TURSCH, 1991), where it is shielded against direct environmental influences. Morphological gaps at the protoconch level are thus likely to be of genetic origin. Another, indirect argument stems from the very rapid changes observed for the small population of *O. smithi* in the lagoon of Laing Island. Such a situation immediately evokes genetic drift, a phenomenon requiring genetic isolation.

One more indirect argument can be found in the morphological stability observed in established *Oliva* populations. This stability sharply contrasts with the rapid changes occurring in the topography of the shallow water biotopes of Hansa Bay. During the last 20 years, the beach at Sisimangum has diminished by some 100 m, the East coast and the northern tip of Laing Island have also considerably regressed, while the beach in the southern part of the lagoon has extended. According to the oral tradition of the local Dawar tribesmen, Laing Island was actually linked to the mainland at the time of their ancestors. Elderly people all say that in their youth Laing island had at least the double of its present size. In addition, sporadic eruptions of the nearby Manam volcano frequently pepper the whole area with large quantities of igneous material. The modifications of the shoreline produce important changes in physical conditions (slope, exposure to waves, etc.), to the point that some of our boat moorings had to be moved over the years. So the morphological stability of most populations shows that many of the discriminant characters used by the *Oliva* taxonomist do not reflect subtle environmental differences but most probably partial genetic isolation.

All the available data thus indicate that there appears to be severe restrictions on gene flow between many of the Hansa Bay conspecific *Oliva* populations. Each of these populations could be considered as a *topogamodeme,* this is a relatively isolated, naturally interbreeding, population (gamodeme) occupying a particular area (LINCOLN *et al.*, 1982).

5. COMMENTS AND DISCUSSION

Although I have no simple solution to offer, it might be worth discussing the mechanism(s) that could explain the partial genetic isolation of the close neighbouring Hansa Bay *Oliva* populations. Interpopulation gene flow depends upon dispersal and this could take place either at the larval or at the adult stage.

Nothing is known about the vagility of *Oliva* larvae, but the present observations suggest that it must generally be low. Indeed, the larval stage lasts several days (OLSSON & CROVO, 1968; TURSCH, 1991) and the seasonally variable currents could easily transport pelagic veligers anywhere in Hansa Bay within hours. It has been shown that the veliger of *Olivella verrauxii* is not pelagic but swims on the bottom (MARCUS & MARCUS, 1959). I could find no report of *Oliva* larvae being caught in plankton hauls. Even if the larvae were effectively dispersed, successful immigration could still be severely restricted by the necessity of settling on a suitable substrate. Effective larval dispersal over large distances certainly does take place, as evidenced by the very large distribution of several *Oliva* species, but it must be quite infrequent.

The *Oliva* populations of Hansa Bay are so closely spaced that immigration could possibly also occur at the adult stage. Very little is known about the actual cruising range of adult *Oliva* species. They can live several years and do easily reach speeds of 25 cm/min (TURSCH, 1991). Tracks several meters long are frequently observed and an *Oliva* could conceivably travel many kilometers in its lifetime. One could even imagine that adult *Oliva* could cross small stretches of moderate depths: they have no pressure-sensitive organ and they could certainly tolerate reduced light (being mainly nocturnal, see VAN OSSELAER & TURSCH, 1993). In addition, they can easily subsist on a wide variety of foods that are completely foreign to them.

In theory, *O. oliva* could thus travel from Boro to the black Sisimangum beach in a matter of days or weeks. But no specimen of the "Boro type" has ever been collected from Kalagima to Awar. Conversely, no specimen of the "Sisimangum type" has ever been caught at Boro Beach. It is doubtful that the mouth of the Sakula river could constitute a serious barrier: it is only about 10-20 m wide and is completely closed by a sand bar at low tide during the dry season. The similar (but smaller) Awar river does not divide the Sisimangum population. It is more likely that the obstacle is constituted by the small rocky point separating Boro from Kalagima, where the soft substrate that all olives require is found at 5-6 m, an environment possibly unsuitable for a species restricted to surf beaches. This same rocky point is no obstacle for *O. smithi* that often lives in deeper water. In practice, adult Olives seem rather sedentary, as shown by the lagoon population of *O. smithi* (see section 3.2, §2). One could conjecture they are prevented from moving by being very sensitive to minute changes in the nature of the substrate, but this is unlikely because in sediment choice experiments, several species of *Oliva* have shown only very slight substrate preferences (VAN OSSELAER & TURSCH, 1993). One could also imagine that the micropopulations are kept together by some cohesive force such as chemical attractants (TURSCH, 1991) but no firm data yet support this hypothesis.

6. CONCLUSIONS

The *Oliva* species of Hansa Bay consist in a mosaic of populations, the map of which fairly reflects the discontinuities of the habitat. These populations are not only ecological races; in many cases they also appear to be temporarily isolated by restricted gene flow, even over very short distances. Neighbouring, conspecific populations frequently differ to the point of complete morphological separation. That different populations could be distinguished by some combination of characters is no great discovery and was indeed fully expected (see MAYR, 1969 and FUTUYMA, 1986), even for shells that are collector's favourites. The observations at Hansa Bay just give a somewhat sharper image of the spatial scale, the extent and the tempo of intraspecific variation in the genus *Oliva*. They also point to the necessity of moderating the current taxonomic approach to this genus.

First, the scale of sympatry in *Oliva* can be much smaller than it is generally considered. The pattern observed in tiny Hansa Bay is certainly not unique and can be expected to occur over the very large distribution areas of many species. In addition to the examples given in the introduction (see TURSCH *et al.*, 1992), the populations of *Oliva oliva* I have sampled in two very similar small bays separated by only 5.8 km on the North coast of Hon Lon Island, off Nha Trang (Vietnam) can be separated at a glance. Many other similar examples could be given and it is a safe bet that morphological discontinuities between close-set populations will be commonly observed in any careful field study of *Oliva*.

Special caution is thus necessary in the application of our most reliable tool for taxonomic decisions at the morphospecies level: the demonstration of morphological gaps between sympatric populations (see Introduction). When comparing populations from a same, broad locality, data such as "New Guinea, shallow water" or even "Hansa Bay, sand, 8 m" are now clearly insufficient to demonstrate sympatry.

We can be sure that *Oliva* populations are sympatric only when they actually overlap in space. This can be known only if specimens of both taxa have been observed together (or within a short distance) in the same, continuous microhabitat. Such a relationship could be described by the word "*syntopic*" in a slightly restricted sense. "Syntopic" has been defined as: "pertaining to populations or species that occupy the same macrohabitat, *are observable in close proximity* (italics are mine) and could thus interbreed" (LINCOLN *et al.*, 1982). Conversely, in the absence of actual spatial overlap, one could use the word "allotopic" in the somewhat restricted sense of "*not observed in close proximity*".

In the case of *Oliva* (at least) it is obviously safer to replace our broad criterion of sympatry by that of syntopy. This does not upset any fundamental concept, as it is only a reduction of spatial scale. It will actually facilitate the task of the taxonomist because differences between similar species will generally be more pronounced wherever these species come into contact (the well-known phenomenon *of character displacement*).

Without this reduction of the commonly accepted scale of sympatry, one could be led to create as many *Oliva* "species" as there are local populations within an arbitrary range of proximity. Many "species" of *Oliva* have indeed been created upon differences smaller than those observed between some of the Hansa Bay conspecific populations. This solution is unfortunately attractive to some (see the criticism of MAYR, 1969) but is demonstrably wrong. In all the cases studied so far in this laboratory and for which enough data were available (for example the protean "*Oliva oliva* complex", see TURSCH *et al.*, 1992), the set of all conspecific populations (considered over the whole distribution range) always form a morphological continuum. The characters discriminating any two given conspecific populations are invariably bridged by at least another population (or by a chain of intergrading populations). This indicates that gene flow, even if restricted, does nevertheless take place.

Some could then be tempted to consider each of the morphologically distinct local populations of *Oliva* as a subspecies in the sense of "local variety". This would lead to obvious nomenclatural excess and the notion of subspecies (largely a category of convenience) would then lose any meaning. The sensible definition of MAYR (1963) restricts subspecies to "aggregates of populations", on much larger spatial scale.

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