

**The "*Oliva miniacea* complex",
with the description of a familiar, unnamed species
(Studies on Olividae. 25).**

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SUMMARY. The status of *Oliva miniacea* (Röding, 1798) and similar taxa is reviewed. *Oliva mascarena* n. sp., a familiar, hitherto unnamed Indian Ocean species, is described. A lectotype is selected for *O. concinna* Marrat, 1870. The taxonomic status of the names used for this group of species (and of names incorrectly associated with them) has been critically examined.

RESUME. Le statut de *Oliva miniacea* (Röding, 1798) et des taxa qui lui sont similaires a été revu. *Oliva mascarena* n.sp., une espèce familière de l'Océan Indien, jusqu'ici non nommée, est décrite. Un lectotype est désigné pour *O. concinna* Marrat, 1870. Le statut taxonomique des noms utilisés pour ce groupe d'espèces (et des noms qui leur ont été erronément associés) a fait l'objet d'un examen critique.

1. INTRODUCTION

1.1. The *O. miniacea* - *O. tremulina* problem.

The large, spectacular *Oliva miniacea* (Röding, 1798) is very common and widespread in the South West Pacific. It exists in an amazing variety of colours, patterns and shapes, and is one of the most protean shells in the genus *Oliva*, itself well known for its variability. Large size and a deep reddish orange aperture are the only two stable characters reported in the recent literature (ZEIGLER & PORRECA, 1969; PETUCH & SARGENT, 1986).

The closely related *Oliva tremulina* Lamarck, 1811, common in the Indian Ocean, has been a controversial taxon for over a century. *O. tremulina* and *O. erythrostoma* Lamarck, 1811 (the name formerly used for *O. miniacea*) were considered as distinct species by WEINKAUFF (1878) and by DAUTZENBERG (1927). In contrast, JOHNSON (1928) considered *O. tremulina* as being a variety of *O. erythrostoma*. More recently, BURCH & BURCH (1967), comparing *O. tremulina* and *O. erythrostoma*, wrote "*O. tremulina* not only have a fleshy-white aperture, but seem to be less swollen at the posterior or shoulder of the shells. They are otherwise close, but we think they are easily separable." ZEIGLER

& PORRECA (1969) wrote of *O. tremulina*: "... it is identical in appearance with *O. miniacea*, differing only in that its aperture is fleshy white." PETUCH & SARGENT (1986) also note the difference of aperture colour, say that *O. tremulina* has a "white, yellowish-cream or creamy pink ground colour" (instead of "cream-yellow or yellow orange" for *O. miniacea*). They do not give any other reliable criterion for discriminating what they consider to be separate species.

1.2. Extension of the problem.

The problem is not confined to the names *miniacea* and *tremulina*. One could predict that the complexity of the biological puzzle, compounded with equivocal nomenclatural practices, would result in taxonomic chaos. This did indeed occur.

O. miniacea is described in the *Museum Boltenianum*, which was rediscovered only in the beginning of this century. So, many earlier citations of this species are under its former name: *O. erythrostoma* Lamarck, 1811. Then, for a period (around 1910-1920) and for reasons unknown to us, *O. miniacea* was called *O. sericea* (Röding, 1798) by American authors, while the true *O. sericea* was designated by its former name, *O. textilina* Lamarck, 1811.

Many distinct species were confused. For instance, *O. tremulina* and *O. erythrostoma* were considered by TRYON (1883) as being only varieties of *O. irisans* Lamarck 1811. Then JOHNSON (1910), reunited (possibly in despair) most of the valid large Indo-Pacific *Oliva* species (*O. miniacea*, *O. ponderosa*, *O. textilina*, *O. tremulina* and others) as varieties of his *O. sericea*; Johnson (not Röding, 1798), 1910. Under his variety *zeilanica* Lamarck (a nomen dubium, see GREIFENEDER, DUCHAMPS & TURSCH, 1995), the author even created a new variety *fordi* - a variety of a variety!. This was not an isolated excess: HIGGINS (1919), amongst others, used names such as "*Oliva sericea miniacea*" and the "*Oliva sericea (tremulina-miniacea* group)".

In the genus *Oliva*, authors have been much more concerned with nomenclature than with biological data, so numerous other names (discussed in section 6: Systematics) have been used for these shells and their various forms.

1.3. Purpose.

The need for a revision will be evident to whoever has been lost in the nomenclatural labyrinth erected around these large, common Indo-Pacific *Oliva* species. These are still habitually confused, even in the best collections.

We had to examine not only the various forms of *O. miniacea* (Röding, 1798) and of *O. tremulina* Lamarck, 1811 but also the related taxa: *Oliva atalina* Duclos, 1835, *O. ponderosa* Duclos, 1840 and a familiar but unnamed *Oliva* from the Central Indian Ocean, described here under. For added safety in the delimitation of the "*O. miniacea* complex", small samples of the outgroups *O. concinna* Marrat, 1870 (considered as *O. tremulina* by BURCH & BURCH, 1960), *O. hirasei* Kira, 1959 and *O. sericea* (Röding, 1798) (considered as a variety of *miniacea* by JOHNSON, 1928) were also examined.

Classical, chronological review of scientific names (most with very vague, if any biological meaning, see section 6) is not the most operational method for solving such a complex problem. Following the general approach outlined in TURSCH, MISSA & BOUILLON (1992), we elected to start by seeking experimental evidence for the existence of separable groups. The next step was the ranking of these groups into species, subspecies and varieties. Nomenclatural decisions could then logically follow objective separation and ranking of taxa, instead of preceding (or simply skipping) these steps.

Abbreviations:

- AMS: Australian Museum, Sydney.
AMNH: American Museum of Natural History, New York.
ANSP: Academy of Natural Sciences, Philadelphia.
BM(NH): The Natural History Museum, London.
IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels.
MCM: Merseyside County Museum, Liverpool.
MNHN: Muséum National d'Histoire Naturelle, Paris.
USNM: National Museum of Natural History (Smithsonian Institution), Washington.

Throughout this text, the convenient device of a semicolon inserted between the specific name and the author [*X-us albus*; Smith (not Brown)] is used to distinguish between a misidentification, which has no nomenclatural status, and a homonym [*X-us albus* Smith (not Brown)], which has (see MAYR & ASHLOCK 1991: 362).

2. MATERIAL EXAMINED

2.1. Type material examined.

- Oliva atalina* Duclos, 1835. 3 syntypes at MNHN.
Oliva azemula Duclos, 1840. 5 syntypes at MNHN.
Oliva berti Terzer, 1986. Paratypes 1 and 2 in Terzer collection, Genoa.
Oliva concinna Marrat, 1870. 2 syntypes at MCM.
Oliva cryptospira Ford, 1891. Holotype n° 15878 at ANSP.
Oliva fulva Marrat, 1871. Holotype at MCM.
Oliva fumosa Marrat, 1871. Holotype at MCM.
Oliva fumosa kremerorum Petuch & Sargent, 1986. Holotype n° 841460 at USNM. Paratype n° C153453 at AMS.
Oliva galeola Duclos, 1840. 3 syntypes at MNHN.
Oliva lamberti Jousseaume, 1884. 3 syntypes at MNHN.
Oliva magnifica Ducros de Saint Germain, 1857. 5 syntypes at MNHN.
Oliva nobilis Reeve, 1850. Type n° 1892.9.24.18 at BM(NH).
Oliva olympiadin Duclos, 1835. 4 syntypes at MNHN.
Oliva ponderosa Duclos, 1840. 9 syntypes at MNHN.
Oliva quersolina Duclos, 1835. 3 syntypes at MNHN.

Oliva sabulosa Marrat, 1868. 2 syntypes at MCM.
Oliva sericea albescens Johnson, 1915. Holotype n° 111753 at ANSP.
Oliva sericea fordii Johnson, 1910. Holotype n° 111612 at ANSP.
Oliva sericea marrati Johnson, 1910. 3 syntypes n° 111862 at ANSP.
Oliva sowerbyi Marrat, 1870. 2 syntypes at MCM.
Oliva stainforthi Reeve, 1850. 2 syntypes n° 1892.9.24.13-14 at BM(NH).
Oliva tenebrosa Marrat, 1870. Holotype at MCM.
Oliva tremulina flammeacolor Petuch & Sargent, 1986. Holotype n° 841458 at USNM. Paratype n° C153546 at AMS.
Oliva tremulina oldi Zeigler, 1969. Holotype n° 147750 at AMNH. Paratype n° C111456 at AMS.

2.2. Other material measured.

The number of specimens that could be completely measured in this study was severely limited by the availability of such large *Oliva* shells with an intact protoconch (the heavier an *Oliva* shell, the more likely it is that its protoconch will be broken). In addition to the measured material, listed here under, well over two thousand specimens (in museums as well as in private hands) have been visually inspected.

DG: indicates specimens from the Dietmar Greifeneder collection; BT: Bernard Tursch collection, JMO: Jean-Marc Ouin collection, JS: Jacques Senders collection, TV: Musée de l'Afrique Centrale collection (Tervueren, Belgium). "noloc." means: no accurate locality. All specimens have an intact protoconch, unless marked with (-). In many cases, some measurements could be obtained on partially damaged protoconchs. For the definition of the provisional phenon, see § 3.3).

Oliva atalina Duclos, 1835. **CARGADOS CARAJOS**: DG-3055/1 (-), DG-3055/2 (-), DG-3055/3 (-), DG-3055/4 (-), DG-3055/5 (-), DG-5639/1 (-), DG-5639/2 (-), DG-6181/1 (-), DG-6181/2 (-), DG-6181/3 (-), DG-6181/4 (-), DG-6181/5 (-). **MAURITIUS**: DG-588 (-), DG-1046 (-), DG-2194 (-), DG-5895/1 (-), DG-5895/2 (-), DG-6180.

Oliva mascarena n. sp. (provisional phenon MS) **CHAGOS, Peros Banhos**: DG-3076. **MAURITIUS, Grand Bay**: DG-5976 (-). **Rivière Noire**: DG-3058/1 (-), DG-3058/2 (-), DG-5786 (-), DG-5977, DG-6179/1 (-), DG-6179/2, DG-7206 (-). **noloc.**: BT-4255, DG-3058/3 (-), DG-3058/4 (-), DG-3058/5 (-).

SEYCHELLES, Beau Vallon: BT-4367 (-), BT-4368, BT-4369, BT-4370.

Oliva miniacea (Röding, 1798). **AUSTRALIA Queensland, Langford Reef, Biesley Is.**: DG-2873/9, DG-2873/g, DG-2873/6, DG-2873/5, DG-2873/7. **CAROLINE Is., Truk Lagoon**: DG-6129/19, DG-6129/15, DG-6129/4, BT-3669. **FIJI Lau Group**: BT-5078, BT-5077, BT-5076, BT-5075, BT-5081. **GUAM, Piti**: BT-3661, DG-6923/2, **Agat**: DG-7979. **INDONESIA**, (provisional phenon IN) **Flores, Larantuka**: BT-1993. **Tanimbar Olilit Lama**: BT-0027. **Bali, Kesuma Sari**: BT-0058, DG-2000, DG-2000-MS1, JS-230, JS-231, JS-232. **JAPAN, Okinawa**: DG-6663/2, DG-6663/1, DG-6663/3, DG-3764/2. **MARSHALL, Kwajalein Atoll**: DG-5400/1, DG-5400/3, BT-2791, BT-2785, BT-2786, DG-6041/2 (-). **NEW CALEDONIA, Nouméa**: BT-2972, BT-2973, BT-2980, BT-3345, BT-3346 (recn. 2377). **Undispensable Reef**: DG-6923/1, DG-6923/2. **PAPUA NEW GUINEA, Hansa Bay**: JMO-004, BT-0908, BT-6549. **Rabaul**: BT-0056, BT-0057, DG-2892/b, DG-2892/c, DG-2892/e. **PHILIPPINES noloc.**: BT-4586, BT-4587, BT-4585, BT-4588, BT-4986. **SAMOA (W)**: DG-898/a, DG-2447, DG-751/a, DG-896/6, DG-751/c. **SOLOMONS Kieta, Loholo Beach**: DG-5440/3, DG-5440/5, DG-5440/1, DG-5440/2, DG-5440/4; **Malaita**: DG-2535/10. **THAILAND, Phuket (Andaman Sea)** (provisional phenon WT): BT-0067, BT-4344, BT-4345, BT-4346. **Ko Chang (Gulf of Thailand)** (provisional phenon ET): BT-5459, BT-5460, BT-5461. **TONGA, Hihifo I.**: BT-0025, BT-0026, **Vava'u I.**: DG-7266/2. **VIETNAM, Nha Trang**: BT-6930, BT-6931, BT-6929, BT-6929.

Oliva miniacea tremulina Lamarck, 1811. **INDIA, Cuddalore**: (form *flammeacolor* Petuch & Sargent, 1986): DG-935/f, DG-1522/e, DG-1522/c, BT-0953. **MAURITIUS Black River**: DG-3064, DG-5978/3, DG-5975, DG-6429, DG-5785. **MADAGASCAR, SW, noloc.**: DG-7468/1. **noloc.**: BT-3322. **Tuléar**: DG-7681/1, DG-7681/2, BT-4770. **MOZAMBIQUE, Nacala**: DG-8018/1, DG-8018/2. **Conducia**: DG-7689/3. **REUNION, noloc.**: BT-4907. **SEYCHELLES, Mahé**: BT-4371, TV-794065, TV-794063, TV-798210. **Praslin**: TV-798700. **SRI LANKA, Negombo** (form *flammeacolor* Petuch & Sargent, 1986): BT-6222, BT-6220, BT-6225, BT-6221 BT-6224. **TANZANIA Dar es Salaam, Fungu Yasin**: DG-7956.

Oliva ponderosa Duclos, 1840. **PERSIAN GULF (?)**, **noloc.**: BT-4900. **MALDIVES, Baros**: DG-2594/e (-). **Farakulufushi**: BT-

1953, BT-1955 (-). **Gan:** BT-1199 (-), BT-1200 (-), BT-2328 (-). **Malé:** BT-3373 (-), BT-6738 (-), BT-6739 (-), DG-5899/1 (-), DG-5899/5, DG-5899/7 (-).

2.3. Outgroups.

The following shells have been used for comparison:

Oliva caerulea (Röding, 1798).

INDONESIA, Bali: BT-0451, BT-0452, BT-0454, BT-0455, BT-1987, **PAPUA NEW GUINEA, Hansa Bay, Awar** (dark form): BT-7124, BT-7126, BT-7127, BT-7129, BT-7130. **Hansa Bay, Laing Island** (light form): BT-0463, BT-0469, BT-7119, BT-7120, BT-7040.

Oliva concinna Marrat, 1870. **PAPUA NEW GUINEA, Hansa Bay:** BT-7095, BT-7096, BT-7097, BT-7098, BT-7099, BT-7101, BT-7103, BT-7104, BT-7111, BT-7112. **PHILIPPINES, Luzon, Manilla Bay:** BT-4342. **SOLOMONS, Honiara:** BT-2440, BT-2441. **Guadalcanal, Marau Sound:** BT-4438. **VANUATU, Port Vila:** BT-4343.

Oliva hirasei Kira, 1959. **PHILIPPINES, Bohol, Panglao:** BT-6194, BT-6196. **Sulu Sea, noloc.:** BT-2184, BT-5021, BT-6202.

Oliva sericea (Röding, 1798).

INDONESIA, Bali: BT-0011, BT-0013, BT-2012, BT-4046. **PAPUA NEW GUINEA, Hansa Bay:** BT-0011. **NEW CALEDONIA, East Coast, noloc.:** BT-3341.

3. METHODS.

This work uses the morphospecies approach, an indirect tool for deducing the existence of biological species. We have so far never observed sexual dimorphism in shells of this group. Neither have we observed significant allometry, with the exception (see TURSCH, GERMAIN & GREIFENEDER, 1986a) of very small juveniles, not considered here. So, at least for sympatric samples, the existence of reproductive barriers can be safely inferred from the observation of gaps in the distribution of shell characters (see § 3.2.2 for limitations).

We have used objective, morphometric characters. Colour patterns (the main classical descriptors) are indeed extremely variable in some of the species, and are very difficult to report accurately. They will be used only as secondary, additional characters.

3.1. Measurements.

3.1.1. The protoconch measurements NW, SPRO, MPRO, LPRO, RES5, PAT17, PAT18

and the teleoconch measurements PNW, H, L, LW, D, R, X, F, FG and SUT that are utilised in this work have been defined in detail by TURSCH & GERMAIN (1985, 1986, 1987). They have been repeatedly tested and demonstrated to be operational in the genus *Oliva* (see TURSCH, GERMAIN & GREIFENEDER, 1986a, 1986b; TURSCH & HUART, 1988; 1990; TURSCH, 1988, 1994; TURSCH & GREIFENEDER, 1989a, 1989b; TURSCH, MISSA & BOUILLON, 1992).

For a quick reminder, these measurements are sketched in Fig. 1. Two important measurements do not appear on this figure. NW is the number of nuclear whorls and PNW is the number of postnuclear whorls. Both are measured to 0.05 whorl.

3.1.2. *Oliva* shells are notoriously variable in size (TURSCH & GERMAIN, 1985) and furthermore we have no sure way of deciding if a shell is adult or not. Therefore, raw teleoconch measurements could simply discriminate large from small specimens. Shape factors are much more informative. Teleoconch measurements will thus always be used as indices (ratio of two linear measurements or ratio of a given linear measurement to PNW). On the contrary, protoconch measurements do not vary with the size of the shell and can be used as such.

3.2. Analysis methods.

These are essentially the same as in TURSCH, MISSA & BOUILLON (1992). Each specimen can be represented by a point in the attribute hyperspace, *i.e.*, a space having as many dimensions as there are variables (attributes) under consideration. Any phenon will thus appear as a cloud of points in the attribute hyperspace, the dimensions of the cloud reflecting the variability.

Two phenon are distinct if their representative clouds are separated by a void region: a morphological gap. In this work, only full separations (with no overlap) will be taken into account.

3.2.1. The attribute hyperspaces where the morphological gaps occur have far too many dimensions to be visualized as such. We can observe these gaps only in reduced spaces (with two or three dimensions). Hence the intensive use of scatter diagrams (projection of the attribute hyperspace on the plane of two selected axes), principal component analysis and factorial discriminant analysis. It is important to keep in mind that if two clouds are separated in a scatter diagram, then they are *a fortiori* separated in the attribute hyperspace.

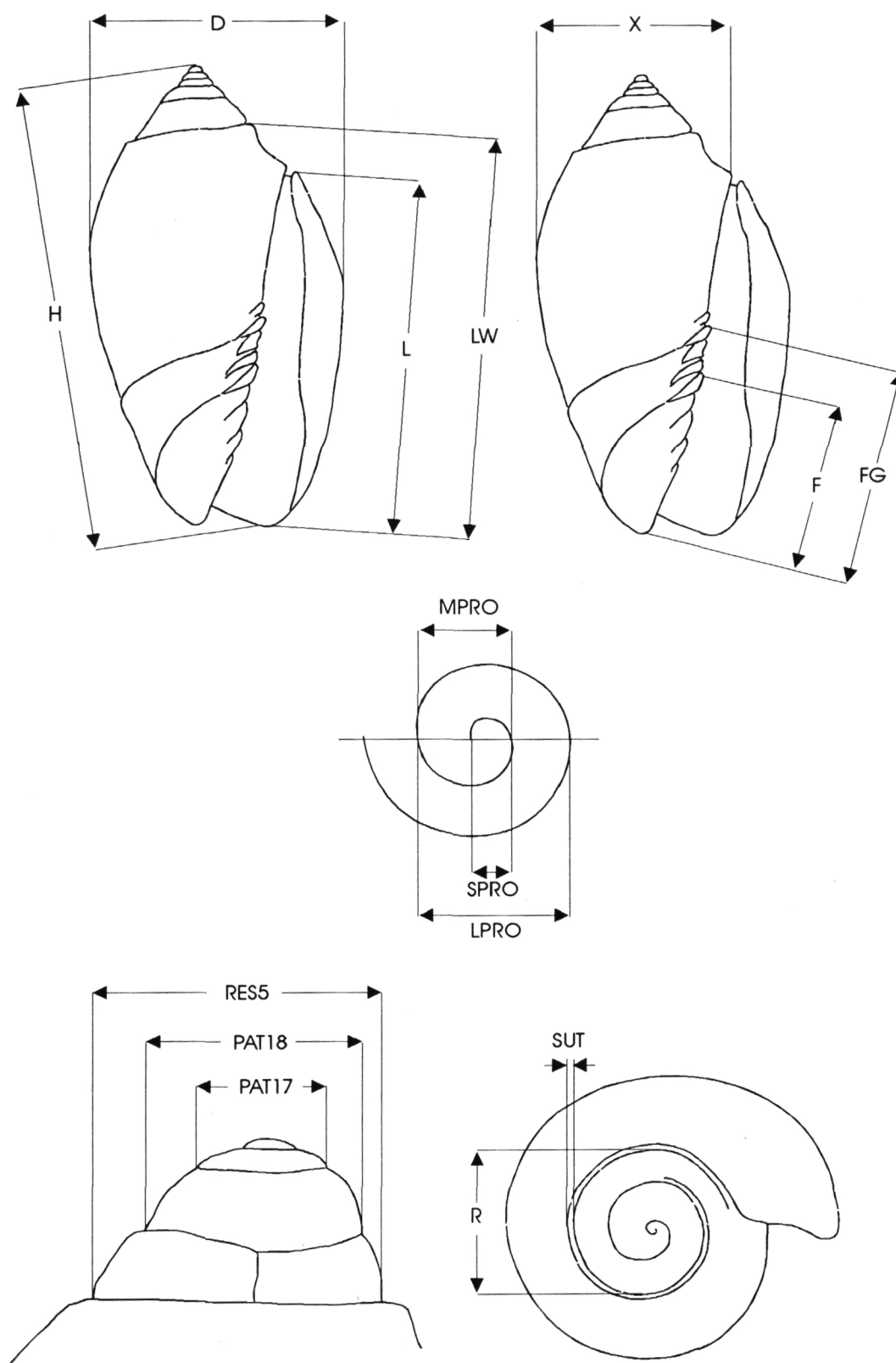


Fig. 1. Shell measurements utilised in this work. See text § 3.1.1.

Finding operational morphological gaps is of course much facilitated if one has an idea of the way in which the taxa are distributed in the multidimensional attribute space. Principal component analysis does provide this kind of information.

3.2.2. Great care should be exercised in the interpretation of the observed separations. First, one has to consider the size of the samples. Weak separations obtained on small samples (from our experience, $N < 5$) might be indicative in scatter diagrams, but must be considered with caution. In contrast, observed overlaps are always significant, as these will persist if the size of the sample is increased. The problem of detecting separations is aggravated in multidimensional hyperspaces, where small gaps observed between small samples should be interpreted with great suspicion.

The interpretation of morphometric separations in terms of distinct species is straightforward only for samples that are syntopic (*i.e.*, actually live together, in the same microbiotope). It has been shown (TURSCH, 1994) that *Oliva* species consist of a mosaic of distinct, rather homogeneous populations. When a number of such local, conspecific populations are compared, they invariably show considerable character overlap. The species is thus represented in the attribute hyperspace by a *morphological continuum*. This is a set in which no population (or groups of populations) can be separated from *all* the others. Even if two populations of the continuum can be easily separated, the gap is invariably bridged by another conspecific population (or a morphologically unbroken chain of populations).

Completely separable populations of one same species can occur even within very short geographic distances (TURSCH, 1994). Separations between pairs of conspecific populations are thus fully expected (see MAYR, 1969 and FUTUYMA, 1986) and do not constitute grounds for specific discrimination. Well on the contrary, observation that very similar *Oliva* phena do never co-occur constitutes a strong indication of their conspecificity (TURSCH, 1995).

In the morphospecies approach, specific discrimination can be established only by the separation of sets containing as many different local populations as possible. Even with a small number of specimens, samples including shells from different localities include much more of the total variability of the species. Clear separations of such samples are most probably significant.

3.3. Preliminary grouping: working hypothesis.

The ideal, objective approach would consist in delimiting objective phena by grouping individual shells, identified only by locality and specimen numbers. This method works very well in studies involving only two or three phena. It becomes unworkable if the number of local phena is large, as it is the case here. It was thus necessary to make a preliminary grouping of our study sample into provisional phena, considered distinct as a *working hypothesis*. The validity of this hypothesis could then be tested by data analysis. Phena that could not be objectively separated were of course grouped together. The taxonomic rank of the remaining, objectively separable phena could then be determined by considerations of geographical distribution.

Many of the shells in this study could easily be classified into commonly admitted taxa. There is today a broad consensus on the identity of *O. hirasei* Kira, 1959, *O. ponderosa* Duclos, 1840 and *O. sericea* (Röding, 1798). Specimens from India and Sri Lanka are easily recognized as *O. tremulina flammeacolor* Petuch & Sargent, 1986 (here after designated as "*O. flammeacolor*", for short). All the South-West Pacific *O. miniacea* s.l. (Röding, 1798) could be grouped without any apparent problem. This was also the case with the "normal" *O. tremulina* Lamarck, 1811 from E. Africa and the Western Indian Ocean. Other shells were not so easy.

O. concinna Marrat, 1870 has different interpretations, depending upon the authors, as the type lot consists of two different species (see *concinna* under section 6, Systematics). The name is here restricted to the shell represented in Fig. 100 of the *Thesaurus* (one of two syntypes, MCM, from New Caledonia). There is also no unanimity on the identity of *Oliva atalina* Duclos, 1935 (see *atalina* under section 6, Systematics).

We could not identify a familiar but unnamed *Oliva* from Aldabra, Chagos, Mauritius and the Seychelles. These shells were kept separate as a temporary phenon *MS*, that will be shown to constitute an unnamed species, *Oliva mascarena* n. sp., described here under. We also had identification problems with *miniacea*-like shells from Indonesia, kept separate as a temporary phenon *IN*, *miniacea*-like shells from West Thailand, kept separate as a temporary phenon *WT* and *miniacea*-like shells from East Thailand, kept separate as a temporary phenon *ET*.

We thus started this study with a working hypothesis consisting of 12 phena: *Oliva atalina* Duclos, 1935, *O. concinna* Marrat, 1870, *O. hirasei* Kira, 1959, *O. ponderosa* Duclos, 1840, *O. sericea* (Röding, 1798), *O. flammeacolor* Petuch & Sargent, 1986, *O. miniacea* s.l. (Röding, 1798), *O. tremulina* Lamarck, 1811, and the phena *MS*, *IN*, *WT* and *ET*. We now had to check whether these phena constitute objectively separable entities or not.

4. THE DELIMITATION OF OBJECTIVE PHENA.

4.1. Principal component analysis.

Principal component analysis was performed separately on teleoconch and protoconch characters. The study sample (here after referred to as List A) consisted of 120 specimens, all with an intact protoconch. This included 50 specimens of *O. miniacea* (4 from Australia, 4 from the Carolines, 3 from Fiji, 3 from Guam, 4 from Japan, 4 from the Marshalls, 4 from New Caledonia, 2 from Undispensable Reef, 6 from Papua New Guinea, 4 from the Philippines, 3 from Samoa, 3 from the Solomons, 3 from Tonga and 3 from Vietnam), 20 *O. tremulina* (5 from Mauritius, 5 from Madagascar, 3 from Mozambique, 1 from Reunion, 5 from the Seychelles and 1 from Tanzania), one *O. atalina* (Mauritius, only specimen available with intact protoconch), 3 *O. ponderosa* (Maldives), 4 specimens of phenon *WT* (W. Thailand), 3 specimens of phenon *ET* (E. Thailand), 9 *O. flammeacolor* (4 from India and 5 from Sri Lanka), 8 specimens of phenon *IN* (Indonesia), 7 specimens of phenon *MS* (3 from Mauritius, 3 from Seychelles and 1 from Chagos), 5 *O. sericea* (3 from Indonesia, 1 from Papua New Guinea, 1 from New Caledonia), 5 *O. concinna* (1 from the Philippines, 3 from the Solomons and 1 from Vanuatu) and 5 *O. hirasei* (from the Philippines, 2 localities).

At this stage, separation of phena can only be suggested, due to the small number of specimens of each local phenon. In contrast, observed overlaps are significant (see § 3.2.2).

4.1.2. Principal components analysis on teleoconch data. The 120 specimens of list A were included in a principal component analysis on 14 teleoconch variables: L/H, D/H, R/H, X/H, F/H, FG/H, SUT/H, SUT/R, (H-L)/H, (D-X)/D, H/PNW, D/PNW, SUT/PNW and F/PNW, selected, after many trials, for their discrimination power. 74.7% of the total variation are accounted for (38% on representation axis 1, 19.2% on axis 2 and 17.5% on axis 3).

4.1.2.1. Plane of axes 1, 2. The quality of representation on axes 1 and 2 (Fig. 2) is mediocre, 57.2% of the total variation being accounted for. It can be seen that *O. miniacea* (M) occupies a very large area and overlaps with all the other phena. *O. tremulina* (T), phenon *WT*, and *O. flammeacolor* (F) form a continuous chain of overlapping phena, distinct from another such chain consisting of *O. ponderosa* (P), phenon *MS*, *O. sericea* (S) and *O. concinna* (C). The two chains are here bridged by the Indonesian phenon *IN*. Not much can be said about *O. atalina* (A), represented by a single specimen. The relatively isolated position of *O. hirasei* (H), overlapping only with *O. miniacea* (M) suggests that this group could be easily isolated.

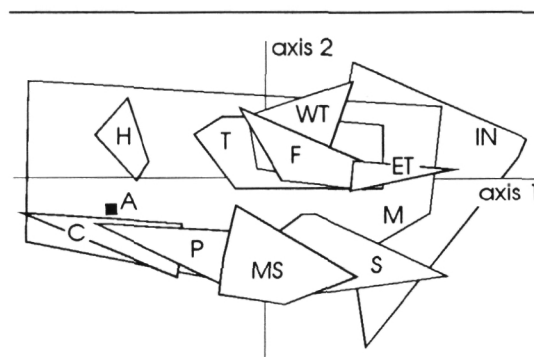


Fig. 2. Principal component analysis on teleoconch data. Plane of axes 1 and 2. 14 variables: L/H, D/H, R/H, X/H, F/H, FG/H, SUT/H, SUT/R, (H-L)/H, (D-X)/D, H/PNW, D/PNW, SUT/PNW and F/PNW.

Representation: minimum convex polygons. 57.2 % of the total variation accounted for.

Total sample: 120 specimens (List A). **A:** *O. atalina* (Mauritius, N=1). **C:** *O. concinna* (Philippines, Solomons, Vanuatu, N=5).

ET: phenon *ET* (E. Thailand, 1 locality, N=3). **F:** *O. flammeacolor* (India, Sri Lanka, N=9). **H:** *O. hirasei* (Philippines, 2 localities, N=5). **IN:** phenon *IN* (Indonesia, 3 localities, N=8). **M:** *O. miniacea* (S.W. Pacific, many localities, N=50). **MS:** phenon *MS* (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, N=7)). **P:** *O. ponderosa* (Maldives, 3 localities, N=3).

S: *O. sericea* (Indonesia, Papua New Guinea, New Caledonia, N=5). **T:** *O. tremulina* (Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania, N=20). **WT:** phenon *WT* (W. Thailand, 1 locality, N=4).

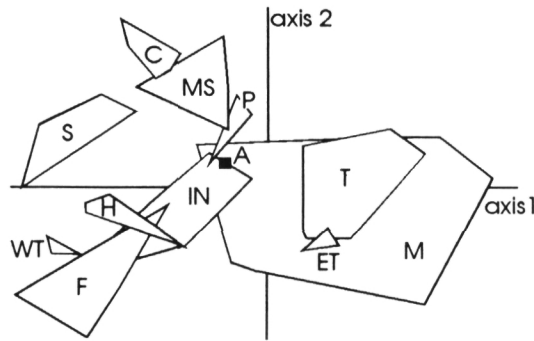


Fig. 3. Principal component analysis on protoconch data. Plane of axes 1 and 2. 7 variables: NW, MPRO, LPRO, (LPRO-SPRO), RES5, PAT17 and PAT18.

Representation: minimum convex polygons. 89.6% of the total variation accounted for. Total sample: 120 specimens (List A). **A:** *O. atalina* (Mauritius, N=1). **C:** *O. concinna* (Philippines, Solomons, Vanuatu, N=5). **ET:** phenon ET (E. Thailand, 1 locality, N=3). **F:** *O. flammeacolor* (India, Sri Lanka, N=9). **H:** *O. hirasei* (Philippines, 2 localities, N=5). **IN:** phenon IN (Indonesia, 3 localities, N=8). **M:** *O. miniacea* (S.W. Pacific, many localities, N=50). **MS:** phenon MS (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, N=7)). **P:** *O. ponderosa* (Maldives, 3 localities, N=3). **S:** *O. sericea* (Indonesia, Papua New Guinea, New Caledonia, N=5). **T:** *O. tremulina* (Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania, N=20). **WT:** phenon WT (W. Thailand, 1 locality, N=4).

4.1.2.2. Plane of axes 2, 3. Only 57.2% of the total variation was accounted for along axes 1 and 2. The representation on the plane of axes 2 and 3 (not given here) accounts for 55.5% of the total variation but does not bring any additional information.

4.1.3. Principal components analysis on protoconch data. The 120 specimens of list A were included in a principal component analysis on 7 protoconch measurements: NW, MPRO, LPRO, (LPRO-SPRO), RES5, PAT17, PAT18. The quality of the representation on axes 1 and 2 (Fig. 3) is very good, 89.6% of the total variation being accounted for (an example of the discriminatory power of protoconch characters). 61% of the total variation are accounted for on axis 1, 28.6% on axis 2, and only 5% on axis 3.

It can now be clearly seen that the sample is heterogeneous. *O. sericea* (S), *O. concinna* (C) and phenon MS are separated from an apparently continuous chain of other taxa. The position of *O. ponderosa* (P) is intermediate and confirms its similarity to *O. miniacea* (M).

The single specimen of *O. atalina* (A) indicates that there is little hope to separate this taxon from *O. miniacea* (M) on protoconch characters.

O. flammeacolor (F) is very close to phenon WT (W. Thailand) and appears well separated from *O. miniacea* (M) but the two groups are bridged by phenon IN (Indonesia). *O. miniacea* (M) completely covers *O. tremulina* (T) and phenon ET (E. Thailand). All these taxa possibly form a single morphological continuum.

4.1.4. Interpretation.

4.1.4.1. The *O. miniacea* populations. On both Figs. 2 and 3, it can be seen that *O. miniacea* (M) occupies a much larger area than the other phenons. In such representations, the size of the area occupied by a given phenon reflects its total variability. The large spread observed for *O. miniacea* raises questions. Is this simply due to the larger number (50) of specimens? Are we dealing with rather similar, but extremely variable local populations? Or are we dealing with a mosaic of many distinct, rather homogeneous populations? Or is our provisional phenon *O. miniacea* heterogeneous, containing populations of other species?

One answer can be found in Fig. 4 (representing the constituents of the *O. miniacea* polygon of Fig. 2) and Fig. 5 (representing the constituents of the *O. miniacea* polygon of Fig. 3, slightly enlarged). We are obviously in presence of a multitude of different local phenons, each rather homogeneous. This was fully expected: an experienced *Oliva* student can often take a rather accurate guess as to the region of origin of a given specimen of *O. miniacea*.

4.1.4.2. The *O. miniacea* continuum. We still have to show that our provisional phenon *O. miniacea* is homogeneous. On both figures 4 and 5, one notices much overlap in the distribution of the characters. The following pairs of groups separated: a-e, e-k, e-c, k-o, a-j and a-i are separated neither by teleoconch (Fig. 4) nor by protoconch characters (Fig. 5). This establishes the existence of a morphologically continuous chain of local populations: i (Papua New Guinea, Hansa Bay), j (Papua New Guinea, Rabaul), a (Australia), e (Japan), c (Fiji), k (Philippines) and o (Vietnam). The

same can be said for the pairs **d-b** and **d-f**, establishing the existence of another chain **d** (Guam), **b** (Caroline Is.) and **f** (Marshall Is.). For each of these groups, we have no choice but to group all the populations into a single minimum convex polygon (see Figs. 6 and 7).

Due to the small size of the samples (see § 3.2.2), the very small separation of groups **h** and **i** (in Figs. 5 and 7) cannot be taken as being of any significance. It then becomes clear (from Figs. 6 and 7) that the grouping of all the samples included under our provisional phenon *O. miniacea* (see § 3.3) is justified. In spite of much effort, all our subsequent attempts to break this group apart by consecutive scatter diagrams did fail. We are in presence of a single, uninterrupted morphological continuum, consisting in a multitude of overlapping, rather homogeneous local phena. This situation was fully expected from previous studies on *Oliva* (TURSCH, 1994). A seeming objection is that we have dealt only with a small number of populations of a very widespread species. Inclusion of more populations could only fill the voids in Figs. 4 and 5, thus reinforcing our conclusion.

With the results of principal component analysis at hand, we can now proceed to select operational discriminants, either for individual taxa or for groups of taxa.

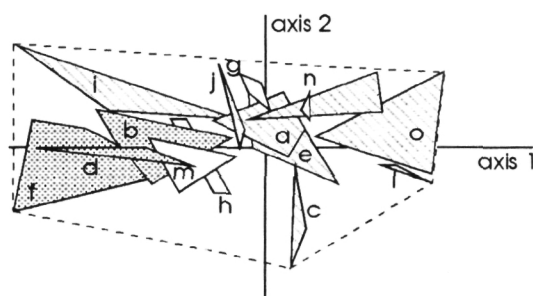


Fig. 4. Principal component analysis on teleoconch data. Plane of axes 1 and 2. Partial view: the constituents of the *O. miniacea* polygon of Fig. 2 (all other groups removed). Sample: 50 specimens (see text § 4.1, list A). **a:** Australia. **b:** Caroline Is. **c:** Fiji. **d:** Guam. **e:** Japan. **f:** Marshall Is. **g:** New Caledonia, main island. **h:** New Caledonia, Undispensable Reef. **i:** Papua New Guinea, Hansa Bay. **j:** Papua New Guinea, Rabaul. **k:** Philippines. **l:** Samoa. **m:** Solomon Is. **n:** Tonga. **o:** Vietnam.

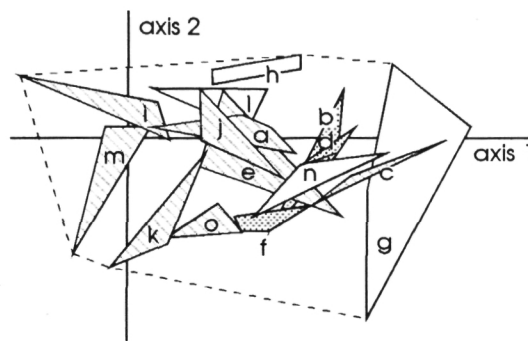


Fig. 5. Principal component analysis on protoconch data. Plane of axes 1 and 2. Partial view: the constituents of the *O. miniacea* polygon of Fig. 3, (slightly enlarged, all other groups removed). Sample: 50 specimens (see text § 4.1, list A). **a:** Australia. **b:** Caroline Is. **c:** Fiji. **d:** Guam. **e:** Japan. **f:** Marshall Is. **g:** New Caledonia, main island. **h:** New Caledonia, Undispensable Reef. **i:** Papua New Guinea, Hansa Bay. **j:** Papua New Guinea, Rabaul. **k:** Philippines. **l:** Samoa. **m:** Solomon Is. **n:** Tonga. **o:** Vietnam.

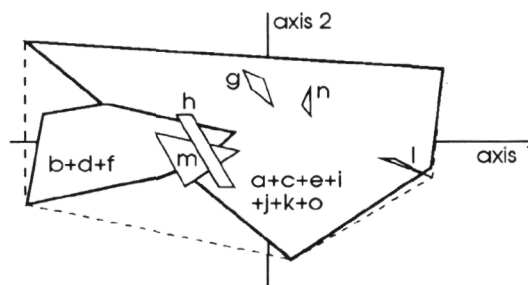


Fig. 6. Principal component analysis on teleoconch data. Plane of axes 1 and 2. Partial view: the constituents of the *O. miniacea* polygon of Fig. 2 (all other groups removed). Same as Fig. 4, but the two groups (a+c+e+i+j+k+o) and (b+d+f) of unseparable populations are now represented by their minimum convex polygons. **a:** Australia. **b:** Caroline Is. **c:** Fiji. **d:** Guam. **e:** Japan. **f:** Marshall Is. **g:** New Caledonia, main island. **h:** New Caledonia, Undispensable Reef. **i:** Papua New Guinea, Hansa Bay. **j:** Papua New Guinea, Rabaul. **k:** Philippines. **l:** Samoa. **m:** Solomon Is. **n:** Tonga. **o:** Vietnam.

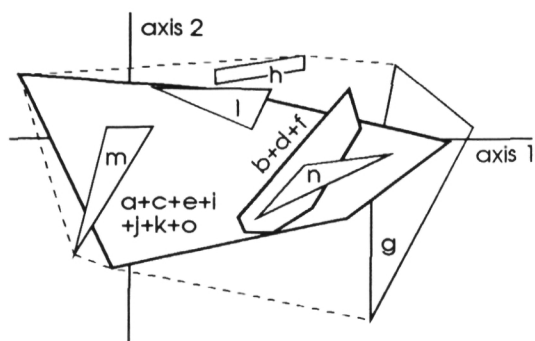


Fig. 7. Principal component analysis on protoconch data. Plane of axes 1 and 2. Partial view: the constituents of the *O. miniacea* polygon of Fig. 3, (slightly enlarged, all other groups removed). Same as Fig. 5, but the two groups (a+c+e+i+j+k+o) and (b+d+f) of unseparable populations are now represented by their minimum convex polygons. **a:** Australia. **b:** Caroline Is. **c:** Fiji. **d:** Guam. **e:** Japan. **f:** Marshall Is. **g:** New Caledonia, main island. **h:** New Caledonia, Undispensable Reef. **i:** Papua New Guinea, Hansa Bay. **j:** Papua New Guinea, Rabaul. **k:** Philippines. **l:** Samoa. **m:** Solomon Is. **n:** Tonga. **o:** Vietnam.

4.2. Separation of *O. hirasei*.

Principal components analysis (§ 4.1.2.1, Fig. 2) suggested that *O. hirasei* (H) could be easily separated from the remainder of the study sample. This is indeed the case. Total, convincing separation is obtained, for instance in a scatter diagram of H/PNW vs. PAT18 (Fig. 8). This establishes *O. hirasei* as an objective, separable taxon. It needs no more to be included in the following separations.

4.3. Separation of *O. sericea*, *O. concinna* and phenon MS.

Principal components analysis (§ 4.1.3, Fig. 3) also suggested that a group formed of *O. sericea* (S), *O. concinna* (C) and phenon MS (*Oliva mascarena* n. sp., see below) could be easily separated from the remainder of the study sample. Total separation is indeed achieved, for instance in the scatter diagram of NW/LPRO vs. H/F (Fig. 9).

The next step was to check if the three phenon that we have just separated (as a group, from the remainder of the sample) constitute separable entities. The much wider protoconch

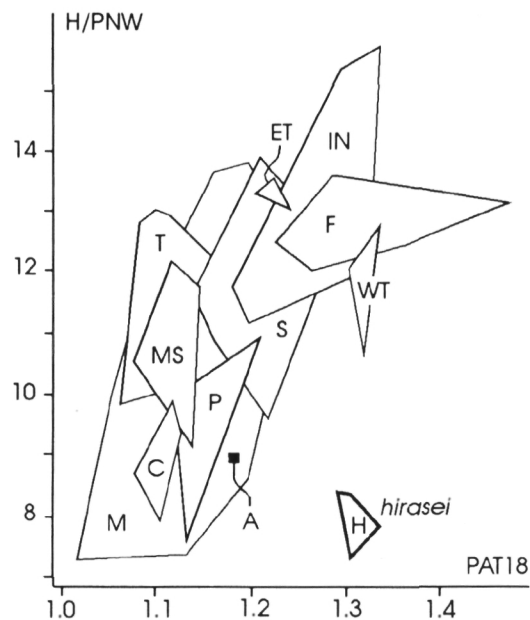


Fig. 8. Separation of *O. hirasei*. Scatter diagram: H/PNW vs. PAT18. Minimum convex polygons. **A:** *O. atalina* (Mauritius, N=1). **C:** *O. concinna* (Philippines, Solomon Is., Vanuatu, N=5). **ET:** Phenon ET (E. Thailand, 1 locality, N=3). **F:** *O. flammeacolor* (India, Sri Lanka, N=9). **H:** *O. hirasei* (Philippines, 2 localities, N=5). **IN:** phenon IN (Indonesia, 3 localities, N=8). **M:** *O. miniacea* (S.W. Pacific, many localities, N=50). **MS:** phenon MS (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, N=7). **P:** *O. ponderosa* (Maldives, 3 localities, N=6). **S:** *O. sericea* (Indonesia, Papua New Guinea, New Caledonia, N=5). **T:** *O. tremulina* (Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania, N=20). **WT:** Phenon WT (W. Thailand, 1 locality, N=4).

of *O. sericea* separates it easily from both phenon MS (*O. mascarena* n. sp.) and *O. concinna*, as evidenced in Fig. 10, the scatter diagram of PAT18 vs. RES5.

In turn, phenon MS (*O. mascarena* n. sp.) and *O. concinna* are totally separated in a scatter diagram of (H-L)/L vs. L/PNW (Fig. 11). Equally good separations are obtained with scatter diagrams (not illustrated here) of X/PNW vs. (H-L)/H, L/PNW vs. (H-L)/D, L/PNW vs. (H-L)/SUT, amongst others.

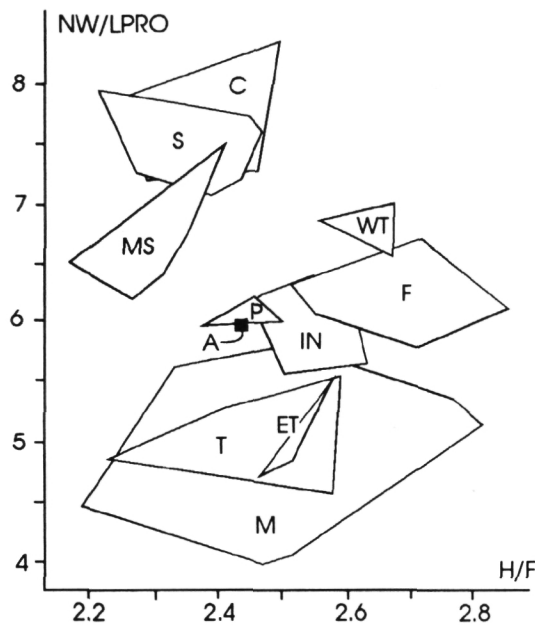


Fig. 9. Separation into two clusters.

Scatter diagram: NW/LPRO vs. H/F. Minimum convex polygons. Total sample: 115 specimens (List A, with *O. hirasei* removed). **A:** *O. atalina* (Mauritius, N=1). **C:** *O. concinna* (Philippines, Solomon Is., Vanuatu, N=5). **ET:** Phenon ET (E. Thailand, 1 locality, N=3). **F:** *O. flammeacolor* (India, Sri Lanka, N=9). **IN:** phenon IN (Indonesia, 3 localities, N=8). **M:** *O. miniacea* (S.W. Pacific, many localities, N=50). **MS:** phenon MS (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, N=7). **P:** *O. ponderosa* (Maldives, N=6). **S:** *O. sericea* (Indonesia, Papua New Guinea, New Caledonia, N=5). **T:** *O. tremulina* (Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania, N=20). **WT:** Phenon WT (W. Thailand, 1 locality, N=4).

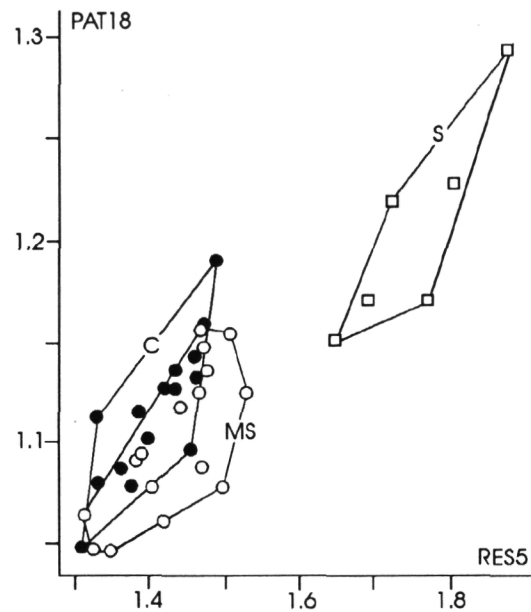
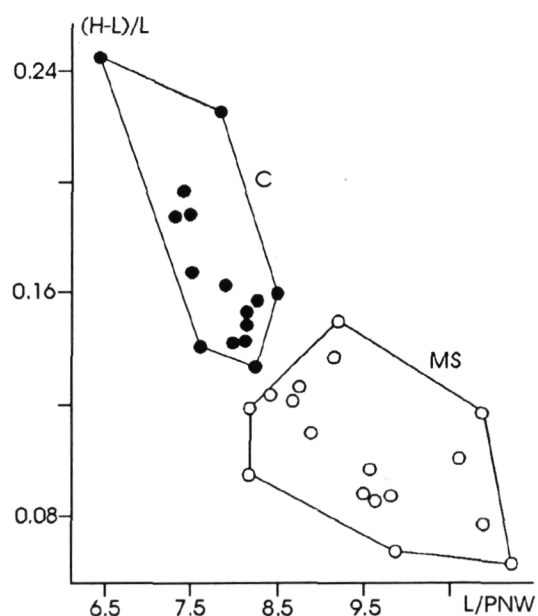


Fig. 10. Separation of *O. sericea* from phenon MS (*O. mascarena* n. sp.) and *O. concinna*. Scatter diagram: PAT18 vs. RES5. Minimum convex polygons. **C:** *O. concinna* (Papua New Guinea, Philippines, Solomon Is., Vanuatu, black circles, N=15). **MS:** phenon MS (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, white circles, N=17). **S:** *O. sericea* (Indonesia, Papua New Guinea, New Caledonia, white squares, N=6).

Fig. 11. Separation of *O. concinna* from phenon MS (*O. mascarena* n. sp.).

Scatter diagram: (H-L)/L vs. L/PNW. Minimum convex polygons. **C:** *O. concinna* (Papua New Guinea, Philippines, Solomon Is., Vanuatu, black circles, N=15). **MS:** phenon MS (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, white circles, N=17).



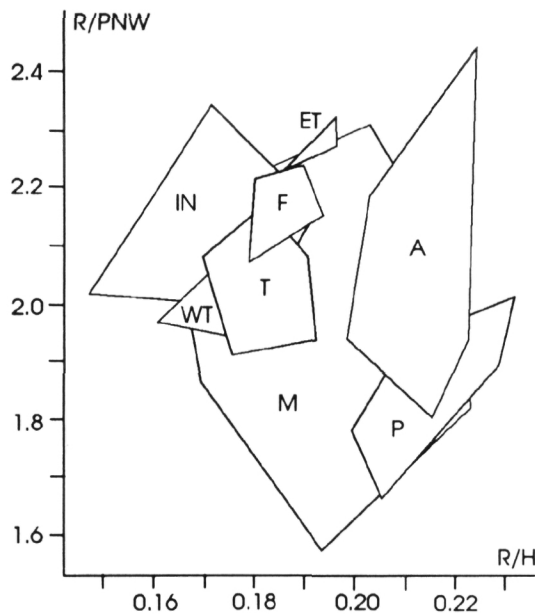


Fig. 12. Example of partial separation. Scatter diagram: R/PNW vs. R/H. Minimum convex polygons. Total sample: 130 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, N=18). **ET:** phenon ET (E. Thailand, 1 locality, N=3). **F:** *O. flammeacolor* (India, Sri Lanka, N=9). **IN:** phenon IN (Indonesia, 3 localities, N=8). **M:** *O. miniacea* (S.W. Pacific, many localities, N=65). **P:** *O. ponderosa* (Maldives, 3 localities, N=13). **T:** *O. tremulina* (Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania, N=20). **WT:** phenon WT (W. Thailand, 1 locality, N=4).

4.4. The "*Oliva miniacea* complex".

At this stage, we have easily separated four recognizable phenon, *O. hirasei*, *O. sericea*, *O. concinna* and phenon MS (*O. mascarena* n. sp.) from the initial sample of 12 provisional phenon.

The 8 remaining provisional phenon are: *Oliva atalina*, *O. flammeacolor*, *O. miniacea*, *O. ponderosa*, *O. tremulina* and the phenon WT (West Thailand), ET (East Thailand) and IN (Indonesia). These closely related phenon form now a much more compact group, where separations are much less evident. For facility, let us call this the "*Oliva miniacea* complex". Does this complex constitute a morphological continuum (in which no group can be separated from *all* the others)? Or does it still contain separable entities?

4.5. The "*Oliva miniacea* complex".

Separation of *O. atalina*.

4.5.1. Principal components analysis of teleoconch characters (§ 4.1.2.1, Fig. 2) suggested that *O. ponderosa* (and possibly *O. atalina*) could be easily separated from *O. tremulina*, *O. flammeacolor*, phenon WT, ET and IN. Many scatter diagrams, such as R/PNW vs. R/H (Fig. 12), including all available specimens, do indeed totally separate a group formed of *O. atalina* and *O. ponderosa* from a compact group formed by *O. tremulina*, *O. flammeacolor*, phenon WT, ET and IN. Both groups are bridged only by *O. miniacea*. So the problem is now reduced to separating *O. atalina* from *O. miniacea* and from *O. ponderosa*.

4.5.2. On the basis of shell measurements, *O. atalina* is not easy to discriminate from *O. ponderosa*, but total separation is achieved in the scatter diagram of FG/F vs. RES5 (Fig. 13), including all specimens on which RES5 could be measured.

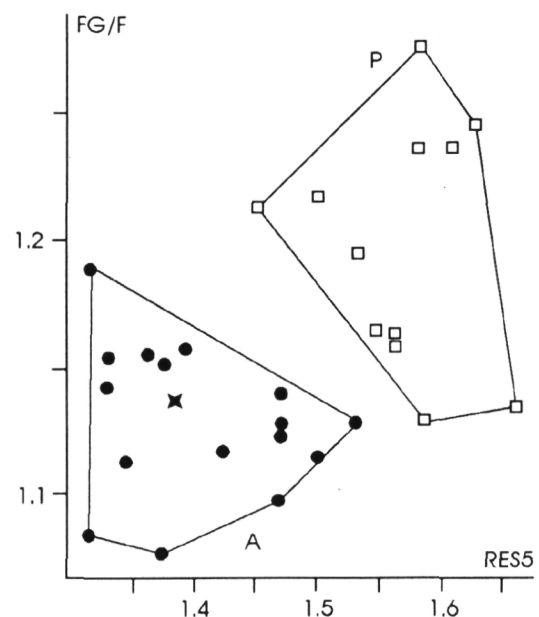


Fig. 13. Separation of *O. atalina* from *O. ponderosa*. Scatter diagram: FG/F vs. RES5. Representation: minimum convex polygons. Total sample: 29 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, black circles, N=16. Largest syntype of *O. stainforthi*: black star). **P:** *O. ponderosa* (Maldives, 3 localities, white squares, N=12).

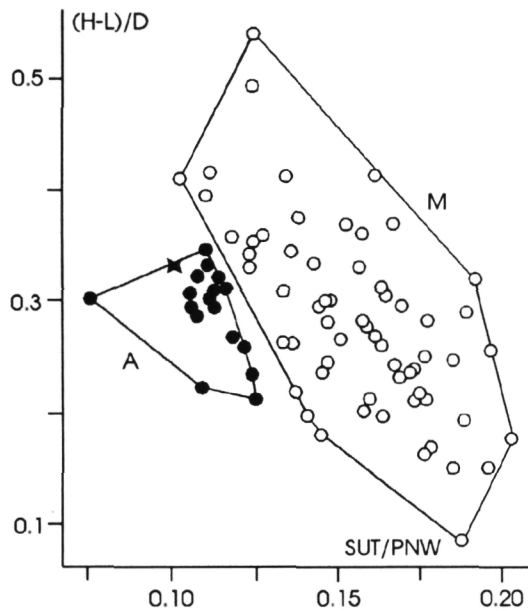


Fig. 14. Separation of *O. atalina* from *O. miniacea*. Scatter diagram: (H-L)/D vs. SUT/PNW. Minimum convex polygons. Total sample: 81 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, black circles, N=16. Largest syntype of *O. stainforthi*: black star). **M:** *O. miniacea* (S.W. Pacific, many localities, white circles, N=65).

4.5.3. *O. atalina* is even more difficult to discriminate from *O. miniacea* by shell measurements. It is indeed quite similar in shape to some populations of *O. miniacea*, and the two phenotypes overlap in many attempts at discrimination. Total separation is nevertheless obtained in the scatter diagram of (H-L)/D vs. SUT/PNW (Fig. 14).

4.5.4. We still have to check whether *O. atalina* is distinct from phenon MS (*O. mascarena* n. sp.), *O. hirasei*, *O. sericea* and *O. concinna*, because these groups were separated on protoconch characters, when only one specimen of *O. atalina* was present. *O. atalina* is so different from phenon MS (*O. mascarena* n. sp.), *O. hirasei* and *O. sericea* that they are totally separated on one single scatter diagram: LW/PNW vs. RES5 (Fig. 15). Complete separation of *O. atalina* from phenon MS (*O. mascarena* n. sp.) is also given in Fig. 16, a scatter diagram of LW/PNW vs. H/R.

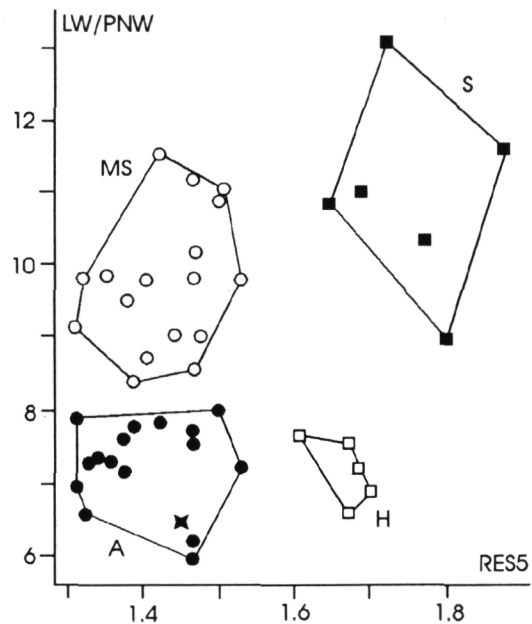


Fig. 15. Separation of *O. atalina*, *O. hirasei*, phenon MS (*O. mascarena* n. sp.) and *O. sericea*. Scatter diagram: LW/PNW vs. RES5. Minimum convex polygons. Total sample: 81 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, black circles, N=16. Largest syntype of *O. stainforthi*: black star). **H:** *O. hirasei* (Philippines, 2 localities, white squares, N=5). **MS:** phenon MS (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles, white circles, N=17). **S:** *O. sericea* (Indonesia, Papua New Guinea, New Caledonia, black squares, N=6).

4.5.5. On the basis of shell measurements, *O. atalina* is also rather close to *O. concinna*, but the two taxa are separated, for instance in the scatter diagram of $100 \times (\text{SUT}/F)$ vs. (H-L)/R (Fig. 17).

4.5.6. There is still a point to be elucidated. Even in the recent literature (BURCH & BURCH, 1960; ZEIGLER & PORRECA, 1969; WAGNER & ABBOTT, 1967), *O. atalina* has repeatedly been considered as being only a white-mouthed form of the common *O. caerulea* (Röding, 1798). This can easily be dispelled by the scatter diagram of $100 \times (\text{SUT}/LW)$ vs. F/L (Fig. 18). We can now consider *O. atalina* a completely distinct phenon.

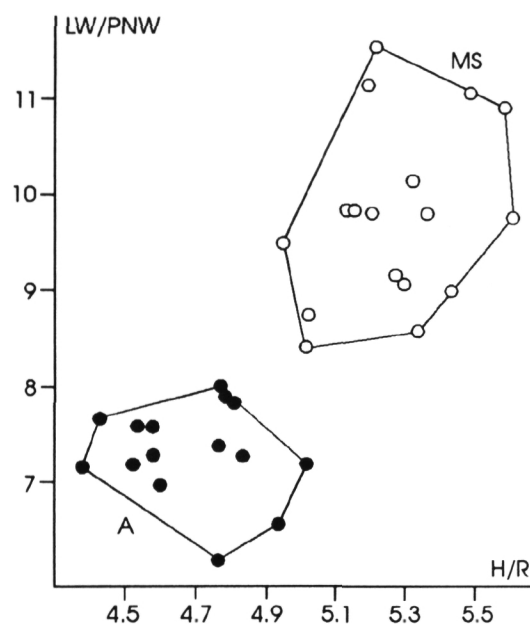


Fig. 16. Separation of *O. atalina* from phenon MS (*O. mascarena* n. sp.). Scatter diagram: LW/PNW vs. H/R. Minimum convex polygons. Total sample: 32 specimens. **A:** *O. atalina* (black circles, N=15, 4 localities, see text § 2.2). **MS:** *O. mascarena* n. sp. (white circles, N=17, 4 localities, see text § 2.2).

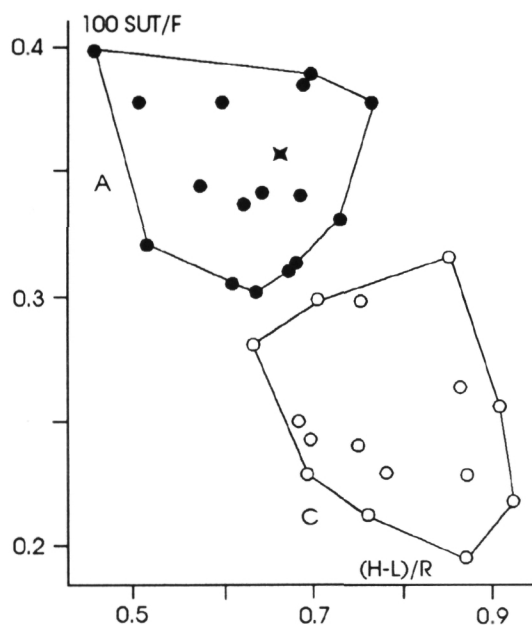


Fig. 17. Separation of *O. atalina* and *O. concinna*. Scatter diagram: 100*SUT/F vs. (H-L)/R. Minimum convex polygons. Total sample: 32 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, black circles, N=16. Largest syntype of *O. stainforthi*: black star). **C:** *O. concinna* (Papua New Guinea, Philippines, Solomon Is., Vanuatu, white circles, N=15).

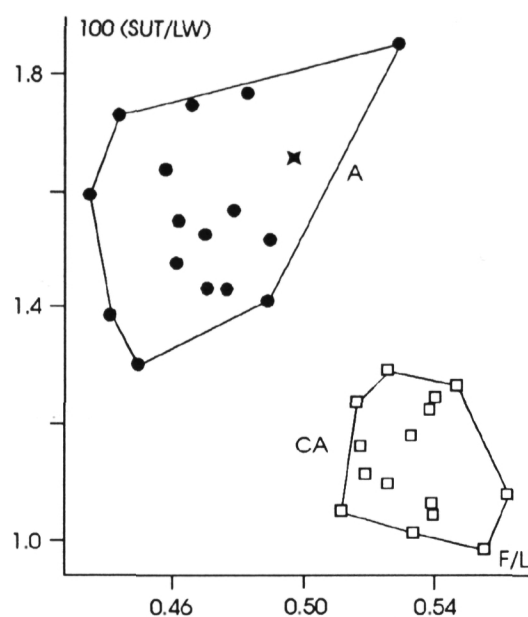


Fig. 18. Separation of *O. atalina* and *O. caerulea*. Scatter diagram: 100 SUT/LW vs. F/L. Minimum convex polygons. Total sample: 31 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, black circles, N=16. Largest syntype of *O. stainforthi*: black star). **CA:** *O. caerulea* (Papua New Guinea, Philippines, Solomon Is., Vanuatu, white squares, N=15).

4.6. The "*Oliva miniacea* complex". Separation of *O. ponderosa*.

We have now to establish whether *O. miniacea* is distinct from *O. ponderosa* or not. This is not as evident as one could believe: some specimens of *O. miniacea* from Micronesia or Northern Bali (see WITTIG-SKINNER, 1981) are quite similar to *O. ponderosa*, excepted for the colour of the aperture. This similarity probably indicates a close phyletic relationship.

A factorial discriminant analysis on the 10 variables RES5, FG/F, (H-L)/D, (H-L)/H, D/H, R/H, SUT/PNW, H/PNW, D/PNW and R/PNW was effected on all available specimens. This yielded 2 canonical discriminant functions F1 and F2. No case was excluded from the analysis. F1 accounts for 89.02% of the variance, (F1+F2) for 100%. The two canonical functions are:

$$F1 = -0.32720 \cdot RES5 - 0.57837 \cdot FG/F + 2.18443 \cdot (H-L)/D - 2.50547 \cdot (H-L)/H + 4.05754 \cdot D/H + 1.76846 \cdot R/H - 0.47104 \cdot SUT/PNW + 13.80281 \cdot H/PNW - 11.63914 \cdot D/PNW - 3.09034 \cdot R/PNW.$$

$$F2 = -0.60497*RES5 - 0.4612*FG/F + 6.58423*(H-L)/D - 5.72022*(H-L)/H + 2.49556*D/H + 1.86125*R/H + 0.30693*SUT/PNW + 10.70283*H/PNW - 5.25453*D/PNW - 5.58134*R/PNW.$$

The resulting graph (Fig. 19) does separate *O. atalina* from *O. ponderosa* and *O. atalina* from *O. miniacea* (confirming the result obtained in § 4.5). It also separates *O. ponderosa* from *O. miniacea*.

That *O. ponderosa* is effectively distinct from *O. miniacea* (in a 10-dimensional attribute hyperspace) is now established. But can we produce simpler discrimination guidelines? There seems to be a possibility of separation with a scatter diagram of MPRO/NW vs. R/H (Fig. 20), but so far this rests only on 3 specimens (*O. ponderosa* are mostly of commercial origin and specimens with perfect protoconch are not easy to obtain).

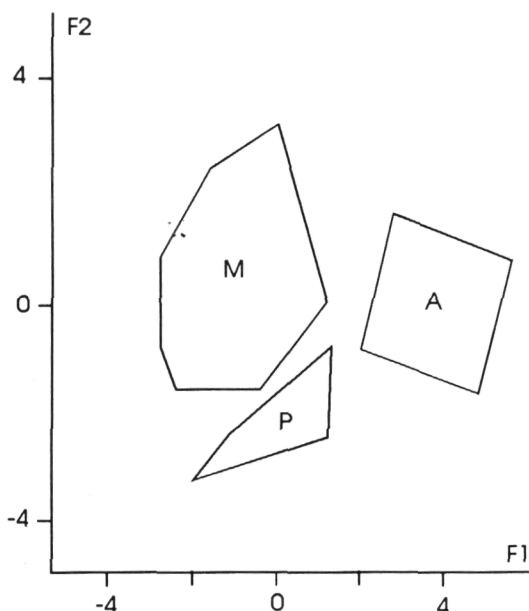


Fig. 19. Separation of *O. atalina*, *O. miniacea* and *O. ponderosa*. Factorial discriminant analysis. 10 variables: RES5, FG/F, (H-L)/D, (H-L)/H, D/H, R/H, SUT/PNW, H/PNW, D/PNW and R/PNW. 91 specimens. **A:** *O. atalina* (Cargados Carajos, Mauritius, N=16). **M:** *O. miniacea* (S.W. Pacific, many localities, N=64). **P:** *O. ponderosa* (Maldives, 3 localities, N=11). Minimum convex polygons. **F1:** first discriminant function, **F2:** second discriminant function (see text, § 4.5).

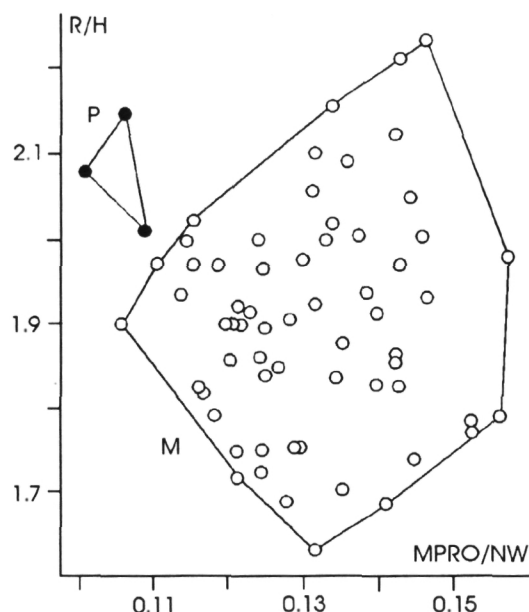


Fig. 20. Separation of *O. ponderosa* from *O. miniacea*. Scatter diagram: R/H vs. MPRO/NW. Minimum convex polygons. Total sample: 68 specimens. **A:** *O. ponderosa* (Maldives, 3 localities, black circles, N=3). **M:** *O. miniacea* (S.W. Pacific, many localities, white circles, N=65).

In practice, there is no real identification problem: *O. ponderosa* is readily separated from all other *miniacea*-like phena of the Indian Ocean, including Indonesia (see § 4.3, 4.5.1 and 4.5.2). It can also be separated from the Pacific *O. miniacea*, as it has always a pale aperture, together with a rather characteristic, stable colour pattern (see section 6: Systematics).

4.7. The "*Oliva miniacea* complex". The remaining phena.

4.7.1. The separations obtained so far are condensed in Table 1. It can be seen that all the remaining phena (*O. flammeacolor*, *O. miniacea*, *O. tremulina*, the phena *WT*, *ET* and *IN*) appear to form a morphological continuum, where no phenon can be clearly separated from all the others. In spite of considerable effort, no convincing separation could be found for breaking apart this group, be it by scatter diagrams, factorial discriminant analysis or principal components analysis. Very weak separations can sometimes be observed for phena *WT* (N=4, same locality) and *ET* (N=3, same locality), but these are clearly not significant (see § 3.2.2).

M	f.7,8 S-											
IN	NO S-	NO S-										
T	f.7 S-	NO S-	f.8(1) S-									
ET	NO(2) S-	NO S-	NO(2) S-	NO(2) S-								
WT	NO S-	f.7,8 S-	f.8 S-	f.7 S-	f.7 S-							
MS	f.7,8 S-	f.8 S-	f.8 S-	f.8 S+	f.8 S-	f.8 S-						
P	f.11 S+	f.14 S-	f.11 S-	f.11 S-	f.11 S-	f.11 S-	f.8 S-					
A	f.11 S-	f.13 S-	f.11 S-	f.11 S+	f.11 S-	f.11 S-	f.13A S+	f.12 S-				
C	f.8 S+	f.8 S+	f.8 S+	f.8 S?	f.8 S?	f.8 S+	f.10 S-	f.8 S?	f.13B S?			
H	f.8 S-	f.8 S+	f.8 S?	f.8 S-	f.8 S-	f.8 S-	f.7 S-	f.8 S-	f.13A S-	f.7 S+		
S	f.8 S+	f.8 S+	f.8 S+	f.8 S+	f.8 S+	f.8 S+	f.9 S+	f.8 S+	f.13A S+	f.9 S+	f.7 S+	
	F	M	IN	T	ET	WT	MS	P	A	C	H	

Table 1. Separable phena. For separable phena, an example of discriminant characters (referring to a text figure) is given. Phena that could not be separated are indicated by a bold border. **A:** *O. atalina* (Cargados, Mauritius). **C:** *O. concinna* (Philippines, Solomon Is., Vanuatu). **ET:** Phenon *ET* (E. Thailand, 1 locality). **F:** *O. flammeacolor* (India, Sri Lanka). **H:** *O. hirasei* (Philippines, 2 localities). **IN:** phenon *IN* (Indonesia, 3 localities). **M:** *O. miniacea* (S.W. Pacific, many localities). **MS:** phenon *MS* (*O. mascarena* n. sp., Chagos, Mauritius, Seychelles). **P:** *O. ponderosa* (Maldives, 3 localities). **S:** *O. sericea* (Indonesia, Papua New Guinea, New Caledonia). **T:** *O. tremulina* (Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania). **WT:** Phenon *WT* (W. Thailand, 1 locality).

(1) doubtful separation. (2) the very weak separations observed in fig. 7 or fig. 8 not significant: WT and ET represent local populations, with very few representatives (see text, § 3.2.2). S+ means broadly sympatric. S- means allopatric. S? means no sympatry data.

We are thus compelled to admit that *O. flammeacolor*, *O. miniacea*, *O. tremulina*, the phena *WT*, *ET* and *IN* constitute one single, highly variable species, for which *Oliva miniacea* s.l. (Röding, 1798) is the oldest name.

4.7.2. This view is reinforced by the observation that all the remaining phena are allopatric (i.e., do never co-occur). Their different aspects can be simply interpreted in terms of geographic variation (genetic and/or environmental). This is in full agreement with the conclusion of JOHNSON (1928): "This (*O. tremulina*) differs from *erythrostoma* only in the

colour of the aperture, and in a large series it is impossible to draw a well defined line separating the two. There are also parallel variations in both, which, aside from the color of the aperture cannot be separated, another strong indication that we are dealing only with only one variable species."

4.7.3. Additional support comes from the observation of a roughly clinal variation in the colour of the shell aperture (the main historical argument for separating *O. miniacea* from *O. tremulina*). This is demonstrated in Fig. 21 where the colour of the aperture is plotted

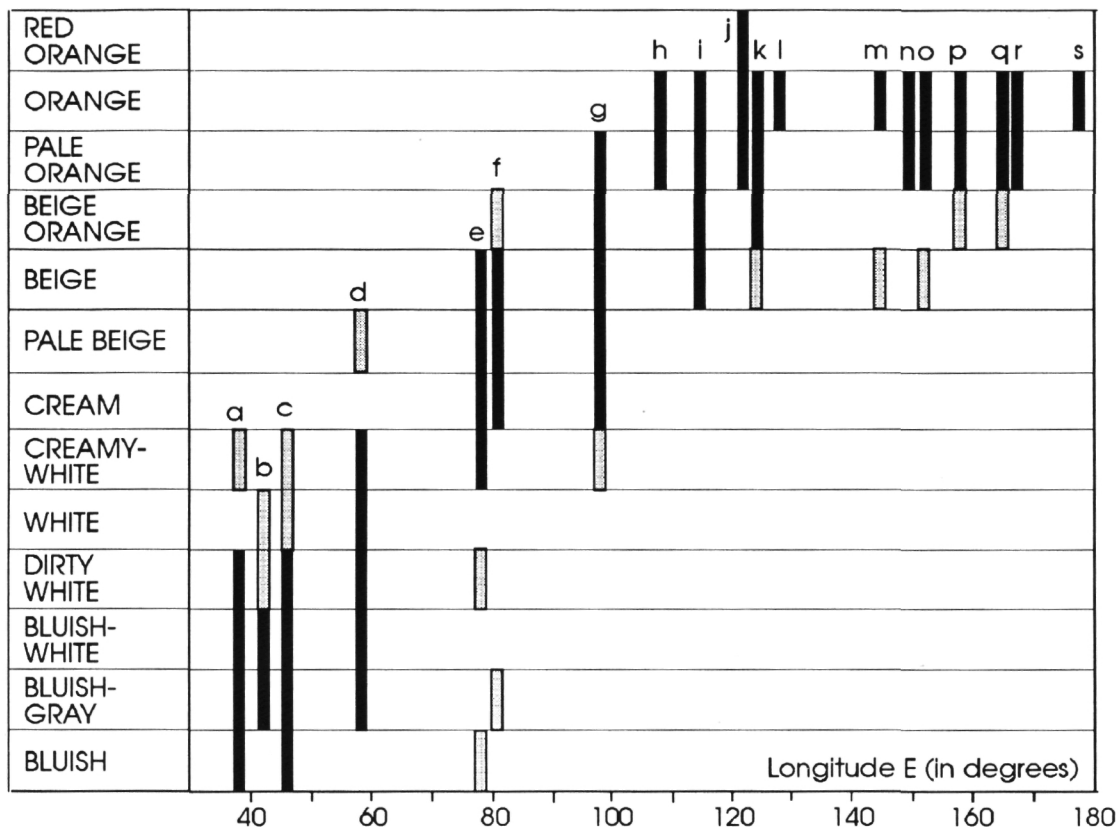


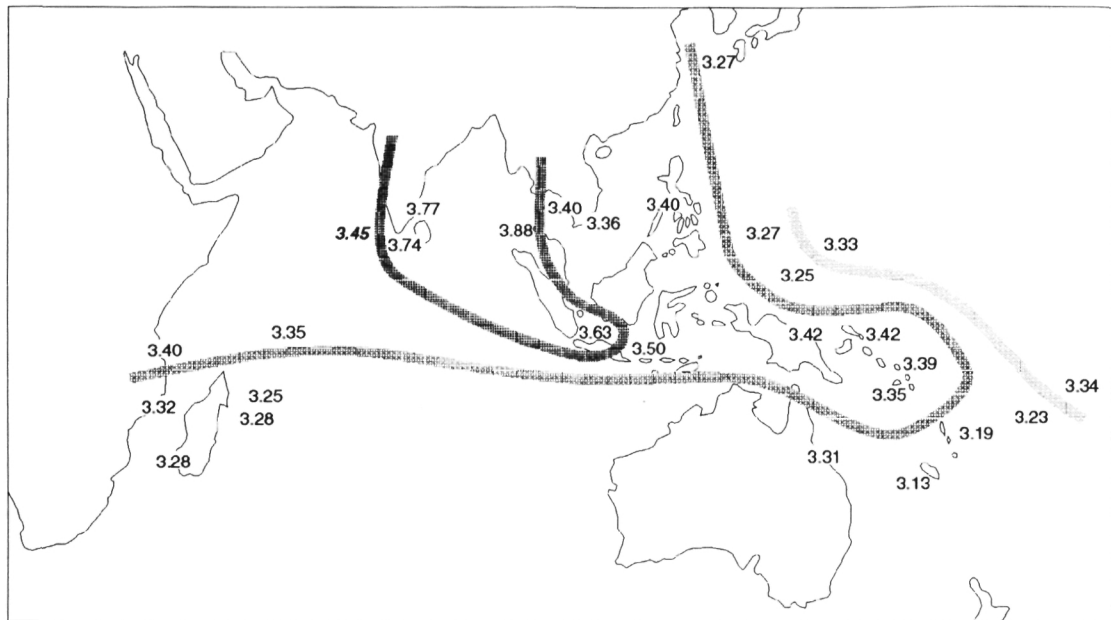
Fig. 21. *O. miniacea* s.l. Clinal variation of aperture colour. Figures are longitudes East (in degrees). For definition of colour classes, see text § 4.6.3. Black bars contain over 85% of each sample. **a.** Tanzania (N = 12). **b.** Mozambique (N = 14). **c.** Madagascar (N = 37). **d.** Mauritius (N = 50). **e.** South India (N = 49). **f.** Sri Lanka (N = 18). **g.** Thailand (N = 40). **h.** Vietnam (n = 12). **i.** Bali (N = 14). **j.** Taiwan (N = 10). **k.** Philippines (N = 80). **l.** Okinawa (N = 10). **m.** Papua New Guinea (N = 18). **n.** Carolines (N = 12). **o.** Queensland (N = 48). **p.** Solomon Is. (N = 32). **q.** New Caledonia (N=60). **r.** Kwajalein (N = 23). **s.** Fiji (N = 13).

against longitude. For reproducibility, the reference colour classes have been defined by their content in red (R), green (G) and blue (B). Bluish: R 89%, G 96%, B 100%; Bluish grey: R 83.5%, G 88%, B: 91%; Bluish white: R 94.5%, G 100%, B 100%; Dirty white: R 95.7%, G 95.7%, B 95.7%; White: R 100%, G 100%, B 100%; Creamy white: R 100%, G 96.5%, B 100%; Cream: R 100%, G 89.5%, B 69.5%; Pale beige: R 100%, G 82.7%, B 62.7%; Beige: R 92.1%, G 67.5%, B 47.5%; Beige orange: R 93.7%, G 51%, B 34.5%; Pale orange: R 100%, G 62.4%, B 15.3%; Orange: R 100%, G 47%, B 0%; Red orange: R 100%, G 29%, B 5.1%.

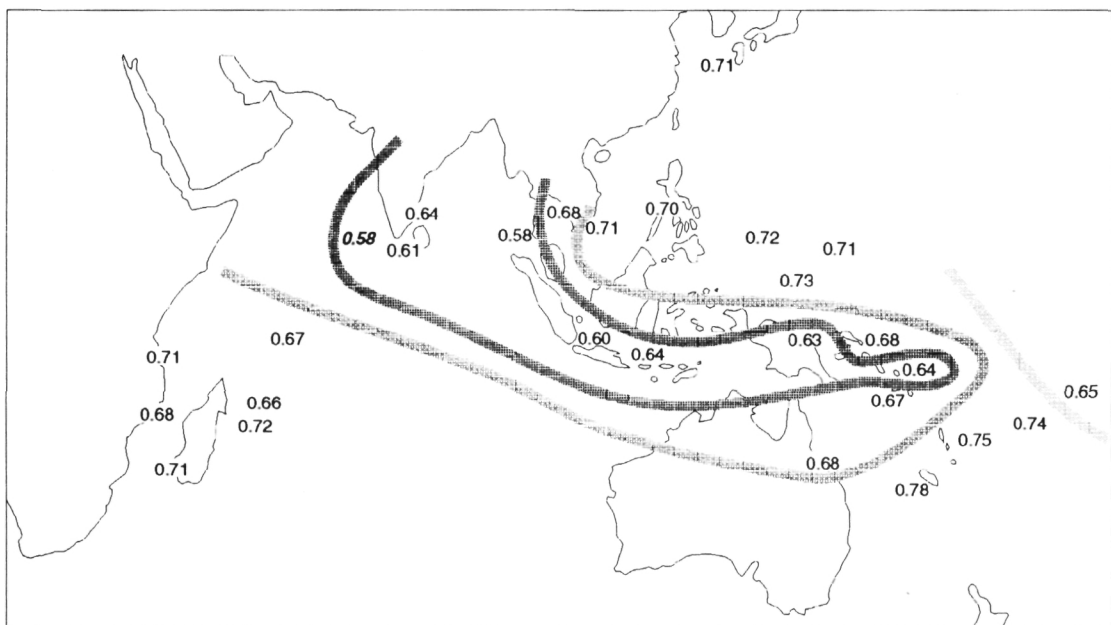
Orange apertures are the rule in the Pacific, whitish apertures are standard in the Western and Central Indian Ocean; intermediate hues (and frequent intrapopulation heterogeneity) are seen in the central part of the distribution area (India, Sri Lanka, West Thailand, Indonesia,

etc.). This character is unlikely to be of direct adaptative significance, as it cannot be seen as long as the animal is alive. The observed variation is far more likely to be of genetic origin.

4.7.4. Further confirmation comes from the observation of a clinal variation in protoconch characters. Mean values observed for NW (and rough isophene lines) are reported on the distribution area (Map 1). Ranges of values for neighbouring populations do frequently overlap and the figures indicate only tendencies of the mean values. It will be seen that mean values decrease regularly with distance from a point located roughly in the Andaman Sea. Mean values observed for LPRO (and isophene lines) are reported on the distribution in Map 2. In this figure also, ranges of values for neighbouring populations do frequently overlap and the figure indicates only tendencies of the mean values.



Map 1. *O. miniacea* s.l., variation of NW. Mean values (see text § 4.7.4). Isophene lines for arbitrary values 3.30 and 3.60. The value for *O. ponderosa* is in italics.



Map 2. *O. miniacea* s.l., variation of LPRO. Mean values (see text § 4.7.4). The value for *O. ponderosa* is in italics. Isophene lines for arbitrary values 0.65 and 0.70.

The parallelism between these two graphs is rather striking. The characters LPRO and NW are geometrically independent variables (see Fig. 1), but appear to be biologically related in the genus *Oliva* (TURSCH, 1988). Clinal variation within a group of populations is of course a very strong argument for their conspecificity.

Here again, the variations of the protoconch are more likely to be genetic than adaptative (see TURSCH, 1994). Maps 1 and 2 could possibly indicate that *Oliva miniacea* s.l. originated somewhere in the North of the Indo-Malayan arc.

4.8. Problems of rank.

It follows from Table 1 that *O. concinna* Marrat, 1870, *O. hirasei* Kira, 1959 and *O. sericea* (Röding, 1798) all obviously constitute separate species. The same goes for phenon *MS* (*O. mascarena* n. sp., described here under). All are broadly sympatric with populations of *Oliva miniacea* s.l.

Within the highly variable species *Oliva miniacea* s.l., all the specimens from India, Sri Lanka and the Maldives that we have examined correspond to *O. flammeacolor*. All the populations of East Africa, Madagascar, Reunion, Mauritius and the Seychelles that we have studied correspond to *O. tremulina*. These two groups of populations clearly stand out in general aspect, are characteristic of given geographic regions and deserve subspecific rank: *Oliva miniacea flammeacolor* Petuch & Sargent, 1986 and *Oliva miniacea tremulina* Lamarck, 1811. Intermediate forms do occur, for instance in Thailand and in Indonesia, as fully expected for subspecies.

O. ponderosa Duclos, 1840 (restricted to the Maldives region) is readily separated by shell measurements from all Indian Ocean shells, but is quite close to some *O. miniacea* populations from the South Pacific. On shell morphological grounds only, it could be just another local phenon of *O. miniacea*. We prefer to consider it a full species because it is broadly sympatric with *O. miniacea flammeacolor* Petuch & Sargent, 1986 (and two subspecies cannot co-occur, by definition).

The same reasoning applies to *O. atalina* Duclos, 1835 (from Cargados and Mauritius), also readily separated from all other Indian Ocean shells, but very close in shell morphology to some *O. miniacea* populations from the South Pacific. It is broadly sympatric with *Oliva miniacea tremulina* Lamarck, 1811 and should therefore be considered as a full species.

5. CONCLUSIONS

The above analysis of both morphometric and distribution data has led us to separate the following 7 species:

- *O. atalina* Duclos, 1835,
- *O. concinna* Marrat, 1870,
- *O. hirasei* Kira, 1959,
- *O. miniacea* (Röding, 1798),
with two subspecies:
 - *O. miniacea flammeacolor* Petuch & Sargent, 1986,
 - *O. miniacea tremulina* Lamarck, 1811,
- *O. ponderosa* Duclos, 1840,

- *O. sericea* (Röding, 1798),
- Another species, the provisional phenon *MS*
(*O. mascarena* n. sp., described here under).

6. SYSTEMATICS

6.1. Affinities.

A close affinity most probably exists between all the taxa considered here. Their shells are quite similar and not readily separable by the shape of the spire and that of the body whorl, both very variable. Most have subchannel marks on the spire. Their suprafasciolar band is divided in two spiral colour zones, the upper one nearly always of lighter colour (excepted in dark specimens), due to additional enamel. In all taxa (with the exception of *O. ponderosa*), the body whorl often has a colour pattern with two prominent darker bands, one near the shoulder and one near the middle of the body whorl. All the shells considered here also have very similar protoconchs and early whorls (see Plate 6). Only *O. sericea* is characterized by its fused early teleoconch whorls (Plate 6, Figs. 9-10). These two figures also illustrate the great intraspecific variability of the angle of the spire, observed in all the species studied here.

In addition to resemblance in shell morphology, the species we had the opportunity of observing alive (*O. concinna*, *O. miniacea*, *O. sericea*) share similarities in the coloration of the animal (pattern formed of large, isolated dark spots). The same pattern is reported for *O. ponderosa* by DUCLOS (1840, Pl. 33, Fig. 8).

Most of the taxa reviewed here are familiar, sometimes under another name. All have been placed in the subgenus *Miniaceoliva* Petuch & Sargent, 1986, also including some species that might be quite unrelated. Awaiting objective data on the limits of the subgenus *Miniaceoliva*, we will (for the time) refrain from using this category.

6.2. Characters.

It must be stressed that, in the genus *Oliva*, there is a fundamental difference of nature between classifications obtained by morphometric methods and classifications based upon ornamentation patterns. As exemplified here above, morphometrics lead to **monothetic taxa**, in which the possession of a unique set of features is both sufficient and necessary for membership. In contrast, the classical "visual" approach (based upon characters as unstable as spire height, colours and colour patterns) generally leads to **polythetic taxa**. In such taxa, organisms that have the greatest number of shared

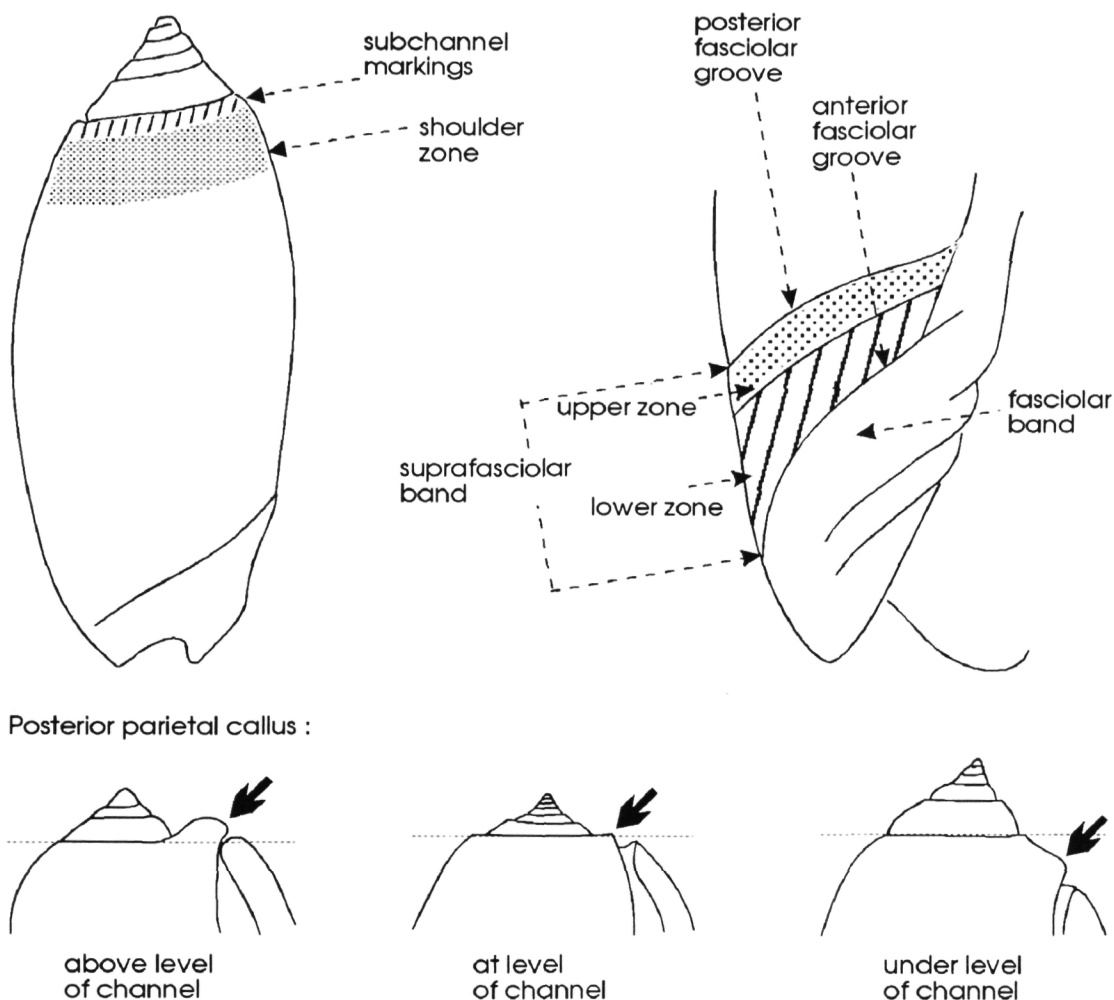


Fig. 22. Descriptive terms for shell.

characters are placed together, but no single character is either necessary or sufficient for group membership (see SNEATH & SOKAL, 1973; PANCHEN, 1992).

In deference to conchological tradition, the following "Diagnosis" paragraphs are largely based upon shell ornamentation, which is notoriously variable in the genus *Oliva*. All characters common to the genus (shell smooth, shiny, etc.) shall be omitted and only features with some discrimination power are reported. Preference has been given to details possessing probably very little or no adaptative value. As just stated here above, very few (if any) of these traits, taken one by one, will allow secure identification of an individual specimen. The probability for achieving this will be much increased by observing the simultaneous presence of such features.

Morphometrics allowed the delimitation of objective, natural taxa. This exploratory task being accomplished, detailed measurements are generally not indispensable any more for identification of individual specimens. *Oliva* species, although highly variable, have nevertheless limited "*répertoires*". Familiarity with the limits of intraspecific variation should allow rapid identification of most (but not all) specimens.

6.3. Notes.

Some descriptive terms used here for the shell (upper and lower zones of the suprafasciolar band, shoulder zone, subchannel markings, the position of the posterior parietal callus relative to the filament channel of the penultimate whorl) are made explicit in Fig. 22. For the use of the term "filament channel"

instead of "suture" see VAN OSSELAER & TURSCH (1994).

In the diagnoses, (++++) stands for "nearly always", (++) for "in most cases" and (+) for "sometimes". The abbreviation "q.v." (*quod vide*) means "see under that name".

The list of localities in the paragraphs "Distribution" is not exhaustive and reports only material seen by us and having reliable data.

In the following section, the names of very frequently cited authors will be abbreviated, to save on space. So, B. & B. stands for BURCH & BURCH, P. & S. for PETUCH & SARGENT, W. & A. for WAGNER & ABBOTT, Z. & P. for ZEIGLER & PORRECA. To avoid confusion, "Pl." and "fig(s)." refer to plates and figures in cited works, while "PL." and "FIG(S)." refer to illustrations in the present paper.

6.4. The species.

Family OLIVIDAE Latreille, 1825

Subfamily OLIVINAE Latreille, 1825

Genus *Oliva* Bruguière, 1789

***Oliva atalina* Duclos, 1835.**

Oliva atalina Duclos, 1835: Pl. 10, Figs. 9 and 10.

Oliva quersolina Duclos, 1835: Pl. 10, Figs. 7 and 8.

Oliva stainforthi Reeve, 1850: sp. 40, Pl. 19, Fig. 40.

Oliva soverbii Marrat, 1870: 13, sp. 61.

Oliva sowerbyi Marrat, 1870: 13, sp. 61, Figs. 114 and 115.

Oliva fulva Marrat, 1871: 42, sp. n° 222, Fig. 471.

TYPE MATERIAL.

Oliva atalina Duclos, 1835: 3 syntypes at MNHN and 3 specimens in the Duclos collection at the Clermont-Ferrand Museum. One syntype figured PL. 1, FIG. 2.

Oliva fulva Marrat, 1871: holotype at MCM, figured PL. 1, FIG. 3.

Oliva quersolina Duclos, 1835: 3 syntypes at MNHN. One syntype figured PL. 1, FIG. 1.

Oliva sowerbyi Marrat, 1870: 2 syntypes at MCM. One syntype figured PL. 1, FIG. 4.

Oliva stainforthi Reeve, 1850: 2 syntypes n° 1892.9.24.13-14 at BM(NH). One syntype figured PL. 1, FIG. 5.

SYNONYMY.

That *O. atalina* Duclos, 1835 constitutes a distinct species is demonstrated here above, in Section 4.

The following names are synonyms:

O. quersolina Duclos, 1835 was *O. episcopalis* Lamarck, 1811 for B. & B. (1960); *O. olarinella* Duclos, 1835 for W. & A. (1967) and (strangely enough) *O. reticularis* Lamarck, 1811 for Z. & P. (1969) and P. & S. (1986). Careful examination of the type material leaves no doubt at all that *O. quersolina* Duclos, 1835 is a **subjective synonym** of *O. atalina* Duclos, 1835.

O. stainforthi Reeve, 1850 was *O. lentiginosa* Reeve, 1850 (a colour form of *O. esiodina* Duclos, 1844, see TURSCH & GREIFENEDER, 1989a) for W. & A. (1967). It was *O. duclosi* Reeve, 1850 (another colour form of *O. esiodina* Duclos, 1844, see TURSCH & GREIFENEDER, 1989a) for Z. & P. (1969) and P. & S. (1986). *O. duclosi* Reeve, 1850 form *stainforthi*; Petuch & Sargent (not Reeve, 1850), 1986 (Pl. 1, Figs. 11, 12) does not even resemble the type material of *O. stainforthi* Reeve (and is clearly the light colour form of *O. esiodina* Duclos, 1844). *O. stainforthii* Reeve (a misspelling) was *O. duclosi* var. *lentiginosa* for B. & B. (1960). One of the two syntypes of *O. stainforthi* (see PL. 1, FIG. 5) is an especially small, "fat", rarely seen form of *O. atalina*. Its identity is evidenced by its position in the scatter diagrams (FIGS. 13, 14, 15 and 17). *O. stainforthi* Reeve, 1850 is therefore a **subjective junior synonym** of *O. atalina* Duclos, 1835.

O. sowerbyi Marrat, 1870 was reported (caption of Marrat's Figs. 114, 115) as originating from Jamaica (an obvious error). This might explain why it has been considered as being *O. reticularis* Lamarck, 1811 (or a color form of this species) by B. & B. (1960), Z. & P. (1969), W. & A. (1967) and P. & S. (1986). It was correctly recognised as being *O. stainforthi* Reeve, 1850 (see here above) by TOMLIN (in FORD, 1953). *O. reticularis* colour form *sowerbyi*; Petuch & Sargent (not Marrat, 1870), 1986 (Pl. 27, Figs. 10, 11) does not at all resemble the type material of *O. sowerbyi* Marrat (and clearly belongs to the American *O. reticularis-fulgurator* group). *O. sowerbyi* Marrat, 1870 (Thesaurus, sp. 61, p. 13) is a misprint, corrected in the caption for Pl. 8, Figs. 114-115 as well as in the Index. *O. sowerbyi* Anton, 1839 is a small fossil from the Paris region. It is probably an *Ancilla*, as it was described (ANTON, 1839: 102) under *hiatula*. "*Oliva*" *sowerbyi* Ducros de Saint Germain, 1857 is not an *Oliva* but an *Olivella*. Careful examination of the type material leaves no doubt that *O. sowerbyi* Marrat, 1870 is a **subjective junior synonym** of *O. atalina* Duclos, 1835.

O. fulva Marrat, 1871 was *O. oliva* (L., 1758) by B. & B. (1960) for W. & A. (1967) and a colour form of *O. leucostoma* Duclos, 1840 for P. & S. (1986). *O. fulva*; Petuch & Sargent (not Marrat, 1871), 1986 (*Atlas*: 162, Pl. 33, Figs. 3, 4) does not even resemble the type and is probably a melanistic *O. elegans* Lam. SOWERBY (Marrat's editor) commented on *O. fulva* (in *Thesaurus*: 42): "This species is allied to a difficult series of Olives viz. *O. atalina*, *O. quersolina*, etc. They may all prove varieties of a common type when the variations are better understood". Study of the sub-adult, worn and discoloured holotype (figured in PL. 1, FIG. 3) established that *O. fulva* Marrat, 1871 is a **subjective junior synonym** of *O. atalina* Duclos, 1835, of which it has the characteristic "double dots" colour pattern (see Diagnosis, here below).

The following names have been mistakenly considered as synonyms:

O. caerulea (Röding, 1798). *O. atalina* Duclos, 1835 was this species for W. & A. (1967). This is not the case, as demonstrated here above (§ 4.5.6 and FIG. 18), but the confusion is understandable. The two species are indeed rather similar in general aspect, except for the typical blue colour of the aperture of *O. caerulea* (Röding, 1798), a **valid species** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

O. episcopalis Lamarck, 1811. *O. atalina* Duclos, 1835 was this species for B. & B. (1960) and Z. & P. (1969). *O. episcopalis* Lamarck, 1811 (see GREIFENEDER, DUCHAMPS & TURSCH, 1995) is a **subjective synonym** of *O. caerulea* (Röding, 1798), discussed in the previous paragraph.

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. atalina*:

Shell up to about 55 mm. Aperture ivory (+++) to faint violet (+). Columella same colour (whitish) as body whorl (+++).

Spire. Profile of spire whorls: variable. In old specimens, posterior parietal callus of variable height in relation to channel of previous whorl.

Body whorl. Subchannel markings: 13 to 18 faint purple axial thin strokes. Background colour ivory white. Shoulder zone: thin band with much reduced pattern. Body whorl colour pattern: characteristic irregular vertical arrangement of elements formed by minute orange dots immediately followed by diffuse bluish spots (+++). In some cases these elements coalesce

into vertical zigzag lines. Darker spiral bands very faint, often consisting in a few, isolated dark spots (+++). Overlay with dark layers not observed.

Suprafasciolar band: pattern in upper zone lacking or very reduced; lower zone with repeating blotches of same colour as body whorl pattern (PL. 5, FIGS. 1, 2).

DISTRIBUTION.

Cargados Carajos, Mauritius.

Oliva concinna Marrat, 1870.

Oliva concinna Marrat, 1870: p. 13, Pl. 7, Figs. 100, 101.

Oliva tremulina; Dautzenberg (not Lamarck, 1811), 1927 var. *chrysoides* Dautzenberg, 1927: 139.

Oliva tremulina; Zeigler (not Lamarck, 1811), forma *oldi* Zeigler, 1969: 14-19.

Oliva fumosa; Petuch & Sargent (not Marrat, 1871), 1986: p. 90, Pl. 10, Figs. 1, 2.

Oliva fumosa; Petuch & Sargent (not Marrat, 1871) *kremerorum* Petuch & Sargent, 1986: 91, Pl. 10, Figs. 3, 4.

TYPE MATERIAL.

O. concinna Marrat, 1870. The type lot (at MCM) consists of two specimens of different species. Of the two figured syntypes, (specimen n° 101, H: 44.2, D: 17.8 mm, figured on PL. 3, FIG. 4, is obviously *O. miniacea tremulina* Lamarck, 1811 (*q.v.*). The other syntype (n° 100, also H: 44.2, D: 17.8 mm, from New Caledonia, figured on PL. 1, FIG. 7, belongs to another species, not yet described at the time. It is here selected as the **lectotype** of *O. concinna* Marrat, 1870.

O. tremulina forma *oldi* Zeigler, 1969. Holotype at AMNH n° 147750, figured PL. 1, FIG. 9. Paratype n° C111456 at AMS.

O. (Miniaceoliva) fumosa kremerorum Petuch & Sargent, 1986. Holotype at USNM (n° 841460), figured PL. 1, FIG. 8. Paratype n° C153453 at AMS.

NOTE. *O. concinna* has been introduced here only as an outgroup for the delimitation of the "*O. miniacea* complex" (see Introduction). The relationships of *O. concinna* Marrat, 1870 with *O. irisans* Lamarck, 1811 and *O. ornata* Marrat, 1867 (both unlikely to be confused with forms of the "*O. miniacea* complex") will be examined elsewhere.

SYNONYMY.

The following names are synonyms:

O. tremulina var. *chrysoides* Dautzenberg, 1927 was a form of *O. tremulina* Lamarck, 1811 for B. & B. (1960, 1967), Z. & P. (1969) and W. & A. (1967). It was a colour form of *O. fumosa*; Petuch & Sargent (not Marrat, 1871), 1986 *concinna* Marrat, 1870 for P. & S. (1986). Study of the material in the Dautzenberg collection (now at IRSNB) established that *O. tremulina*; Dautzenberg (not Lamarck, 1811), 1927 var. *chrysoides* Dautzenberg, 1927 is a colour form of *O. concinna* Marrat, 1870. A specimen from the Dautzenberg collection is figured PL. 1, FIG. 6.

O. tremulina forma *oldi* Zeigler, 1969. Study of the holotype (from the Solomon Islands, figured PL. 1, FIG. 9) shows that *O. tremulina*; Zeigler (not Lamarck, 1811), 1969 forma *oldi* Zeigler, 1969 is a dark-patterned colour form of *O. concinna* Marrat, 1870, a form linked to the type by many intergrades. This was a form of *O. tremulina* Lamarck, 1811 for Z. & P. (1969) and W. & A. (1967) to be. It was considered a colour form of *O. fumosa*; Petuch & Sargent (not Marrat, 1871) *concinna* Marrat, 1870 (see here under) for P. & S. (1986).

O. fumosa kremerorum Petuch & Sargent, 1986. Study of the holotype established that *O. fumosa*; Petuch & Sargent (not Marrat, 1871), 1986 *kremerorum* Petuch & Sargent, 1986 is a form of *O. concinna* Marrat, 1870 found in South India and Sri Lanka. Nearly identical specimens are commonly found in Melanesia.

The following names have been mistakenly considered as synonyms or constitute errors in identification:

O. tremulina Lamarck, 1811. *O. concinna* Marrat, 1870 was a synonym of this name (*q.v.*) for TOMLIN (in FORD, 1953), B. & B. (1967), Z. & P. (1969) and W. & A. (1967). This is understandable, due to the heterogeneity of the type lot of *O. concinna* (see Type Material).

O. pica Lamarck, 1811 was a possible synonym of *O. concinna* Marrat, 1870 for W. & A. (1967). *O. pica*; Johnson (not Lamarck, 1811), 1928 was a possible synonym of *O. concinna* Marrat, 1870 for B. & B. (1967). *O. pica* Lamarck, 1811 is a **nomen dubium** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

O. zeilanica Lamarck, 1811. *O. concinna* Marrat, 1870 was placed by KÜSTER (in WEINKAUFF, 1878) in the synonymy of this name, which is also a **nomen dubium** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

O. tenebrosa Marrat, 1870 was a synonym of *O. concinna* Marrat, 1870 for W. & A., 1967.

The holotype (figured PL. 3, FIG. 5) is just a dark specimen of *O. miniacea tremulina* Lamarck, 1811 (*q.v.*).

O. fumosa Marrat, 1871. P. & S. (1986) considered *O. concinna* Marrat, 1870 to be a subspecies of this taxon. *O. fumosa*; Petuch & Sargent (not Marrat, 1871), 1986, Pl. 89, Figs. 1, 2 is indeed *O. concinna* Marrat, 1870. But the holotype of *O. fumosa* Marrat, 1871 (figured PL. 3, FIG. 3) is undoubtedly *O. miniacea tremulina* Lamarck, 1811 (*q.v.*). *O. fumosa*; Petuch & Sargent (not Marrat, 1871), 1986 *kremerorum* Petuch & Sargent (not Marrat, 1871), 1986, discussed here above, is yet another facet of the same imbroglio.

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. concinna*:

Shell up to about 55 mm. Aperture whitish, not characteristic. Lower part of columella diffused with salmon or orange (+++), smoky brown in dark specimens.

Spire. Profile of spire whorls: variable, but not concave (++). In old specimens, posterior parietal callus mostly below, not above the filament channel of the previous whorl.

Body whorl. Subchannel markings: variable in number (can be absent) and aspect.

Background colour: ivory to light greyish beige. Shoulder zone: thin (3-5 mm) band generally without any pattern (+++). Body whorl pattern: most generally vertical zigzag of smoky grey to brown. Occasional specimens partly or completely overlaid with dark brown, black or orange.

Suprafasciolar band: upper zone with pattern lacking or very reduced, lower zone with many thin elements often coalescent in a continuous grey band (++) (PL. 5, FIGS. 9, 10). Width of fasciolar band very large (mean: 11.3% of lip length) (+++).

DISTRIBUTION.

Fiji, S. India, Indonesia (Bali), Sri Lanka, New Caledonia, Papua New Guinea, Philippines, Samoa, Solomons, W. Thailand, Vanuatu.

Oliva hirasei Kira, 1959.

Oliva hirasei Kira, 1959: Pl. 32, Fig. 8.

Oliva tremulina; Zeigler & Porreca (not Lamarck, 1811) *fumosa*; Zeigler & Porreca (not Marrat, 1871), 1969: Pl. 12, Fig. 8.

TYPE MATERIAL.

We are not aware of the existence of any type material.

SYNONYMY.

This is a distinctive shell, now unanimously recognized as a valid species, and most specimens are correctly identified. Two representative specimens are figured PL. 1, FIGS. 10, 11. B. & B. (1960) listed *O. hirasei* Kira, 1959 as a possible synonym of *O. tremulina* Lamarck, 1811.

Specimens of other species have sometimes been mistaken for this species. For instance, *Oliva tremulina*; Zeigler & Porreca (not Lamarck, 1811) *fumosa*; Zeigler & Porreca (not Marrat, 1871), 1969: Pl. 12, Fig. 8 is a typical *O. hirasei* Kira, 1959.

DIAGNOSIS.

In addition to the discriminants reported in Table 1, the following features are useful for recognising *O. hirasei*:

Shell up to about 60 mm. Aperture dirty white (+++). Lower tip of columella with smoky-grey diffuse blotch (+++). In old specimens posterior parietal callus variable, sometimes reaching or even surpassing level of apex.

Spire: no pattern at all (+++) except for occasional subchannel marks. Profile of spire whorls: not convex (++).

Body whorl. Subchannel markings: variable small elements, often coalescent into a thin dark line along the external rim of the channel (++). Background colour: light beige to apricot. Shoulder zone: broad band generally devoid of pattern (+++). Body whorl pattern: brown, most generally large vertical zigzag patterns. Most often very bold streaks just under shoulder zone. Overlay with dark layers not observed.

Suprafasciolar band: upper zone with pattern lacking or very reduced; lower zone with many thin elements often coalescent in a continuous grey band (++) (PL. 5, FIGS. 11, 12).

DISTRIBUTION.

Japan, New Caledonia, Papua New Guinea, Philippines, Solomons, Taiwan.

REMARKS.

This species is referred to as *hirasei* "Kuroda & Habe, 1952" Kira, 1959 (WAGNER & ABBOTT, 1967) or *hirasei* Kira, 1959 (PETUCH & SARGENT, 1986). According to Z. & P. (1969: 71), Kuroda & Habe proposed this new name in 1952, based on a figure of HIRASE (1909: 3, Pl. 4, Fig. 26) in *The Conchological Magazine*, a short-lived publication that appeared in Japan early in the century. Apparently, there is no written description of the shell by KURODA and

HABE (1952). The species was then described by KIRA (1959).

***Oliva mascarena* n. sp.**

Oliva olympiadin; Reeve (not Duclos, 1835) 1850: Pl. 3, Figs. 5a, 5b, 5d, 5e.

Oliva ponderosa; Zeigler & Porreca (not Duclos, 1840) 1969: Pl. 12, Fig. 9.

Oliva tremulina olympiadin; Zeigler & Porreca (not *tremulina* Lamarck, 1811, not *olympiadin* Duclos, 1835) 1969: Pl. 12, Fig. 6.

Oliva olympiadin; Kaicher (not Duclos, 1840), 1989. Card n° 5513.

Oliva pica; Petuch & Sargent (not Lamarck, 1811) 1986: Pl. 13, Figs. 7, 8.

Oliva pica colour form *olympiadin*; Petuch & Sargent (not *pica* Lamarck, 1811, not *olympiadin* Duclos, 1835) 1986: Pl. 13, Figs. 9, 10.

TYPE MATERIAL.

Holotype (PL. 4, FIG. 1) in BM(NH) n° 1953.3.4.203 (H: 75.1 mm; D: 35.1 mm), collected at Aldabra, June 1938. From Winckworth collection, with old label "*O. pica*".

Paratype 1 (PL. 4, FIG. 2) in BM(NH) n° 1953.3.4.204 (H: 68.5 mm; D: 31.0 mm), collected at Aldabra, June 1938. From Winckworth collection, with old label "*O. pica*".

Paratype 2 (PL. 4, FIG. 3) in IRSNB, (H: 71.5 mm; D: 32.0 mm) Dautzenberg collection, "probably from Mauritius".

Paratype 3 (PL. 4, FIG. 4) in MNHN, (H: 67.8; D: 32.0 mm), ex coll. D. Greifeneder n° DG-3921a, Seychelles.

Paratype 4 (PL. 4, FIG. 5) in D. Greifeneder coll., n° DG-3076, (H: 59.8 mm; D: 27.3 mm), Peros Banhos, Chagos Archipelago.

Paratype 5 (PL. 4, FIG. 6) in B. Tursch coll., n° BT-4370, (H: 65.6 mm; D: 29.5 mm), dredged 15 m, Beau Vallon, Seychelles, 1973.

SYNONYMY.

That *O. mascarena* n. sp. constitutes a distinct species has been demonstrated here above (in Section 4). If recognised once, this shell will later be identified at a glance. The existence and the variation range of this rather obvious species were already recognised in 1850 by Reeve, on the basis of a large series of specimens (about 200) from Mauritius. Reeve unfortunately thought that the species was already described and even selected a fine specimen (BMNH n° 1984149, from the Cuming collection) to illustrate what he believed to be *O. olympiadin* Duclos, 1835 (the identity of *O. olympiadin* is

now clear: the two figured syntypes are colour forms of *O. miniacea tremulina* Lamarck, 1811, q.v.).

Ever since Reeve's days, students were apparently convinced that such a large, striking species *must* already have been named (which is not the case). Specimens, present in large numbers in many old collections, have thus been invariably shoehorned into many of the taxa created for shells of the Western region of the Indian Ocean. Even in one of the world's most prestigious Museums, specimens of this species bear the labels *O. miniacea*, *O. olympiadin*a, *O. pica*, *O. ponderosa*, *O. sericea* and *O. tremulina*.

The rather frequent use of the name *O. pica* Lamarck, 1811 deserves some comment. This is a nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH, 1995). In any case, the original description "*Sur une couleur brune ou d'un fauve très-rembruni, cette olive présente des taches d'un beau blanc, irrégulières, et dont plusieurs sont trigones ou deltoïdes*" does not apply to any of the several hundred specimens of *O. mascarena* n. sp. that we have examined.

O. ponderosa ; Zeigler & Porreca (not Duclos, 1840), 1969, *O. tremulina* ; Zeigler & Porreca (not Lamarck, 1811) *olympiadin*a; Zeigler & Porreca (not Duclos, 1835), 1969, *O. pica* ; Petuch & Sargent (not Lamarck, 1811), 1986, *O. pica* ; Petuch & Sargent (not Lamarck, 1811), 1986 colour form *olympiadin*a ; Petuch & Sargent (not Duclos, 1835), 1986 are some other examples (amongst more) of misidentification of *O. mascarena* n. sp. *O. olympiadin*a ; Kaicher (not Duclos, 1840), 1989 is also this species.

DESCRIPTION.

GENERAL ASPECT. The rather cylindrical shell is of medium to large size, (40 to probably 80 mm), with an average ratio of diameter (D) to lip length (L) of $D/L = 0.49$. The spire is flat-conical to onion-shaped. The average height of the spire is 7% of the total shell length (H). In adult shells, the posterior parietal callus reaches (or more often protrudes above) the level of the channel of the previous whorl. The protoconch and the width of the filament channel are similar to those of the other large *Oliva* species of the Indian Ocean, such as *O. miniacea tremulina* and *O. ponderosa*. The columellar plaits are flat and smooth in adult shells, whereas 20 distinct plaits were counted on an immature specimen. The upper margin of the

suprafasciolarian band meets the columella outline at an average relative height of 0.49 of the lip length (L). The uppermost callus zone of the fasciolar band has a mean breadth of 8.3% of the lip length (L). This zone is thus generally broader than in *O. miniacea tremulina* (mean 5.6%) or in *O. miniacea* (mean 6.0%). In large, adult specimens the inner part of the lip is thickened over a large stretch, in which the lip runs straight, parallel to the shell axis. The siphonal notch is mostly more oblique than in *O. miniacea tremulina*. For an equal size, the shell of *O. mascarena* n. sp. is generally much heavier than *O. miniacea tremulina* or *O. miniacea*, but lighter than *O. atalina* and *O. ponderosa*.

COLOUR PATTERN. The ground colour of all parts of the shell is ivory white or brilliant white, the latter mainly in populations from Aldabra, the Seychelles or Tanzania. The columella and the fasciolar band can show a touch of cream. Prevalent blurred and diffuse pattern elements are purplish-grey, the additional blotches are brown, dark brown or even black. The whorls of the spire show few tangential strokes or chevrons. The subchannel rim has 9 to 17 faint oblique chevrons. Then follows a small zone with a reduced density of pattern elements. On the body whorl, the blurred purplish-grey pattern elements (mostly degenerated chevrons and strokes) are arranged more or less axially. There are two darker spiral bands, which are mainly formed by additional dark blotches. Occasionally, the shells are partly overlaid with dark chocolate brown. In the upper zone of the suprafasciolarian band, the pattern density is reduced. The lower part of the same band is decorated with 6 to 12 dark blotches or oblique strokes, forming in some cases a "tiger pattern".

NUMERICAL VALUES.

Some morphometric data of *O. mascarena* n. sp. are reported in Table 2. None of these values, if taken alone, will ensure secure identification. Appropriate combinations of these data will do so, as shown in Section 4 (Delimitation of objective phenon).

One should note the very high values of the coefficient of variability (CV) for all data involving (H-L), expressing the relative height of the spire. This feature, heavily emphasized in nearly all classical descriptions of *Oliva* species, is nearly useless, being possibly the most variable quantitative character in all the taxa we have examined.

	mean	CV	min.	max.
Protoconch (<i>N</i>=7)				
LPRO (mm)	0.54	4.92	0.51	0.59
LPRO-SPRO (mm)	0.37	4.70	0.34	0.4
MPRO (mm)	0.34	6.22	0.31	0.36
MPRO/NW	0.09	7.35	0.08	0.11
NW	3.56	2.74	3.45	3.75
PAT17 mm)	0.67	7.04	0.6	0.72
PAT18 (mm)	1.13	2.51	1.09	1.16
RES5 (mm)	1.47	3.09	1.38	1.53
SPRO (mm)	0.18	9.67	0.15	0.19
Teleoconch (<i>N</i>=17)				
(D-X)/D	0.28	6.09	0.24	0.30
(H-L)/D	0.21	23.14	0.13	0.30
(H-L)/H	0.10	23.17	0.06	0.15
(H-L)/R	0.50	20.92	0.32	0.70
D/H	0.46	3.21	0.42	0.48
D/PNW	4.77	9.85	4.08	5.56
F/H	0.43	3.55	0.40	0.46
F/L	0.49	3.26	0.44	0.50
F/PNW	4.51	11.28	3.64	5.41
FG/F	1.13	1.04	1.20	3.61
FG/H	0.49	2.27	0.46	0.51
H/PNW	10.47	9.07	8.98	12.16
L/H	0.91	2.19	0.87	0.94
L/PNW	9.49	10.08	8.20	11.23
LW/H	0.93	1.54	0.91	0.96
LW/PNW	9.78	9.59	8.39	11.53
R/H	0.19	3.60	0.18	0.20
R/PNW	1.99	1.72	2.34	8.69
(100*SUT)/F	2.73	10.11	2.14	3.35
(100*SUT)/H	1.17	8.29	0.93	1.39
(100*SUT)/LW	1.26	8.87	0.96	1.49
(100*SUT)/PNW	12.28	11.02	9.82	14.73
X/H	0.33	2.96	0.31	0.35

Table 2. *Oliva mascarena*, n.sp.: morphometric data. The meaning of the measurements is sketched in Fig. 1. CV is the coefficient of variability, it is equal to (100 x standard deviation)/mean (MAYR, 1969).

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. mascarena* n. sp.:

Shell up to about 80 mm. Aperture white (+++). Columella and fasciole white or creamy (+++).

Spire. Profile of spire whorls: variable. In mature and old specimens: posterior parietal callus always above the filament channel of the previous whorl (+++).

Body whorl. Subchannel markings: 9 to 17 oblique chevrons (pointed upwards) short pur-

plish-grey elements. Background colour: ivory to pure brilliant white (+++). Shoulder zone: thin band with much reduced pattern (++). Body whorl pattern: blurred purplish-grey elements, mostly arranged axially. Darker spiral bands formed by additional dark brown to black blotches. Occasional specimens partly overlaid with chocolate brown.

Suprafasciolar band: upper zone with pattern lacking or very reduced; lower zone very close to *O. atalina*, but with dark dots more frequent (++) (see PL. 5, FIGS. 3, 4).

COMPARISONS.

O. mascarena n. sp. can be distinguished from:

- *O. atalina* by never having the "orange and blue double dots" pattern elements characteristic of this species (*q.v.*). Complete morphometric separation is shown in FIG. 16 (H/R vs. LW/PNW).

- *O. concinna* by lacking the suprafasciolar pattern and the columella tip coloration typical of this species (*q.v.*). Complete morphometric separation is given in FIG. 11 ((H-L)/L vs. L/PNW).

- *O. hirasei* by not possessing the broad, unadorned shoulder zone, the columella tip coloration and the bold streaks colour pattern typical of this species (*q.v.*). Complete morphometric separation is shown in FIG. 8 (H/PNW vs. PAT18) and FIG. 15 (LW/PNW vs. RES5).

- *O. miniacea miniacea* by lacking the bright orange to beige aperture colour, the columella colour, the suprafasciolar pattern typical of this species (*q.v.*) and by having a very different pattern. Complete morphometric separation is shown in FIG. 9 (NW/LPRO vs. H/F).

- *O. miniacea flammeacolor* by lacking the deep beige aperture colour, the suprafasciolar pattern typical of this species (*q.v.*) and by having a very different colour pattern on the body whorl. Complete morphometric separation is shown in FIG. 9 (NW/LPRO vs. H/F).

- *O. miniacea tremulina* by lacking the suprafasciolar pattern typical of this species (*q.v.*) and by having a very different colour pattern on the body whorl. Complete morphometric separation is shown in FIG. 9 (NW/LPRO vs. H/F).

- *O. ponderosa* by lacking the pale pink or orange aperture, the violet tinge on the fasciole margin typical of this species (*q.v.*) and by frequently having a pattern of dark blotches, nearly always lacking in *O. ponderosa*. Complete morphometric separation is shown in FIG. 9 (NW/LPRO vs. H/F).

- *O. sericea* by lacking the cream aperture, the very convex spire whorls, the fused postnuclear whorls, the suprafasciolar pattern typical of this species (*q.v.*) and by having a very different colour pattern on the body whorl. Complete morphometric separation is shown in FIG. 10 (PAT18 vs. RES5).

ETYMOLOGY.

Named after the Mascarene Islands.

DISTRIBUTION.

Aldabra, Cargados Carajos, Chagos (Peros Banhos), Mauritius (several localities), Mozambique (Nacala Bay), Reunion, Seychelles (Beau Vallon), Tanzania (Dar es Salaam). In Mauritius, *O. mascarena* is reported to be syntopic with *O. atalina* and *O. tremulina*.

Oliva miniacea (Röding, 1798).

Porphyria miniacea Röding, 1798: 32, sp. n° 391.

Porphyria miniata Link, 1807: 95.

Oliva porphyracea Perry, 1811: Pl. 41, Fig. 2.

Oliva erythrostoma Lamarck, 1811: 309, sp. n° 3.

Oliva aurantiaca Schumacher, 1817: 244.

Oliva masaris Duclos, 1835: 17, Pl. 20, Figs. 7-8 and Pl. 11, Fig. 9.

Oliva azemula Duclos, 1840: Pl. 14, Figs. 1, 2 (*pars*).

Oliva sylvia Duclos, 1845: 17, Pl. 14, Figs. 10-13.

Oliva magnifica Ducros de St. Germain, 1857: 30, Pl. 1, Fig. 4,a-d.

Oliva porphyritica Marrat, 1870: 12, Pl. 7, Figs. 105-110, sp. n° 55.

Oliva lamberti Jousseaume, 1884: 180.

Oliva sericea ; Johnson (not Röding, 1798) var. *miniacea* Johnson, 1910: 51.

Oliva sericea ; Johnson (not Röding, 1798) var. *marrati* Johnson, 1910: 51.

Oliva sericea ; Higgins (not Röding, 1798) var. *johnsoni* Higgins, 1919: 58.

Oliva erythrostoma var. *efasciata* Dautzenberg, 1927: 39.

Oliva erythrostoma var. *saturata* Dautzenberg, 1927: 39.

Oliva berti Terzer, 1986: 24.

TYPE MATERIAL.

Oliva azemula Duclos, 1840 : 6 syntypes at MNHN.

Oliva magnifica Ducros de St. Germain, 1857: holotype at MNHN.

Oliva lamberti Jousseaume, 1884: holotype at MNHN.

Oliva berti Terzer, 1986: holotype at Museum of Natural History, Genoa (not seen). Paratypes 1 and 2 in Terzer collection, Genoa.

SYNONYMY.

For the validity of the name *O. miniacea* (Röding, 1798), see TURSCH, DUCHAMPS & GREIFENEDER (1994).

The following names are synonyms:

O. miniata (Link, 1807) is an **objective junior synonym** of *O. miniacea* (Röding, 1798), both taxa being based upon the same illustrations (TURSCH, DUCHAMPS & GREIFENEDER, 1994). This is in agreement with W. & A. (1967) and P. & S. (1986).

O. porphyraea Perry, 1811 is a **subjective junior synonym** of *O. miniacea* (Röding, 1798) (see TURSCH, DUCHAMPS & GREIFENEDER, 1994), in agreement with B. & B. (1960). This was *O. porphyria* (L., 1758) for Z. & P. (1969), W. & A. (1967) and P. & S. (1986).

O. erythrostoma Lamarck, 1811. The original description is compatible with *O. miniacea* (Röding, 1798) and refers to the figures 476 and 477 of Martini, upon which this species is based. *Oliva erythrostoma* Lamarck is thus an **objective junior synonym** of *O. miniacea* (Röding, 1798). The species is clearly described and illustrated by DUCLOS (1840), who was familiar with Lamarck's specimens (see GREIFENEDER, DUCHAMPS & TURSCH, 1995). It was also *O. miniacea* (Röding, 1798) for B. & B. (1960), W. & A. (1967) and P. & S. (1986).

O. aurantiaca Schumacher, 1817. The laconic description consists only in "*Olive à bouche d'orange*" and a reference to figures 476 and 477 of Martini, previously used for *O. miniacea* (Röding, 1798). *O. aurantiaca* Schumacher, 1817 is therefore an **objective junior synonym** of *O. miniacea* (Röding, 1798), as for B. & B. (1960) and W. & A. (1967). Although there is no indication whatsoever, P. & S. (1986, p. 95) interpreted this as a colour form of *O. miniacea* (Röding, 1798).

O. masaris Duclos, 1835, for which no type specimens could be retrieved, has long been a puzzle. According to DUCROS (1857: 29) "*O. masaris*, Duclos" (misspelling for *masaris*) is a discoloured shell of *O. erythrostoma* Lamarck. This contradicts the description of Duclos ("... onze specimens d'une fraîcheur extrême. ... L'ouverture, d'une extrême longueur, est carnicole, rien n'égale sa fraîcheur. ...", italics ours). According to B. & B. (1967: 506) the figures of "*O. messaris* Duclos, 1835" (another misspelling for *masaris*) depict one large *O. tremulina* Lamarck, 1811, and one worn and discolored *O. miniacea* (Röding, 1798). The taxon was (in part) *O. miniacea* (Röding, 1798) for B. & B. (1960) and W. & A. (1967) and was a colour form of the same for P. & S. (1986). "*O. messaris* Marrat, 1871" cited as a synonym of *O. miniacea* (Röding, 1798) in P. & S. (1986:

94) is both a misspelling and a misquotation. The original description and figures of *O. masaris* Duclos, 1835 as well as the locality ("Habite les mers de la Chine") correspond to specimens from the intergradation zone between *O. miniacea* s.s. and *O. miniacea tremulina* (see § 4.7). It is thus best to consider *O. masaris* Duclos, 1835 as a **subjective junior synonym** of *O. miniacea* (Röding, 1798).

O. azemula Duclos, 1840 (Hist. Nat., Pl. 14, Figs. 1, 2; description in Illustr. Conch., p. 17, a text referring to Pl. 15, Figs. 1, 2, 10, 11 and also to Pl. 14, Fig. 7, a figure bearing the caption *O. erythrostoma*). The type lot is a heterogeneous. 3 of the syntypes (see PL. 2, FIG. 7) are *O. ponderosa* Duclos, 1840, 2 are *O. miniacea* (Röding, 1798) (see PL. 2, FIG. 1) and one is *O. miniacea tremulina* Lamarck, 1811 (see PL. 3, FIG. 1). The taxon *O. azemula* Duclos was a mixture of *O. ponderosa* Duclos, 1840 and *O. miniacea* (Röding, 1798) for DAUTZENBERG (1927) and B. & B. (1967), was *O. miniacea* (Röding, 1798) for B. & B. (1967) and W. & A. (1967); a colour form of *O. miniacea* (Röding, 1798) for P. & S. (1986).

O. sylvia Duclos, 1845. There is no type material available for this taxon, considered as a form of *O. miniacea* (Röding, 1798) by B. & B. (1960, 1967), Z. & P. (1969), W. & A. (1967) and P. & S. (1986). This cannot be a colour form, because the author described it as occurring in various colourations (all white, all black, etc.). Duclos' good colour plates and his description (aperture "*de couleur aurore ou souci*") indicate that *O. sylvia* Duclos, 1845 should be considered as a **subjective junior synonym** of *O. miniacea* (Röding, 1798).

O. magnifica Ducros de St. Germain, 1857. The holotype (see PL. 2, FIG. 4) leaves no doubt that this is a **subjective junior synonym** of *O. miniacea* (Röding, 1798), as for B. & B. (1960), Z. & P. (1969), W. & A. (1967) and P. & S. (1986).

O. porphyritica Marrat, 1870 (authorship is correct, since the previous *porphyritica* of Martini is in a rejected work) was *O. miniacea* var. *johnsoni* Higgins, 1919 for B. & B. (1960) and *O. miniacea* (Röding, 1798) for Z. & P. (1969), W. & A. (1967) and P. & S. (1986). Marrat's description ("Quam *O. tremulinae* magis acuminatâ, variè picta; aperturâ intus aurantiâ") and his figures leave no doubt that this is a **subjective junior synonym** of *O. miniacea* (Röding, 1798).

O. lamberti Jousseaume, 1884. Examination of the holotype (PL. 2, FIG. 3, from New

Caledonia) leaves no doubt that this is a **subjective junior synonym** of *O. miniacea*. This was a valid species for W. & A. (1967), a subspecies of *O. miniacea* for P. & S. (1986).

O. sericea var. *miniacea* Johnson, 1910. The description "aperture a bright red" in JOHNSON (1910: 51) leaves no doubt that *O. sericea*; Johnson (not Röding, 1798) var. *miniacea* Johnson, 1910 is the same as *O. miniacea* (Röding, 1798).

O. sericea var. *marrati* Johnson, 1910. JOHNSON (1910: 51 and 1915: 97) states that this name applies to "the dark brown red-mouthed form as figured by Marrat (*Thesaurus Conch.* pl. 7, f. 109)", which clearly depicts a very dark *O. miniacea* (Röding, 1798). One can thus consider *O. sericea*; Johnson (not Röding, 1798) var. *marrati* Johnson, 1910 as a **colour form** of *O. miniacea* (Röding, 1798), as for B. & B. (1960, 1967), Z. & P. (1969), W. & A. (1967) and P. & S. (1986). This is entirely confirmed by examination of the tree syntypes at ANSP.

O. sericea var. *johnsoni* Higgins, 1919. The original description states this is the shell represented by Marrat in Pl. 7, Fig. 110 of the *Thesaurus*. This shell (with the caption *O. porphyritica*, see here above) is a somewhat dark specimen of *O. miniacea* (Röding, 1798), of which *Oliva sericea*; Higgins (not Röding, 1798) var. *johnsoni* Higgins, 1919 is a **subjective junior synonym**. This is in agreement with B. & B. (1960), Z. & P. (1969), W. & A. (1967). It is a colour form for P. & S. (1986).

O. erythrostoma var. *efasciata* Dautzenberg, 1927. This name was given by DAUTZENBERG (1927: 39) to "the part of *O. azemula* Duclos, 1840 (q.v.) which is not *O. ponderosa* Duclos, 1840". It was a synonym of *O. miniacea* (Röding, 1798) for B. & B. (1960), a form of the same for B. & B. (1967), Z. & P. (1969), W. & A. (1967) and a subspecies for P. & S. (1986). No type specimen was designated, and no specimen with such label could be found in the Dautzenberg collection (now at IRSNB). Study of the collection leaves no doubt on the author's concept of *O. erythrostoma* and it follows that the variety *efasciata* Dautzenberg, 1927 is a **colour form** of *O. miniacea* (Röding, 1798).

O. erythrostoma var. *saturata* Dautzenberg, 1927. No type specimen was designated, but examination of Dautzenberg's specimens (now at IRSNB) leaves no doubt (see PL. 2, FIG. 5) that this is a **colour form** of *O. miniacea* (Röding, 1798), as for B. & B. (1960, 1967), Z.

& P. (1969), W. & A. (1967) and P. & S. (1986).

O. berti Terzer, 1986. This taxon (Paratype 1 is figured PL. 2, FIG. 2) is based upon very small (about 30 mm) specimens of *O. miniacea* (Röding, 1798) from Kwajalein, Marshall Islands. In this locality, the size reached by "adult" (thick lipped) specimens is extremely variable. We have examined a large, homogeneous syntopic series including specimens up to 87.67 mm and were unable to find any reliable discriminant character. *Oliva berti* Terzer, 1986, the remarkable dwarf variant occurring in Micronesia, is a **local form** of *O. miniacea* (Röding, 1798). The author (*personal communication*) now agrees with this disposition.

The following names have been mistakenly considered as synonyms or constitute errors in identification:

O. sericea (Röding, 1798) (q.v.). This **valid species** (q.v.) was a form of *O. miniacea* (Röding, 1798) for JOHNSON (1910).

O. tremulina Lamarck, 1811 (q.v.). This was a form of *O. miniacea* (Röding, 1798) for JOHNSON (1910). We now treat it as a **subspecies** (see below). It is most probably the same as "*tremulina* Duclos, 1835" cited by B. & B. (1960) and W. & A. (1967) as a synonym of *O. miniacea* (Röding, 1798). DUCLOS, who was familiar with Lamarck's specimens (see GREIFENEDER, DUCHAMPS & TURSCH, 1995), after stating "*ore pallido*" in his Latin diagnosis of *O. tremulina* Lamarck, 1811, describes it as having a very variable aperture colouration: "*J'ai des individus qui l'ont blanche; d'autres l'ont chamois, mauve, violette, bleue; enfin une dernière qui l'a d'une teinte qui peut rivaliser la plus belle feuille de rose*" (DUCLOS 1840: 17). This is probably the cause of the confusion. The problem is unimportant: as expected, there is an intergradation zone between the two subspecies, where individuals of intermediate hues do occur.

O. titea Duclos, 1845 (DUCLOS in Chenu, p.20, Pl. 36, Figs. 3, 4) is a small (15 mm), white American fossil (possibly an *Olivella* ?) from the Walnut Hills, near Vicksburgh. It is indeterminate for W. & A. (1967). Why P. & S. (1986: 95) consider this minute American fossil as being the white colour form of *O. miniacea* (Röding, 1798) is not clear to us.

O. sericea var. *zeilanica* Johnson, 1910 was *O. miniacea* (Röding, 1798) for B. & B. (1960), W. & A. (1967) and P. & S. (1986). The spire in the adult shell is said by JOHNSON (1910: 51)

to be "covered with a callus". The author also states that "it merges into ... the var. *ornata* Marr." This indicates that the name *O. sericea*; Johnson (not Röding, 1798), 1910 var. *zeilanica*; Johnson (not Lamarck, 1811), 1910 is a **subjective junior synonym** of *O. irisans* Lamarck, 1811. (for this name, see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. miniacea*:

Shell up to about 90 mm. Aperture orange to orange beige (+++). Lower part of columella often diffused with same colour as the aperture (++), not characteristic. In old specimens posterior parietal callus variable, but most often at level with the filament channel of previous whorl.

Spire. Profile of spire whorls: variable, mostly straight, not convex (++).

Body whorl. Subchannel markings: oblique linear or chevron markings, very variable in number (6 to 23), colour and shape. Background colour very variable: cream, beige to apricot. Shoulder zone: thin band with reduced pattern. Body whorl pattern: very variable. In many populations the grey brown vertical pattern elements are often foreshadowed by adjacent, parallel orange forerunners. Occasional specimens partly or completely overlaid with dark brown, black or orange.

Suprafasciolar band: upper zone with pattern lacking or very reduced; lower zone with many different patterns, rarely coalescent (see PL. 5, FIGS. 17-20). Width of fasciolar band very narrow (mean: 6.0% of lip length) (+++).

DISTRIBUTION.

Very large distribution in the Western Pacific. East to Samoa, North to Okinawa and Marshall Is., West to Indonesia and Gulf of Thailand, South to Queensland.

Oliva miniacea flammeacolor

Petuch & Sargent, 1986.

Oliva (Miniaceoliva) tremulina flammeacolor

Petuch & Sargent, 1986: 100, Pl. 15, Figs. 5-7.

TYPE MATERIAL.

Holotype in USNM, n° 841458 (figured PL. 2, FIG. 6). Paratype n° C153546 at AMS.

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are

useful for recognising *O. miniacea flammeacolor*:

Shell up to about 90 mm, often light for its size. Aperture greyish-beige inside. Margin of lip apricot to dull orange(+++). Lower part of columella apricot to dull orange (+++), often with smoky grey at upper margin of fasciole (++). In old specimens, posterior parietal callus mostly below channel of previous whorl.

Spire. Profile of spire whorls: variable, mostly concave, not convex (++). Strokes on spire whorls generally darker than in *O. miniacea tremulina* (++).

Body whorl. Subchannel markings: 10 to 18 very variable markings, often with complex structure. Background colour: pale to vivid apricot (+++). Shoulder zone: thin band with reduced pattern. Body whorl pattern: less variable and darker than in *O. miniacea tremulina* (++). Very occasional specimens partly overlaid with black or dark brown.

Suprafasciolar band: upper zone with pattern lacking or very reduced; lower zone with "tiger pattern" of repeating very dark strokes, stronger than in *O. miniacea tremulina* (++) (see PL. 5, FIGS. 15,16). Fasciolar band very narrow (mean: 6.2% of lip length) (+++).

DISTRIBUTION.

South India, Sri Lanka, Maldives.

Oliva miniacea tremulina

Lamarck, 1811.

Oliva tremulina Lamarck, 1811: 310, sp. n° 5.

Oliva olympiadin Duclos, 1835: Pl. 12, Figs. 10-12.

Oliva azemula Duclos, 1840: Pl. 14, Figs. 1, 2. (*pars*).

Oliva nobilis Reeve, 1850: Pl. 2, Fig. 3.

Oliva concinna Marrat, 1870: 12, Pl. 7, Fig. 101, sp. 60 (*pars*).

Oliva tenebrosa Marrat, 1870: 13, Fig. 177, sp. n° 58*.

Oliva fumosa Marrat, 1871: 13, Fig. 119, sp. n° 58.

TYPE MATERIAL.

Oliva olympiadin Duclos, 1835: two figured syntypes at MNHN.

Oliva azemula Duclos, 1840: six syntypes at MNHN.

Oliva nobilis Reeve, 1850: type n° 1892.9.24.18 at BM(NH).

Oliva concinna Marrat, 1870: one (n° 101) of two figured syntypes, at MCM.

Oliva tenebrosa Marrat, 1870: holotype at MCM.

Oliva fumosa Marrat, 1871: holotype at MCM.

SYNONYMY.

For the validity of the name *O. tremulina* Lamarck, 1811, see GREIFENEDER, DUCHAMPS & TURSCH (1995). As discussed under *O. miniacea* s.s. (q.v.), "*O. tremulina* Duclos 1835", cited by B. & B. (1960) and W. & A. (1967) as a synonym of *O. miniacea* (Röding, 1798), is most probably the same.

The following names are synonyms:

O. olympiadin Duclos, 1835. This was a colour form of *O. pica* Lamarck, 1811 (which is a nomen dubium, see GREIFENEDER, DUCHAMPS & TURSCH, 1995) for P. & S. (1986), and *O. tremulina* Lamarck, 1811 (or a form of this) for B. & B. (1960), Z. & P. (1969) and W. & A. (1967). The latter considered "*O. olympiadin* Duclos, 1844" as being *O. fulgurator* (Röding, 1798), a very distinct Western Atlantic species. The two figured syntypes of *O. olympiadin* Duclos, 1835 (H: 69.0, D: 29.3 mm and H: 74.0, D: 33.8 mm, figured PL. 3, FIGS. 6, 7) are undoubtedly different colour forms of *O. miniacea tremulina* Lamarck, 1811, of which *O. olympiadin* Duclos, 1835 is a **subjective junior synonym**.

O. azemula Duclos, 1840 (*pars*). One of the six syntypes at MNHN (H: 60.0, D: 27.2 mm, figured PL. 3, FIG. 1) is undoubtedly *O. miniacea tremulina* Lamarck, 1811.

O. nobilis Reeve, 1850. This was *O. tremulina* Lamarck, 1811 for B. & B. (1960, 1967), Z. & P. (1969), W. & A. (1967) and P. & S. (1986). The type, at BM(NH) (H 63.2, D 27.6 mm, figured PL. 3, FIG. 2) is undoubtedly a colour form of *O. miniacea tremulina* Lamarck, 1811, of which *O. nobilis* Reeve, 1850 is a **subjective junior synonym**. Two other syntypes figured by Reeve (Figs. 4b, 4c, from the Steere and Cole collections) were not located.

O. concinna Marrat, 1870. This **valid species** was a form of *O. tremulina* Lamarck, 1811 for TOMLIN (in FORD, 1953), B. & B. (1967), Z. & P. (1969), W. & A. (1967). This is true for one of the figured specimens, n° 101 (H: 44.2, D: 17.8 mm, illustrated PL. 3, FIG. 4) of the heterogeneous type lot (see discussion under *O. concinna* Marrat, 1870).

O. tenebrosa Marrat, 1870 (Thesaurus, p. 13, Fig. 177, sp. n° 58, locality "Borneo" very doubtful) was a synonym of *O. concinna* Marrat for W. & A. (1967). The holotype (H: 66.5, D: 27.0 mm, figured PL. 3, FIG. 5) is just a dark specimen of *O. miniacea tremulina* Lamarck,

1811, of which *O. tenebrosa* Marrat, 1870 is a **subjective junior synonym**, as correctly stated by B. & B. (1960) and Z. & P. (1969). In any case, *O. tenebrosa* Marrat, 1870 is a junior homonym of *O. tenebrosa* Wood, 1828, itself a junior synonym of *O. undatella* Lamarck, 1811, as for B. & B. (1960), Z. & P. (1969), KEEN (1971), W. & A. (1967) and P. & S. (1986). *O. tenebrosa*; Petuch & Sargent (not Marrat, 1870), 1986 is a colour form of *O. elegans* Lamarck, 1811.

O. fumosa Marrat, 1871. The holotype (H: 73.0, D: 31.3 mm, figured PL. 3, FIG. 3), probably from the S.W. Indian Ocean, is undoubtedly *O. tremulina* Lamarck, 1811, of which *O. fumosa* Marrat, 1871 is a **subjective junior synonym**, as correctly stated by TOMLIN (in FORD, 1953), B. & B. (1960), Z. & P. (1969) and W. & A. (1967).

The following names have been mistakenly considered as synonyms or constitute errors in identification:

O. hepatica Lamarck, 1811 (Ann. Mus.: 320, sp. n° 35) was a synonym of *O. tremulina* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), W. & A. (1967) and P. & S. (1986). This was already the interpretation of DUCLOS (1840: 17). *O. hepatica* Lamarck, 1811 is a **nomen dubium** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

Oliva pica Lamarck, 1811 was a synonym of *O. tremulina* Lamarck, 1811 for B. & B. (1960), a probable form of the same for Z. & P. (1969) and a valid species for P. & S. (1986). This is also a **nomen dubium** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

O. zeilanica Lamarck, 1811 was *O. tremulina* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969) and W. & A. (1967). It has been shown to be a **nomen dubium** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

O. sericea var. *zeilanica* Johnson, 1910. The description refers to a "smaller race quite readily separated in the adult but completely connected with *tremulina* in younger specimens." See *zeilanica* under *O. miniacea*.

O. obtusaria Lamarck, 1822 was a synonym of *O. tremulina* Lamarck, 1811 for B. & B. (1960), W. & A. (1967) and P. & S. (1986) and was impossible to identify for B. & B. (1967). This is again a **nomen dubium** (see GREIFENEDER, DUCHAMPS & TURSCH, 1995).

O. masaris Duclos, 1835 (*pars*) was *O. tremulina* Lamarck, 1811 for B. & B. (1967). This, together with the misspelling "*O.*

messaris" has been discussed under *O. miniacea* s.s (q.v.).

"*O. irisans* Duclos, 1835" was possibly (*in pars*) *O. tremulina*; Zeigler & Porreca (non Lamarck, 1811), 1969 forma *chrysoides* Dautzenberg, 1927 for Z. & P. (1969), and *O. cryptospira* Ford, 1891 for B. & B. (1960). "*O. irisans* Duclos, 1835" is the same as *O. irisans* Lamarck, 1811, a valid species (see GREIFENEDER, DUCHAMPS & TURSCH, 1995). From the original illustrations of FORD (1891: p. 136, Figs. 3, 4) it is clear that *O. cryptospira* Ford, 1891 is *O. irisans* Lamarck, 1811.

O. hirasei Kira, 1959 was listed as a possible synonym of *O. tremulina* Lamarck, 1811 by B. & B. (1960). That it constitutes a separate, valid species is clear from the evidence presented in section 4.2.

O. tremulina forma *oldi* Zeigler, 1969 was a form of *O. tremulina* Lamarck, 1811 for Z. & P. (1969) and W. & A. (1967). *O. tremulina*; Zeigler (not Lamarck, 1811), 1969 forma *oldi* Zeigler, 1969 has been discussed under *O. concinna* Marrat, 1870 (q.v.), where it belongs.

O. tremulina var. *chrysoides* Dautzenberg, 1927. The case of *O. tremulina*; Dautzenberg (not Lamarck, 1811), 1927 var. *chrysoides* Dautzenberg, 1927 has also been discussed under *O. concinna* Marrat (q.v.), 1870, where it belongs.

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. miniacea tremulina*:

Shell up to about 90 mm. Aperture white to bluish and cream (+++). Lower part of columella cream, to faint smoky (++). In old specimens, posterior parietal callus mostly below filament channel of previous whorl.

Spire. Profile of spire whorls: variable, mostly concave, not convex (++).

Body whorl. Subchannel markings: 10 to 18 very variable markings, often with complex structure. Background colour: generally cream to beige (+++). Shoulder zone: thin band with reduced pattern. Body whorl pattern: very variable. Occasional specimens partly or completely overlaid with black or dark brown.

Suprafasciolar band: upper zone with pattern lacking or very reduced; lower zone with "tiger pattern" of repeating dark strokes (++) (see PL. 5, FIGS. 13, 14). Fasciolar band very narrow (mean: 5.6% of lip length).

Note: As it could be expected, intergrades between the subspecies *O. miniacea tremulina* and the typical *O. miniacea* are found at the

common border of their distribution zones, along the Indonesian arc.

DISTRIBUTION:

Madagascar, Mauritius, Mozambique, Reunion, Seychelles, Tanzania.

Oliva ponderosa Duclos, 1840

Oliva ponderosa Duclos, 1840: Pl. 13, Figs. 8, 9.

Oliva azemula Duclos, 1840: Pl. 14, Figs. 1, 2. (*pars*).

TYPE MATERIAL:

Oliva ponderosa Duclos, 1840: 9 syntypes at MNHN (Figured syntype, H: 57.3, D: 30.8 mm, illustrated PL. 2, FIG. 8).

Oliva azemula Duclos, 1840: 6 syntypes at MNHN.

SYNONYMY.

O. azemula Duclos, 1840 (*pars*). Three of the six syntypes (one of these, H: 59.9, D: 28.9 mm, is figured PL. 2, FIG. 7) are undoubtedly *O. ponderosa* Duclos. For the others, see *O. azemula* Duclos, 1840 under *O. miniacea* (Röding, 1798).

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. ponderosa*:

Shell up to about 70 mm. Large specimens very heavy. Aperture pale pink or pale orange (+++).

Spire. Profile of spire whorls: mostly straight (++). In old specimens, posterior parietal callus mostly below, not above channel of previous whorl.

Body whorl. Subchannel markings: 9 to 12 faint purplish, oblique linear or chevron markings. Background colour light cream. Shoulder zone: thin band with reduced pattern. Body whorl pattern: Light brown to greyish-purple markings arranged more or less vertically. Spiral darker bands mostly insignificant. Overlay with dark layers not observed.

Suprafasciolar band: upper zone with pattern lacking or very reduced; lower zone with repeating strokes "tiger pattern" of same colour as body whorl pattern, no very dark dots (see PL. 5, FIGS. 5, 6). Upper margin of white fasciole (just below posterior fasciolar groove) often tinged violet (++).

DISTRIBUTION.

Thought to be restricted to the Maldives region. Specimens very similar to *O. ponderosa* Duclos, 1840 (and possibly this species) have been reported from Pulau Mendjangan, Bali, Indonesia by WITTIG-SKINNER (1981).

***Oliva sericea* (Röding, 1798).**

Porphyria sericea Röding, 1798: 33, sp. n° 390.

O. granitella Lamarck, 1811: 314, sp. n° 18.

Oliva textilina Lamarck, 1811: 309, sp. n° 2.

Oliva galeola Duclos, 1840: 30, Pl. 28, Figs. 4-6.

Oliva sabulosa Marrat, 1868 (2): 213.

O. textilina var. *albina* Melvill & Standen, 1897: 304.

TYPE MATERIAL.

Oliva galeola Duclos, 1840: three syntypes at MNHN.

Oliva sabulosa Marrat, 1868: two syntypes at MCM.

SYNONYMY.

For the validity of the name *O. sericea* (Röding, 1798), see TURSCH, DUCHAMPS & GREIFENEDER (1994). For the historical confusion around this name, see Introduction.

The following names are synonyms:

O. textilina Lamarck, 1811, a name still considered valid by Z. & P. (1969), is an **objective junior synonym** of *O. sericea* (Röding, 1798), both species being based upon the same figure of Martini (see GREIFENEDER, DUCHAMPS & TURSCH, 1995). This is in agreement with W. & A. (1967) and P. & S. (1986).

O. galeola Duclos, 1840. This was *O. funebris* Lamarck, 1811 (a nomen dubium, see GREIFENEDER, DUCHAMPS & TURSCH, 1995) for B. & B. (1960), Z. & P. (1969) and W. & A. (1967). Of the three syntypes of *O. galeola* Duclos, 1840 at MNHN, two are juvenile *O. sericea* (Röding, 1798) (one of these, H: 28.8, D: 13.8 mm, is figured in PL. 3, FIG. 8). The third specimen (possibly adventitious, as DUCLOS, 1840: 30 describes his species as "*l'ouverture est blanche*") is *O. reticulata* (Röding, 1798). *O. galeola* Duclos, 1840 is thus a **subjective junior synonym** of *O. sericea* (Röding, 1798). *O. galeola*; Petuch & Sargent (not Duclos, 1840), 1986 is represented (Pl. 6, Figs. 16, 17) by an entirely different shell, possibly *O. dactyliola* Duclos, 1840. As for *O. galeola*; Petuch & Sargent (not Duclos, 1840), 1986 color form *lutea*; Petuch & Sargent (not

Marrat, 1871), 1986 (Pl. 6, Figs. 21, 22), this is yet another, entirely different shell, possibly *O. elegans* Lamarck, 1811.

O. sabulosa Marrat, 1868. The type material (one of the two syntypes, H: 52.0, D: 22.0 mm is figured PL. 3, FIG. 9) shows that this is undoubtedly a **subjective junior synonym** of *O. sericea* (Röding, 1798), as for WILKINS (in FORD, 1953), B. & B. (1967), Z. & P. (1969), W. & A. (1967) and P. & S. (1986). MARRAT himself was probably aware of this, as the name is not cited any more in the *Thesaurus*.

O. textilina var. *albina* Melvill & Standen, 1897. The very short description clearly indicates that this is a **subjective junior synonym** of *O. sericea* (Röding, 1798). This was *O. textilina* for B. & B. (1960), a variety of *O. textilina* for Z. & P. (1969), a form of *O. sericea* for B. & B. (1967) and W. & A. (1967).

O. granitella Lamarck, 1811. This is a **subjective junior synonym** of *O. sericea* (Röding, 1798) (see GREIFENEDER, DUCHAMPS & TURSCH, 1995), as for B. & B. (1967), W. & A. (1967) and P. & S. (1986). It was *O. textilina* Lamarck, 1811 for B. & B. (1960) and Z. & P. (1969).

The following names have been mistakenly considered as synonyms or constitute errors in identification:

O. sericea var. *miniacea* Johnson, 1910. The case of *O. sericea*; Johnson (not Röding, 1798), 1910 var. *miniacea* Johnson, 1910 has been discussed under *O. miniacea* (Röding, 1798) (*q.v.*), where it belongs.

O. sericea var. *fordi* Johnson, 1910: 51. Under his variety *zeilanica* Lamarck, 1822 (a nomen dubium, see GREIFENEDER, DUCHAMPS & TURSCH, 1995), JOHNSON created a new variety *fordi* (a variety of a variety!). It was defined as the dark brown form of *O. cryptospira* Ford, 1891, resembling *O. tenebrosa*; Johnson (not Marrat, 1870), 1910. This is the shell figured by MARRAT on Pl. 9, Fig. 126 in the *Thesaurus* with the correct caption *O. irisans* Lamarck, 1811. Therefore *O. sericea*; Johnson (not Röding, 1798), 1910 var. *fordi* Johnson, 1910 is expected to be a **colour form** of *O. irisans* Lamarck, 1811. This was also the conclusion of P. & S. (1986) and it is entirely confirmed by examination of the type specimen of *O. sericea* var. *fordi* Johnson, 1910. It was a form of *O. lignaria* Marrat, 1868 for B. & B. (1967), Z. & P. (1969) and W. & A. (1967). The "var. *fordii* Johnson" is a misspelling in JOHNSON (1915: 98).

O. sericea var. ***marrati*** Johnson, 1910. The case of *O. sericea*; Johnson (not Röding, 1798), 1910 var. *marrati* Johnson, 1910 has been discussed under *O. miniacea* (Röding, 1798), where it belongs.

O. sericea var. ***johnsoni*** Higgins, 1919. The case of *O. sericea*; Higgins (not Röding, 1798), 1919 var. *johnsoni* Higgins, 1919 has also been discussed under *O. miniacea* (Röding, 1798) (*q.v.*), where it belongs.

O. sericea var. ***albescens*** Johnson, 1915. This was described as a form of *Oliva sericea* (*sensu* Johnson, 1915) var. *cryptospira* Ford, 1891. *Oliva sericea* (*sensu* Johnson, 1915) is a mixture of many taxa, but the one line description: "There is also a pure white, callous-spined form (*albescens*)" fortunately leaves no doubt that *O. sericea*; Johnson (not Röding, 1798), 1915 var. *cryptospira* Ford, 1891 forma *albescens* Johnson, 1915 is a colour form of *O. irisans* Lamarck, 1811, as correctly deduced by P. & S. (1986) and confirmed by examination of the type specimens of *O. cryptospira* Ford, 1891 and *O. sericea albescens* Johnson, 1915, both at ANSP. This was *O. textilina* Lamarck, 1811 for B. & B. (1960), and a form of *O. lignaria* Marrat, 1868 for B. & B. (1967) and W. & A. (1967).

DIAGNOSIS.

In addition to the numerical discriminants reported in Table 1, the following features are useful for recognising *O. sericea*:

Shell up to 90 mm, quite thick and heavy (++). Aperture creamy-beige (+++). Faint smoky diffusion on fasciole. In old specimens, callus at upper end of pillar above channel of previous whorl (+++).

Spire. Profile of spire whorls: convex (+++). First postnuclear whorls fused (filament channel filled with glassy material) (++).

Body whorl. Subchannel markings: numerous fine, short oblique linear or chevrons markings. Background colour: cream. Shoulder zone: upper band of body whorl pattern reaching or nearly reaching subchannel pattern (+++). Body whorl pattern: very fine network of grey-brown lines, often finely punctulate. Overlay with dark layers not observed.

Suprafasciolar band: upper zone with irregular mottlings (++); lower zone with irregular "tiger pattern" (++) (see PL. 5, FIGS. 7, 8).

DISTRIBUTION.

Sri Lanka, Fiji, Samoa, Solomons, Papua New Guinea, Maldives, Philippines, Indonesia, Taiwan, Okinawa, Vietnam, Queensland.

Index to names. (valid taxa in bold).

albescens Johnson, 1915: colour form of *O.*

irisans Lamarck, 1811.

albina Melvill & Standen, 1897: subjective junior synonym of *O. sericea* (Röding, 1798).

atalina Duclos, 1835: valid species.

aurantiaca Schumacher, 1817: objective junior synonym of *O. miniacea* (Röding, 1798).

azemula Duclos, 1840 (*pars*): subjective junior synonym of *O. miniacea* (Röding, 1798).

azemula Duclos, 1840 (*pars*): subjective junior synonym of *O. miniacea tremulina* Lamarck, 1811.

azemula Duclos, 1840 (*pars*): subjective junior synonym of *O. ponderosa* Duclos, 1840.

berti Terzer, 1986: local form of *O. miniacea* (Röding, 1798).

caerulea (Röding, 1798): valid species.

chrysoides Dautzenberg, 1927: colour form of *O. concinna* Marrat, 1870.

concinna Marrat, 1870: valid species.

concinna Marrat, 1870 (*pars*): subjective junior synonym of *O. miniacea tremulina* Lamarck, 1811.

cryptospira Ford, 1891: subjective junior synonym of *O. irisans* Lamarck, 1811.

efasciata Dautzenberg, 1927: colour form of *O. miniacea* (Röding, 1798).

episcopalis Lamarck, 1811: subjective junior synonym of *O. caerulea* (Röding, 1798).

erythrostoma Lamarck, 1811: objective junior synonym of *O. miniacea* (Röding, 1798).

flammeacolor Petuch & Sargent, 1986:

subspecies of *O. miniacea* (Röding, 1798).

fordi Johnson, 1910: colour form of *O. irisans* Lamarck.

fordini Johnson, 1910: misspelling for *fordi* Johnson, 1910.

fulva Marrat, 1871: subjective junior synonym of *O. atalina* Duclos, 1835.

fumosa Marrat, 1871: subjective junior synonym of *O. miniacea tremulina* Lamarck, 1811.

fumosa; Zeigler & Porreca (not Marrat, 1871), 1969: subjective junior synonym of *O. hirasei* Kira.

fumosa; Petuch & Sargent (not Marrat, 1871), 1986: subjective junior synonym of *O. concinna* Marrat, 1870.

galeola Duclos, 1840: subjective junior synonym of *O. sericea* (Röding, 1798).

granitella Lamarck, 1811: subjective junior synonym of *O. sericea* (Röding, 1798).

hepatica Lamarck, 1811: nomen dubium.

hirasei Kira, 1959: valid species.

johnsoni Higgins, 1919: subjective junior synonym of *O. miniacea* (Röding, 1798).

kremerorum Petuch & Sargent, 1986: form of *O. concinna* Marrat, 1870.
lamerti Jousseume, 1884: subjective junior synonym of *O. miniacea* (Röding, 1798).
magnifica Ducros de St. Germain, 1857: subjective junior synonym of *O. miniacea* (Röding, 1798).
marrati Johnson, 1910: colour form of *O. miniacea* (Röding, 1798).
masaris Duclos, 1835: subjective junior synonym of *O. miniacea* (Röding, 1798).
mascarena n. sp. valid species.
mazaris, Duclos 1835: misspelling for *masaris*, Duclos, 1835.
messaris Marrat, 1871: misspelling and misquotation for *masaris*, Duclos, 1835.
miniacea (Röding, 1798): valid species.
miniata (Link, 1807): objective junior synonym of *O. miniacea* (Röding, 1798).
nobilis Reeve, 1850: subjective junior synonym of *O. miniacea tremulina* Lamarck, 1811.
O. obtusaria Lamarck, 1822: nomen dubium.
oldi Zeigler, 1969: colour form of *O. concinna* Marrat, 1870.
olympiadina Duclos, 1835: subjective junior synonym of *O. miniacea tremulina* Lamarck, 1811.
pica Lamarck, 1811: nomen dubium.
ponderosa Duclos, 1840: valid species.
porphyracea Perry, 1811: subjective junior synonym of *O. miniacea* (Röding, 1798).
porphyritica Marrat, 1870: subjective junior synonym of *O. miniacea* (Röding, 1798).
quersolina Duclos, 1835: subjective synonym of *O. atalina* Duclos, 1835.
sabulosa Marrat, 1868: subjective junior synonym of *O. sericea* (Röding, 1798).
saturata Dautzenberg, 1927: colour form of *O. miniacea* (Röding, 1798).
sericea (Röding, 1798): valid species.
soverbii Marrat, 1870: misspelling for *O. sowerbyi* Marrat, 1870.
sowerbyi Anton, 1839: small fossil from the Paris region, probably an *Ancilla*.
sowerbyi Ducros de Saint Germain, 1857 is an *Olivella*.
sowerbyi Marrat, 1870: subjective junior synonym of *O. atalina* Duclos, 1835.
stainforthi Reeve, 1850: subjective junior synonym of *O. atalina* Duclos, 1835.
stainforthii Reeve, 1850: misspelling for *O. stainforthi* Reeve, 1850.
sylvia Duclos, 1845: subjective junior synonym of *O. miniacea* (Röding, 1798).
tenebrosa Marrat, 1870: subjective junior synonym of *O. miniacea tremulina* Lamarck, 1811 and junior homonym of *O. tenebrosa* Wood, 1828.

tenebrosa Wood, 1828: subjective junior synonym of *O. undatella* Lamarck, 1811.
textilina Lamarck, 1811: objective junior synonym of *O. sericea* (Röding, 1798).
titea Duclos, 1845: small American fossil, possibly an *Olivella*.
tremulina Lamarck, 1811: subspecies of *O. miniacea* (Röding, 1798).
zeilanica Lamarck, 1811: nomen dubium.
zeilanica ; Johnson (not Lamarck, 1811), 1910: subjective junior synonym of *O. irisans* Lamarck, 1811.

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We are most grateful to Dr. Ph. BOUCHET and Dr. A. TILLIER (Muséum National d'Histoire Naturelle, Paris), Ms. K. WAY (The Natural History Museum, London), Dr. Dr. I. WALLACE, (Merseyside County Museum, Liverpool), Dr. M.G. HARASEWYCH and Ms. Raye N. GERMON [National Museum of Natural History (Smithsonian Institution), Washington], Dr. W. EMERSON (American Museum of Natural History, New York), Dr. G. ROSENBERG (Academy of Natural Sciences, Philadelphia), Dr. W.F. PONDER and Dr. I. LOCH (Australian Museum, Sydney) and Dr. J. VAN GOETHEM (Institut Royal des Sciences Naturelles de Belgique, Brussels) for allowing us to study type material and specimens from historical collections. We thank Mr. Gianluigi TERZER (Genoa, Italy) for the loan of paratypes of *O. berti* and Dr. F. PUYLAERT, Musée Royal de l'Afrique Centrale (Tervueren, Belgium) for loan of specimens. We are deeply indebted to Mme Eda COUACAUD (Quatre Bornes, Mauritius) for sharing most valuable observations on the *Oliva* fauna of the South-Western Indian Ocean; to Christian VAN OSSELAER for much help in discussions and in the first, exploratory measurements and to Mr. A. LIEVROUW (IRSNB) for his kind assistance. We are grateful to Geo BAYER (D-Munich), Manfred BLÖCHER (D-Duisburg), Oscar BOLL (D-Duisburg), Renate DÜNKEL (D-Köngerheim), Kapitän Felix LORENZ (D-Lauenburg), Jean-Marc OUIN (B-Brussels), Dr. Jacques SENDERS (B-Brussels), the late (and not forgotten) Renate Wittig SKINNER, Margrit WIDMER (CH-Würenlingen) for the loan or gift of samples. We are grateful to the Fonds National de la Recherche Scientifique (F.N.R.S.) and BIOTEC, S.A. for material assistance. We are much indebted to Dr. C. MASSIN (IRSNB) for his outstanding care in correcting our text.

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Plate 1 (opposite page).

Figs. 1-5. *Oliva atalina* Duclos, 1835.

1. *O. quersolina* Duclos, 1835. Syntype, MNHN (H: 36.5 mm, D: 16.2 mm).
2. *O. atalina* Duclos, 1835. Syntype, MNHN (H: 54 mm, D: 24.7 mm).
3. *O. fulva* Marrat, 1871. Holotype, MCM (H: 32.3 mm, D: 15.0 mm).
4. *O. sowerbyi* Marrat, 1870. Syntype, MCM (H: 32.2 mm, D: 15.0 mm).
5. *O. stainforthi* Reeve, 1850. Syntype, BM(NH) (H: 34.2 mm, D: 17.0 mm).

Figs. 6-9. *Oliva concinna* Marrat, 1870.

6. *O. tremulina* var. *chrysoides* Dautzenberg, 1927. Specimen from Dautzenberg collection (IRSNB) (H: 46.3 mm, D: 19.1 mm). No locality.
7. *O. concinna* Marrat, 1870. Figured syntype, MCM (H: 44.2 mm, D: 17.8 mm). Selected as lectotype.
8. *O. (Miniaceoliva) fumosa kremerorum* Petuch & Sargent, 1986. Holotype, USNM n° 841460. (H: 52.9 mm, D: 21.4 mm). near Zamboanga, Philippines.
9. *O. tremulina* forma *oldi* Zeigler, 1969. Holotype, AMNH n° 147750 (H: 56.6 mm, D: 24.7 mm). Buin, Bougainville, Solomon Is..

Figs. 10-11. *Oliva hirasei* Kira, 1959.

10. *O. hirasei* Kira, 1959. BT-4154, (H: 43.7 mm, D: 20.4mm), Calapan, Philippines.
11. *O. hirasei* Kira, 1959. BT-4150, (H: 49.4 mm, D: 22.6 mm), dredged off Kaoshiung, Taiwan, 1962.

Scale bars: 10 mm.

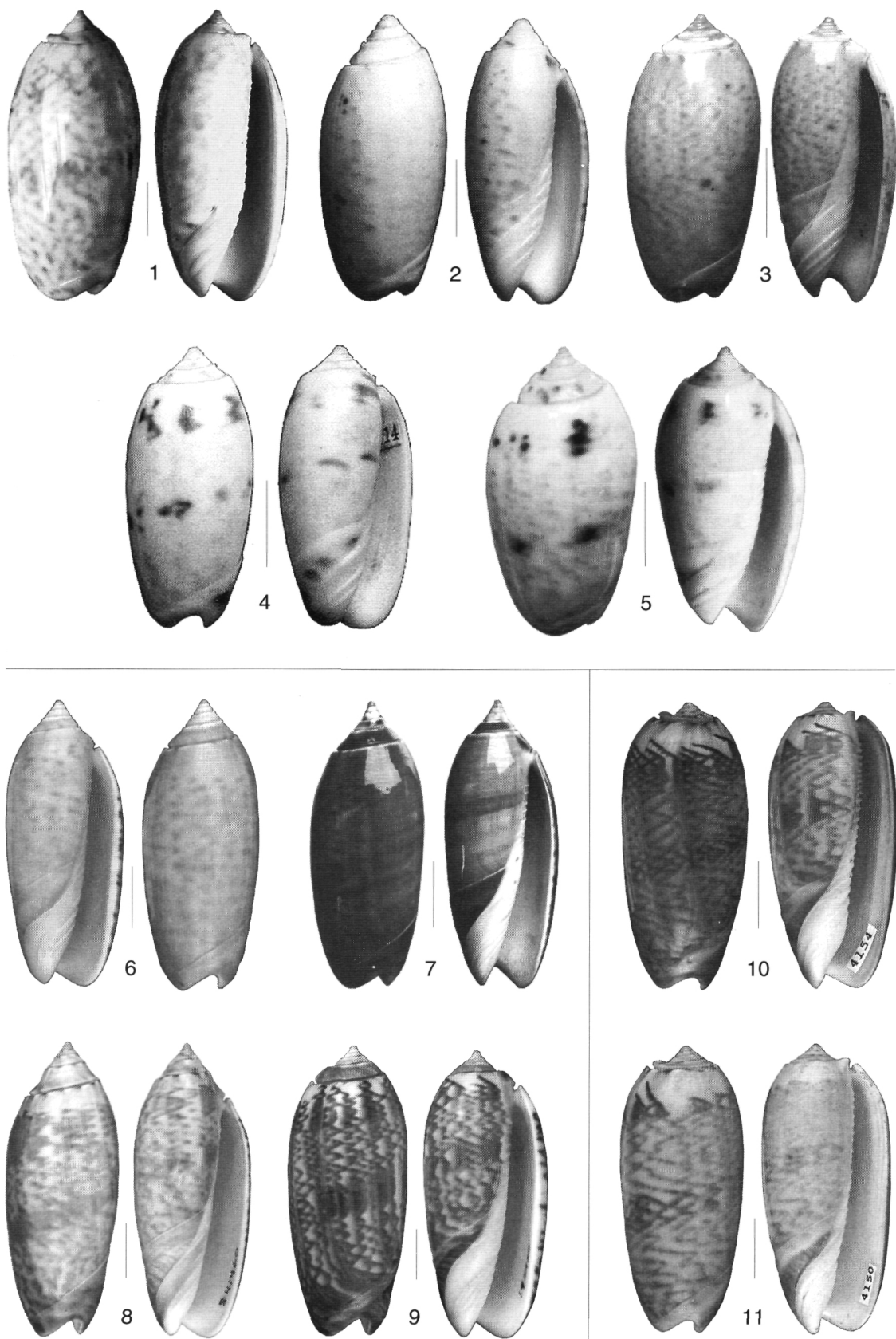


Plate 2 (opposite page).

Figs. 1-5. *Oliva miniacea* (Röding, 1798).

1. *O. azemula* Duclos, 1840. Syntype, MNHN (H: 65.8 mm, D: 31.7 mm).
2. *O. berti* Terzer, 1986. Paratype n° 1, Terzer collection (H: 29.8 mm, D: 12.4 mm). Kwajalein Atoll, Marshall Islands.
3. *O. lamberti* Jousseaume, 1884. Syntype, MNHN (H: 72.5 mm, D: 30.0 mm).
4. *O. magnifica* Ducros de St.Germain, 1857. Syntype, MNHN (H: 63.8 mm, D: 26.7 mm).
5. *O. miniacea* var. *saturata* Dautzenberg, 1927. Specimen from Dautzenberg collection (IRSNB) (H: 67.3 mm, D: 28.4 mm). New Caledonia.

Fig. 6. *Oliva miniacea flammeacolor* Petuch & Sargent, 1986.

6. *O. (Miniaceoliva) flammeacolor*, Petuch & Sargent, 1986. Holotype n° 841458, USNM (H: 67.1 mm, D: 29.1 mm).

Figs. 7-8. *Oliva ponderosa* Duclos, 1840.

7. *O. azemula* Duclos, 1840. Syntype, MNHN (H: 59.9 mm, D: 28.9 mm).
8. *O. ponderosa* Duclos, 1840. Figured syntype, MNHN (H: 57.3 mm, D: 30.8 mm).

Scale bars: 10 mm.

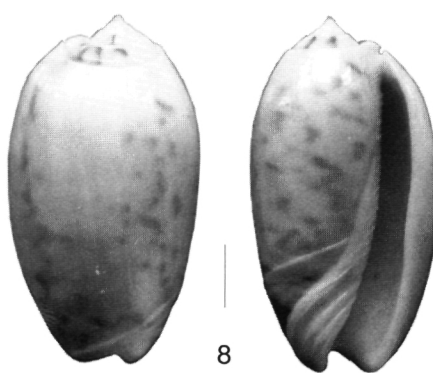
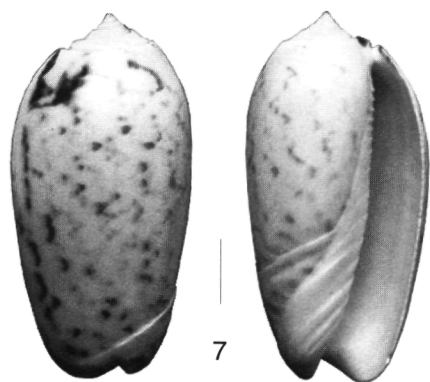
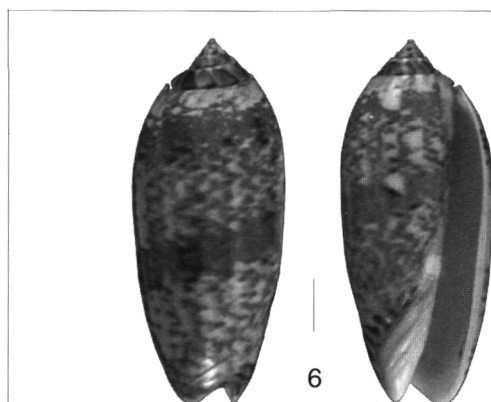
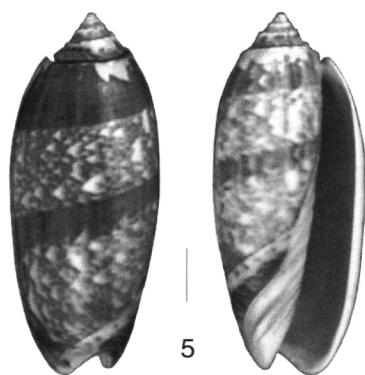
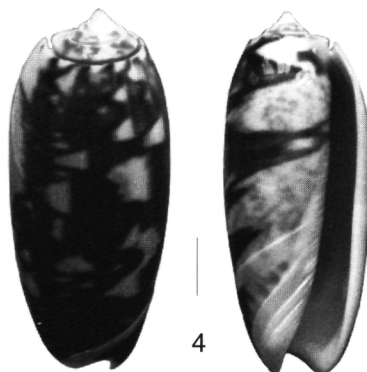
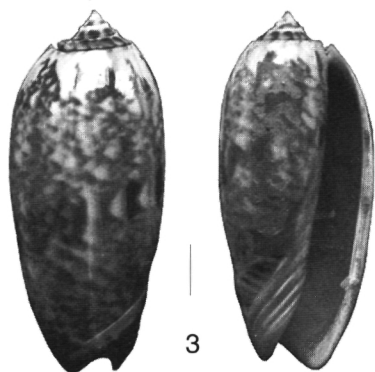
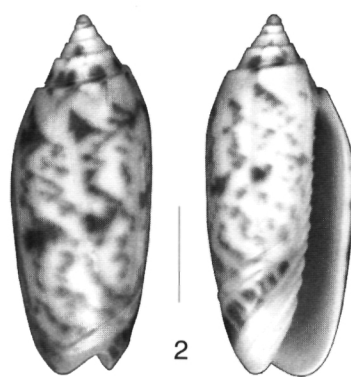
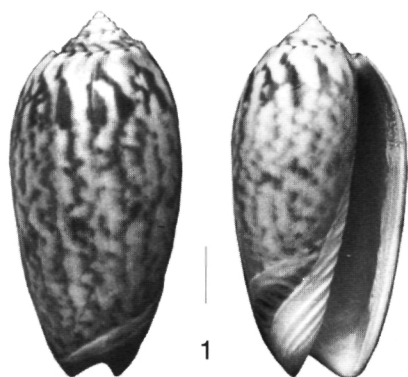


Plate 3 (opposite page).

Figs. 1-7. *Oliva miniacea tremulina* Lamarck, 1811.

1. *O. azemula* Duclos, 1840. Syntype, MNHN (H: 60.0 mm, D: 27.2 mm).
2. *O. nobilis* Reeve, 1850. Syntype, BM(NH) n° 1892.9.24.18 (H: 63.2 mm, D: 27.6 mm).
3. *O. fumosa* Marrat, 1871. Holotype, MCM (H: 73.0 mm, D: 31.3 mm).
4. *O. concinna* Marrat, 1870. Figured syntype, MCM (H: 44.2 mm, D: 17.8 mm).
5. *O. tenebrosa* Marrat, 1870. Holotype, MCM (H: 66.5 mm, D: 27.0 mm).
6. *O. olympiadinina* Duclos, 1835 . Figured syntype, MNHN (H: 74.0 mm, D: 33.8 mm).
7. *O. olympiadinina* Duclos, 1835 . Figured syntype, MNHN (H: 69.0 mm, D: 29.3 mm).

Figs. 8-9. *Oliva sericea* (Röding, 1798).

8. *O. galeola* Duclos, 1840 . Syntype, MNHN (H: 28.8 mm, D: 13.8 mm).
9. *O. sabulosa* Marrat, 1868. Syntype, MCM (H: 52.0 mm, D: 22.0 mm).

Scale bars: 10 mm.

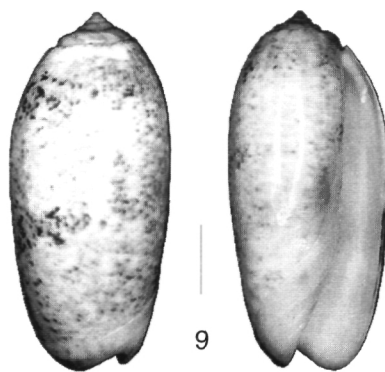
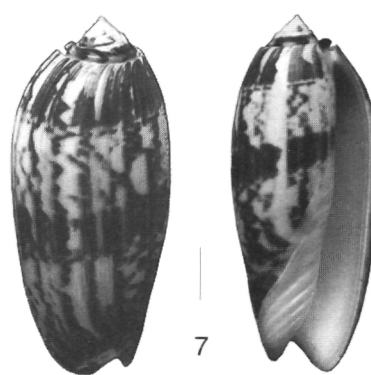
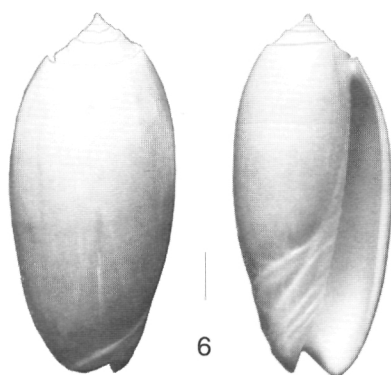
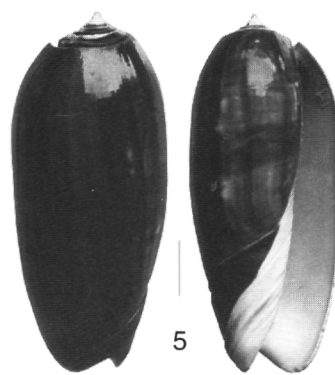
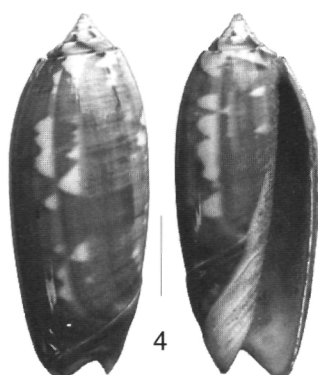
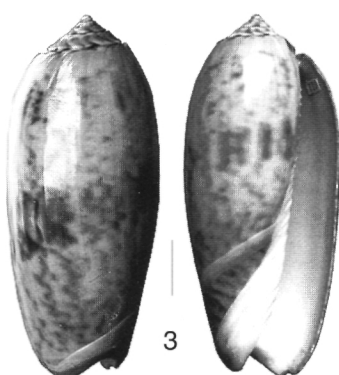
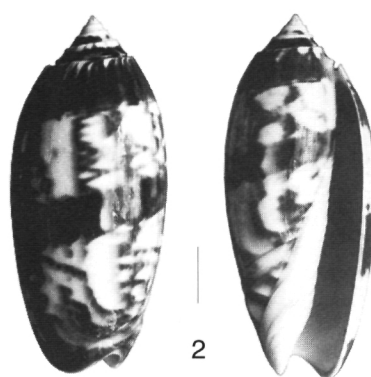
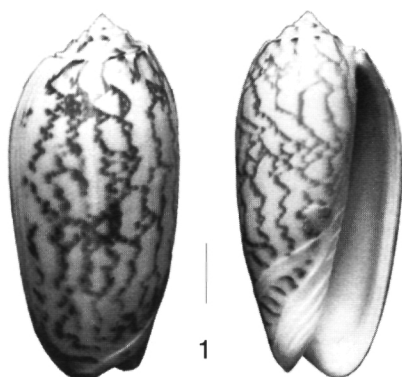
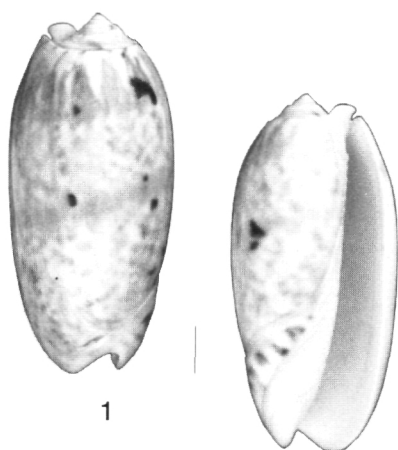


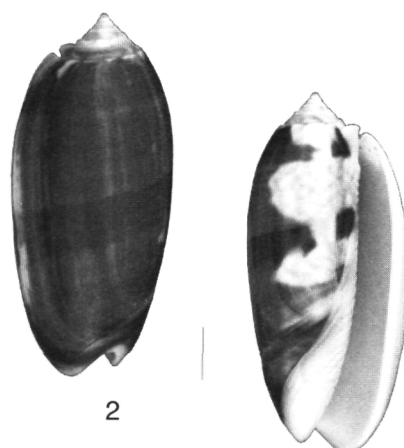
Plate 4 (opposite page).Figs. 1-6. *Oliva mascarena* n. sp.

1. *Oliva mascarena*, holotype, BM(NH) n° 1953.3.4.203 (H: 75.1 mm; D: 35.1 mm), from Winckworth collection, with old label "*O. pica*". Collected at Aldabra, June 1938.
2. *Oliva mascarena* n. sp., paratype 1, BM(NH) n° 1953.3.4.204, (H: 68.5 mm; D: 31.0 mm), from Winckworth collection, with old label "*O. pica*". Collected at Aldabra, June 1938.
3. *Oliva mascarena* n. sp., paratype 2, IRSNB, (H: 71.5 mm; D: 32.0 mm), ex coll. Dautzenberg, (with old label "*O. pica*, probably from Mauritius").
4. *Oliva mascarena* n. sp., paratype 3, MNHN, (H: 67.8; D: 32.0 mm), ex coll. D. Greifeneder n° DG-3921a, Seychelles.
5. *Oliva mascarena* n. sp., paratype 4, D. Greifeneder coll., n° DG-3076, (H: 59.8 mm; D: 27.3 mm), Peros Banhos, Chagos.
6. *Oliva mascarena* n. sp., paratype 5, B. Tursch coll., n° BT-4370, (H: 65.6 mm; D: 29.4 mm), dredged 15 m, Beau Vallon, Seychelles, 1973.

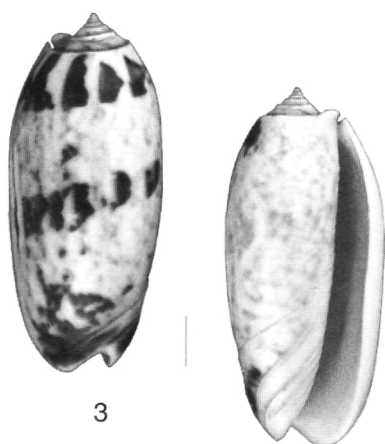
Scale bars: 10 mm.



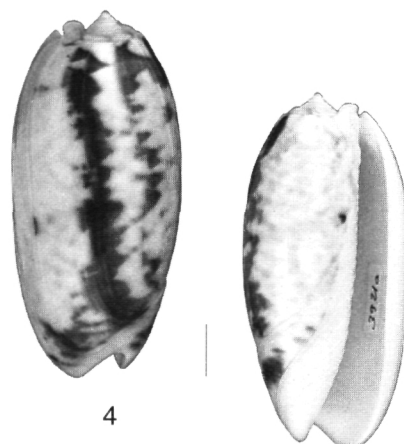
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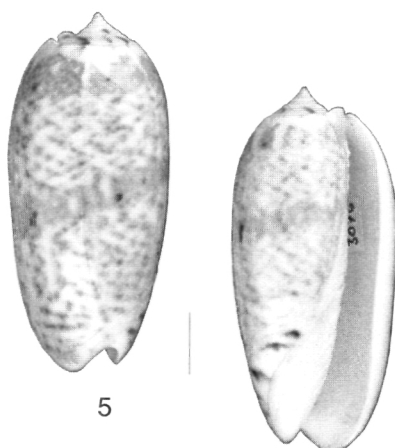
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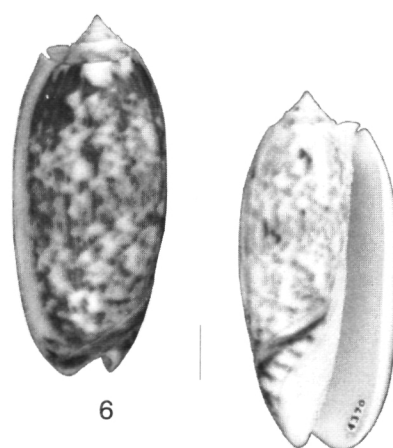
3



4



5



6

Plate 5 (opposite page).**Figs. 1-20. Patterns in the suprafasciolar zone.**

1. *O. atalina* Duclos, 1835, Mauritius.
2. *O. atalina* Duclos, 1835, Cargados.
3. *O. mascarena* n. sp., Seychelles.
4. *O. mascarena* n. sp., Mauritius.
5. *O. ponderosa* Duclos, 1840, Maldives.
6. *O. ponderosa* Duclos, 1840, Maldives.
7. *O. sericea* (Röding, 1798), Philippines.
8. *O. sericea* (Röding, 1798), Philippines.
9. *O. concinna* Marrat, 1870, New Caledonia.
10. *O. concinna* Marrat, 1870, New Britain.
11. *O. hirasei* Kira, 1959, Taiwan.
12. *O. hirasei* Kira, 1959, Philippines.
13. *O. miniacea tremulina* Lamarck, 1811.
14. *O. miniacea tremulina* Lamarck, 1811.
15. *O. miniacea flammeacolor* Petuch & Sargent, 1986, South India.
16. *O. miniacea flammeacolor* Petuch & Sargent, 1986, South India.
17. *O. miniacea* (Röding, 1798), Vietnam.
18. *O. miniacea* (Röding, 1798), Philippines.
19. *O. miniacea* (Röding, 1798), Philippines.
20. *O. miniacea* (Röding, 1798), Gilbert Is.



Plate 6 (opposite page).

Figs. 1-10. **Protoconchs**. (all figures at same scale).

1. *O. atalina* Duclos, 1835. Mauritius, DG-6180.
2. *O. concinna* Marrat, 1870. Philippines, BT-4342.
3. *O. hirasei* Kira, 1959. Philippines, BT-5025.
4. *O. mascarena* n. sp. Seychelles, BT-4368.
5. *O. miniacea* (Röding, 1798). Philippines, BT-5081.
6. *O. miniacea flammeacolor*, Petuch & Sargent, 1986. India, BT-0953.
7. *O. miniacea tremulina* Lamarck, 1811. Madagascar, BT-4710.
8. *O. ponderosa* Duclos, 1840. Maldives, BT-1953.
9. *O. sericea* (Röding, 1798). New Caledonia, BT-3341.
10. *O. sericea* (Röding, 1798). Bali, BT-0013.

