A puzzle of highly multiform species:
Oliva fulgurator Röding, 1798)
and related American taxa

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A puzzle of highly multiform species:
Oliva fulgurator (Röding, 1798) and related American taxa [1]

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ABSTRACT. The taxonomic status of the members of the Western Atlantic "*Oliva fulgurator-reticularis* complex", the Eastern Pacific "*Oliva spicata* complex" and of some related taxa is reviewed. *O. foxi* Stingley, 1984, *O. fulgurator* (Röding, 1798), *O. polpasta* Duclos, 1833, *O. scripta* Lamarck, 1811 and *O. spicata* (Röding, 1798) are shown to be distinct species. *O. spicata deynzerae* Petuch & Sargent, 1986 is a distinct subspecies. The available type material of many synonymous taxa has been studied and illustrated.

RÉSUMÉ. Le statut taxonomique des membres du "complexe *Oliva fulgurator-reticularis*" de l'Atlantique-Ouest, du "complexe *Oliva spicata*" du Pacifique-Est et de quelques espèces apparentées est revu. *O. foxi* Stingley, 1984, *O. fulgurator* (Röding, 1798), *O. polpasta* Duclos, 1833, *O. scripta* Lamarck, 1811 and *O. spicata* (Röding, 1798) sont démontrées être des espèces distinctes. *O. spicata deynzerae* Petuch & Sargent, 1986 est une sous-espèce distincte. Le matériel type accessible de nombreux taxa synonymes a été étudié et illustré.

1. INTRODUCTION

1.1. The problem

1.1.1. The number of species

Authors differ widely in opinion on the number of *Oliva* species in the Western Atlantic. ZEIGLER & PORRECA (1969) as well as ABBOTT (1974) admit the existence of four species [*Oliva fulgurator* (Röding, 1798), *O. reticularis* Lamarck, 1811, *O. sayana* Ravenel, 1834 and *O. scripta*, Lamarck, 1811]. PETUCH & SARGENT (1986) recognise no less than twenty-one species and ten subspecies.

Many Western Atlantic taxa share common characteristics and appear to be closely related, forming the "*O. reticularis* complex" of TURSCH & HUART (1990) (this shall here be called the "*O. fulgurator-reticularis* complex", for reasons that will become apparent in § 5.1). The numerous, controversial taxa erected for the members of this group are the elements of an old and intricate nomenclatural puzzle, possibly the best example of the notorious taxonomic chaos prevailing in the genus *Oliva*. With the exception of the new species described by PETUCH & SARGENT (1986) and by PETUCH (1987,1988,1990), not hitherto revised, nearly every Caribbean taxon of the complex has already been synonymised (this will be seen in the section Systematics). Only *O. fulgurator* and *O. reticularis* were generally considered to be distinct species. The existence, the nature and the difficulty of the problem raised by the "*O. fulgurator-reticularis*

complex" were already clearly grasped well over a century ago:

"*Oliva reticularis* is, without question, the most variable species in the genus and we warn conchologists that one should have access to a very rich, very abundant collection in order to understand the unions [of taxa] that we are suggesting . . . Let us repeat that such a work requires a considerable collection as well as extreme tenacity".

DUCROS DE SAINT GERMAIN (1857: 53)
(translation ours)

The subsequent naming of many vague and ill-defined forms only added to the confusion. The difficulties encountered in matching shells with names are familiar to every student of Caribbean *Oliva*.

In the Eastern Pacific, ZEIGLER and PORRECA (1969) recognise nine species, while PETUCH & SARGENT (1986) list twenty-one species (and six subspecies). The Eastern Pacific *Oliva* fauna is much richer in species than its Western Atlantic counterpart. It contains a few very distinct species [*O. porphyria* (L., 1758), *O. peruviana* Lamarck, 1811, *O. splendidula* Sowerby, 1825, *O. incrassata* (Lightfoot in Solander, 1786), *O. julieta* Duclos, 1840, *O. kaleontina* Duclos, 1835, *O. undatella* Lamarck, 1811, etc.) which are outstanding in aspect and pose no serious identification problem.

In addition, there is a large group of obviously cognate nominal taxa [the "*O. spicata* complex" based

upon *O. spicata* (Röding, 1798), see Tursch & Huart 1990]. This poses much the same problems as its Western Atlantic counterpart, the "*O. fulgurator-reticularis* complex".

1.1.2. The distribution of species

The geographical distribution of many named taxa in both the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" is poorly known. The limits of their variation are indeed so imprecise that correct identification is often possible only for material from type localities.

Further taxonomic complications arise because several cognate *Oliva* taxa of the two faunas (especially in the "*O. spicata* complex" and in the "*O. fulgurator-reticularis* complex") are quite similar in appearance. Early locality data are often questionable, and in several instances (see examples in Table 1) authors have considered a same taxon to have an Atlantic or a Pacific distribution.

Furthermore, some taxa such as *O. olorinella* Duclos, 1835 (*q.v.*) have been erected upon a mixture of Atlantic and Pacific shells.

1.1.3. Previous quantitative results.

Using morphometric analysis, Tursch & Huart (1990) demonstrated that the Atlantic *Oliva* specimens fall into four objective groups. One of these groups is the West African *O. flammulata* Lamarck, 1811. The three others live in the Western Atlantic: *O. scripta* Lamarck, 1811, *O. sayana* Ravenel, 1834 and a highly variable group then called the "*O. reticularis* complex" (now the "*O. fulgurator-reticularis* complex"). None of these groups could be split into smaller, objective units, although the complex contains very dissimilar populations. The only possible candidate for segregation was *O. oblonga* Marrat, 1870, of which only a small sample was available to us at the time, so that no definite conclusion could be drawn.

Most Eastern Pacific specimens were easily separated into the objective groups *O. porphyria, O. splendidula, O. kaleontina, O. undatella, O. polpasta* Duclos,1833 and a large, highly variable group called the "*O. spicata* complex". Further analysis tentatively separated only a sample of *O. polpasta* from a small allopatric sample of *O. kerstitchi* da Motta, 1985. The specific status of the latter was considered to be only a working hypothesis, awaiting further confirmation.

taxon	Eastern Pacific distribution for	Atlantic distribution for
O. brunnea Marrat, 1870	Burch & Burch (1960), Wagner & Abbott (1978) (as a synonym of *O. spicata*)	Petuch & Sargent (1986) (as a subspecies of *O. jamaicensis*)
O. graphica Marrat, 1870	Burch & Burch (1960) (as a synonym of *O. spicata*) Wagner & Abbott(1978) (as a synonym of *O. scripta*)	Zeigler & Porreca (1969), Keen (1971) (as a synonym of *O. julieta*) Petuch & Sargent (1986) (as a full species)
O. oblonga Marrat, 1870	Burch & Burch (1960), Keen (1971), Wagner & Abbott (1978) (as a synonym of *O. spicata*)	Petuch & Sargent (1986), Petuch (1987) (as a form of *O. tisiphona*)
O. oriola ; Duclos (not Lamarck, 1811), 1835.	Burch & Burch (1960), Zeigler & Porreca (1969), Keen (1971) (as a synonym of *O. spicata*)	Wagner & Abbott (1978) (as a synonym of *O. reticularis, pars*)
O. oniska Duclos, 1845	Wagner & Abbott (1978) (as a synonym of *O. fulgurator*) Petuch & Sargent (1986) (as a subspecies of *O. tisiphona*)	Zeigler & Porreca (1969) (as a form of *O. spicata*)
O. porcea Marrat, 1870	Wagner & Abbott(1978) (as a synonym of *O. scripta*)	Burch & Burch (1960) (as a synonym of *O. spicata*) Zeigler & Porreca (1969), Keen (1971) (as a synonym of *O. julieta*)

Table 1. Some examples of divergent geographical attributions.

It was stressed that nearly all the many controversial taxa erected for American species appear:

1/ to have a restricted geographical distribution.

2/ to belong either to the "*O. fulgurator-reticularis* complex" or to the "*O. spicata* complex" (see TURSCH & HUART 1990).

1.2. Aim.

The present paper is the continuation and the extension of the exploratory quantitative survey of living American *Oliva* species by TURSCH & HUART (1990). In that preliminary study, some species were not represented; other required larger samples and nomenclatural problems were not treated in any detail.

The causes of the discrepancy of opinions in the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" will be analysed and discussed. A critical review of the type material will now be presented.

The very distinct species *O. porphyria, O. peruviana, O. splendidula, O. incrassata, O. julieta, O. kaleontina, O. undatella* will be mentioned in the present paper only as references for the delimitation of the "*O. spicata* complex". The West African species *O. flammulata* will also be considered for comparison because it is the type species of the genus *Strephona* Mörch, 1852, in which many American taxa have been

placed (for reasons not clear to us). The taxa *O. schepmani* Weissbord, 1962 [most probably a form of *O. fulgurator* (Röding, 1798)], *O. davisae* Durham, 1950 (most probably a form of *O. polpasta* Duclos, 1833) and *O. callosa* Li, 1930 (a subjective junior synonym of *O. polpasta* Duclos, 1833) all based upon fossil material, will not be examined here.

2. MATERIAL EXAMINED

2.1. Specimens.

372 specimens, from many localities, have been added to the 419 specimens measured in detail and listed in TURSCH & HUART (1990). In addition to the material measured, several thousand specimens, from a large number of localities, have been examined in public and private collections. Broad localities for specimens of the "*O. fulgurator-reticularis* complex", the main object of this study are shown on the map of Fig. 1. The complete list of the examined material would take many pages and (contrary to our habit) we have preferred to list only the type material. 35 measurements (17 used in this paper) have been determined on each intact specimen measured, so this work rests upon a databank of well over twenty thousand high-precision measurements (see section 3.1), accumulated over many years.
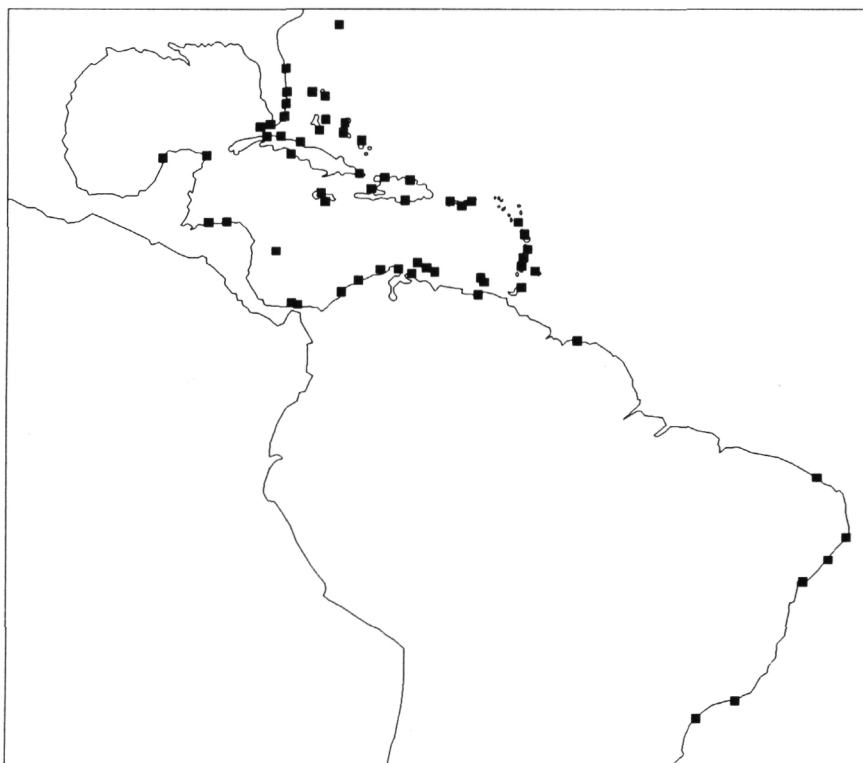

Fig. 1. The "*O. fulgurator-reticularis* complex". Localities of material examined. Localities in close vicinity (less than 20 miles) not separated.

2.2. 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.

MCM: Merseyside County Museum, Liverpool.

MCZ:Museum of Comparative Zoology, Harvard University.

MNHN: Muséum National d'Histoire Naturelle, Paris.

MHNG: Muséum d'Histoire Naturelle, Genève.

USNM: National Museum of Natural History (Smithsonian Institution), Washington.

SBMNH: Santa Barbara Museum of Natural History.

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt.

2.3. Type material examined.

Oliva foxi Stingley, 1984.

Oliva foxi Stingley, 1984. Holotype ANSP 358356 (H: 36.98 mm, D: 14.82 mm) (see PL. 4, FIG. 1). One paratype ANSP 358357 (H: 37.60 mm, D: 15.17 mm) (see PL. 4, FIG. 2). One paratype AMNH 264800 (H: 34.9 mm, D: 14.1 mm) (see PL. 4, FIG. 3). One paratype AMS C.170890 (H: 33.35 mm; D: 13.36 mm) (see PL. 4, FIG. 4).

Oliva fulgurator (Röding, 1798).

Oliva olorinella Duclos, 1835. Eight heterogeneous syntypes at MNHN. One syntype (H: 28.7 mm; D: 12.1 mm) illustrated PL. 9, FIG. 2.

Oliva obesina Duclos, 1840. Figured syntype (H: 44.0; D: 26.3 mm) (see PL. 6, FIG. 1), and 2 syntypes at MNHN.

O. timoria Duclos, 1840 (*pars*). Figured syntype (out of 3) (H: 62.0 mm; D: 33.1 mm), MNHN. (see PL. 7, FIG. 1).

Oliva aldinia Duclos, 1845. Figured syntype (H: 55.6 mm, D: 30.3 mm), (see PL. 6, FIG. 2) + 3 syntypes at MNHN.

Oliva broderipi Ducros de St. Germain, 1857. Holotype at MNHN (H: 27.8 mm; D: 13.4 mm) (see PL. 7, FIG. 3).

Oliva jamaicensis Marrat, 1867. Holotype at MCM (H: 37.7 mm, D: 18.4 mm) (see PL. 6, FIG. 6).

Oliva oblonga Marrat, 1867. Holotype at MCM (H: 63.2 mm, D: 29.2 mm) (see PL. 6, FIG. 7).

Oliva bewleyi Marrat, 1870. Holotype at MCM (H: 41.8, D: 18.1 mm) (see PL. 7, FIG. 10).

Oliva figura Marrat, 1870. Holotype at MCM (H: 41.2 mm, D: 18.1 mm) (see PL. 8, FIG. 3).

Oliva formosa Marrat, 1870. Holotype at MCM (H: 45.23 mm; D: 19.52 mm) (see PL. 9, FIG. 6).

Oliva graphica Marrat, 1870. Holotype at MCM (H: 44.6 mm, D: 22.2 mm) (see PL. 6, FIG. 4).

Oliva porcea Marrat, 1870. Holotype at MCM (H: 42 mm, D: 20.8 mm) (see PL. 6, FIG. 3).

Oliva sowerbyi Marrat, 1870. Syntype (out of 2) at MCM (H:32.2 mm; D:15.0 mm). This taxon is not related to *O. fulgurator* (see Systematics).

Oliva bullata Marrat, 1871. Holotype at MCM (H: 60.83 mm; D: 26.21 mm) (see PL. 9, FIG. 3).

Oliva mercatoria Marrat, 1871. Two syntypes at MCM (H: 41.0 mm, D: 19.5 mm and H: 44.2 mm, D: 20.5 mm) (see PL. 6, FIG. 9).

Oliva nivosa Marrat, 1871. Holotype (H: 49.2 mm, D: 22.0 mm) (see PL. 7, FIG. 9) and one possible paratype at MCM.

Oliva reclusa Marrat, 1871. Holotype at MCM (H: 43.2 mm, D: 18.1 mm) (see PL. 9, FIG. 7).

Oliva circinata Marrat, 1871. Holotype at MCM (H: 55.4, D: 23.4 mm) (see PL. 9, FIG. 8), with 4 possible paratypes. One probable paratype (as stated on an additional label written by N. McMillan in 1978) ANSP 15940 (H: 47.02 mm, D: 19.64 mm).

Oliva bifasciata Küster in Weinkauff, 1878. Figured specimen SMF 9353 (H: 61.39 mm, D: 26.73 mm) (see PL. 8, FIG. 4).

Oliva cribraria Marrat, 1883? Holotype (H: 48.22 mm; D: 22.12 mm) at MCM (see PL. 9, FIG. 10).

Oliva reticularis bollingi Clench, 1934. Holotype MCZ 76656 (H: 61.95 mm, D: 28.52 mm) (see PL. 7, FIG. 8).

Oliva reticularis greenwayae Clench, 1937. Holotype MCZ 115455 (H: 59.65 mm, D: 25.18 mm) (see PL. 8, FIG. 5).

Oliva pattersoni Clench, 1945. Holotype MCZ 151166 (H: 62.57 mm, D: 28.29 mm) (see PL. 8, FIG. 6).

Oliva drangai Schwengel, 1951. Holotype ANSP 247107 (H: 40.47 mm, D: 18.62 mm) (see PL. 7, FIG. 7). Paratype ANSP 247093 (H: 18.56 mm, D: 8.46 mm).

Oliva antillensis Petuch & Sargent, 1986. Holotype USNM 841425 (H: 28.05 mm; D: 11.47 mm) (see PL. 9, FIG. 1).

Oliva ionopsis Berry, 1969. Holotype SMBNH 34656 (H: 30.54 mm; D: 13.76 mm) (see PL. 11, FIG. 10) and seven paratypes SMBNH 34657.

Oliva bahamasensis Petuch & Sargent, 1986. Holotype USNM 841426 (H: 44.58 mm; D: 20.62 mm) (see PL. 8, FIG. 10).

Oliva barbadensis Petuch & Sargent, 1986. Holotype USNM 841427 (H: 47.05 mm; D: 20.32 mm) (see PL. 9, FIG. 4).

Oliva bifasciata jenseni Petuch & Sargent, 1986. Holotype USNM 859302 (changed from USNM 841453, R. GERMON *in litt.*) (H: 50.30 mm; D: 24.12 mm) (see PL. 7, FIG. 6).

Oliva finlayi Petuch & Sargent, 1986. Holotype USNM 841432 (H: 39.98 mm; D: 18.71 mm) (see PL. 8, FIG. 8).

Oliva goajira Petuch & Sargent, 1986. .Holotype USNM 841433 (H: 36.79 mm; D: 15.49 mm) (see PL. 8, FIG. 2).

Oliva jamaicensis zombia Petuch & Sargent, 1986. Holotype USNM 841454 (H: 23.87 mm; D: 12.61 mm) (see PL. 7, FIG. 2).

Oliva magdae Petuch & Sargent, 1986. Holotype USNM 841441 (H: 37.57 mm; D: 18.62 mm) (see PL. 6, FIG. 8).

Oliva maya Petuch & Sargent, 1986. Holotype USNM 859301 (changed from USNM 841453, R. GERMON *in litt.*) (H: 57.81 mm: D: 24.97 mm) (see PL. 8, FIG. 1).

Oliva bifasciata sunderlandi Petuch, 1987. Holotype USNM 859904 (H: 22.02 mm; D: 9.56 mm) (see PL. 9, FIG. 5).

Oliva circinata tostesi Petuch, 1987. Holotype USNM 859865 (H: 46.20 mm; D: 21.37 mm) (not H: 41 mm as in description) (see PL. 9, FIG. 9).

Oliva sargenti Petuch, 1987. Holotype USNM 859864 (H: 28.60 mm; D: 14.03 mm) (see PL. 7, FIG. 5).

Oliva contoyensis Petuch, 1988. Holotype USNM 859945 (H: 36.71 mm; D: 18.42 mm) (see PL. 7, FIG. 4).

Oliva ernesti Petuch, 1990. Holotype USNM 860535 (H: 33.66 mm, D: 15.45 mm) (not H: 38 mm, as in description) (see PL. 8, FIG. 7).

Oliva polpasta Duclos, 1833.

Oliva polpasta Duclos, 1833. Six syntypes at MNHN. Figured syntype (H: 40.1 mm; D: 21.0 mm) (see PL. 4, FIG. 6).

Oliva truncata Marrat, 1867. Holotype at MCM (H: 37 mm, D: 18 mm) (see PL. 4, FIG. 7).

Oliva kerstitchi da Motta, 1985. Holotype MHNG 984.631 (H: 24.5 mm, D: 11.2 mm) (see PL. 4, FIG. 8).

Oliva olssoni Petuch & Sargent, 1986. Holotype USNM 841444 (H: 35.03 mm; D: 19.57 mm) (see PL. 4, FIG. 9).

Oliva sayana Ravenel, 1834.

Oliva circinata var. *citrina* Johnson, 1911. Paratype MCZ 6267 (H: 60.51 mm, D: 23.56 mm) (see PL.5, FIG. 4).

Oliva sayana sarasotensis Petuch & Sargent, 1986. Holotype USNM 841450 (H: 40.60 mm; D: 17.90 mm) (see PL. 5, FIG. 3).

Oliva sayana texana Petuch & Sargent, 1986. Holotype USNM 841465 (H: 43.60 mm; D: 17.54 mm) (see PL. 5, FIG. 2).

Oliva scripta Lamarck, 1811.

Oliva caribaeensis Dall & Simpson, 1901. Holotype USNM 159672 (H: 31.61 mm; D: 14.93 mm) (see PL. 5, FIG. 6).

Oliva trujilloi Clench, 1938. Holotype MCZ 57240 (H: 40.52 mm, D: 17.95 mm) (see PL. 5, FIG. 7). One paratype AMNH 79010 (H: 34.8, D: 15.5 mm) (see PL. 5, FIG. 8). Five paratypes AMS C.095147 (one H: 39.57 mm; D: 18.59 mm, illustrated PL. 5, FIG. 9).

Oliva (Cariboliva) scripta venezuelana Petuch & Sargent, 1986. Holotype USNM 841451 (H: 44.22 mm; D: 22.02 mm) (see PL. 5, FIG. 10).

Oliva spicata (Röding, 1798).

Oliva oniska Duclos, 1845. Nine syntypes at MNHN. Figured syntype (H: 61.0 mm; D: 26.2 mm) (see PL. 11, FIG. 4).

Oliva pindarina Duclos, 1840. Three syntypes at MNHN. Figured syntype (H: 53.4 mm; D: 27.3 mm) (see PL. 10, FIG. 2).

O. timoria Duclos, 1840 (*pars*). Figured syntype (out of 3) (H: 55.8 mm; D: 39.1 mm), MNHN. (see PL. 10, FIG. 1).

Oliva subangulata Philippi, 1848. One syntype (H: 59.62 mm; D: 26.38 mm) out of 2, BM(NH) 1924.1.5.98-99. (see PL. 11, FIG. 6).

Oliva cumingii Reeve, 1850. Three syntypes BM(NH) 1987008, (one H: 48.4 mm; D: 24.2 mm) (see PL. 11, FIG. 1).

Oliva ligneola Reeve, 1850. Two heterogeneous syntypes BM(NH) 1892.9.24.4-5. One (H: 21.36 mm; D: 10.67 mm) is *O. tigrina fallax* Johnson 1911, the other (H: 25.60 mm; D: 13.09 mm) (see PL. 10, FIG. 3) is a bleached *O. spicata* (Röding), 1798.

Oliva intertincta Carpenter, 1857. Two syntypes USNM 716187 (largest: H: 19.68 mm; D: 9.70 mm, see PL. 11, FIG. 9). 3 additional syntypes in BM(NH), Carpenter collection, tablet 2121.

Oliva violacea Marrat, 1867. Holotype at MCM (H: 39.3 mm, D: 17.3 mm) (see PL. 11, FIG. 8).

Oliva brunnea Marrat, 1870. Holotype at MCM (H: 34,0 mm, D: 16.1 mm) (see PL. 11, FIG. 3).

Oliva punctata Marrat, 1870. One of two syntypes (H: 35.35 mm; D: 17.24 mm) at MCM (see PL. 10, FIG. 4).

Oliva fuscata Marrat, 1870. Three syntypes at MCM, one of which (H: 42.66 mm; D: 20.30 mm) is figured PL. 11, FIG. 2 and another (H: 39.76 mm; D: 18.62 mm) PL. 11, FIG. 7.

Oliva spicata var. *hemphilli* Ford in Johnson, 1911. Five syntypes ANSP 111697. One (H: 54.05 mm, D: 23.38 mm) is figured PL. 10, FIG. 8.

Oliva spicata var. *perfecta* Johnson, 1911. Three syntypes ANSP 111729. One (H: 59.06 mm, D: 25.73 mm) is figured PL. 11, FIG. 5.

Oliva rejecta Burch & Burch, 1962. One paratype USNM 667317 (H: 37.24 mm; D: 16.01 mm) (see PL. 10, FIG. 10). One paratype at MNHN (H: 31.3, D: 13.6 mm) (see PL. 10, FIG. 9).

Oliva (Strephona) radix Petuch & Sargent, 1986. Holotype USNM 841446 (H: 36.62mm; D: 22.51 mm) (see PL. 10, FIG. 6).

Oliva subangulata corteziana Petuch & Sargent, 1986. Holotype USNM 841457 (H: 32.33 mm; D: 16.21 mm) (see PL. 10, FIG. 7).

Oliva spicata deynzerae Petuch & Sargent, 1986.

Oliva (Strephona) spicata deynzerae Petuch & Sargent, 1986. Holotype USNM 841452 (H: 53.19 mm; D: 21.95 mm) (see PL. 4, FIG. 5).

3. METHODS

3.1. Measurements.

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 utilized 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. 2. 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. The way in which *Oliva* shell measurements are best used is discussed in TURSCH & GREIFENEDER (1996).

3.2. Analysis methods.

These are essentially the same as in TURSCH, MISSA & BOUILLON (1992) and TURSCH & GREIFENEDER (1996). 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 variability.

Separations (voids between clouds of points) in hyperspace cannot be visualized directly. These voids can be detected by special techniques of space reduction, such as Principal Component Analysis (PCA) or Factorial Discriminant Analysis (FDA). In favourable situations, however, only two of the many variables can be sufficient for evidencing the separation of two or several groups. This can then be represented on bidimensional graphs (scatter diagrams). Such separations constitute conclusive evidence: groups that are separated in two dimensions

are necessarily separated in the multidimensional attribute hyperspace. From our experience, patient search for operational characters (the number of possible combination of measurements can be very large) will generally yield a clean-cut bidimensional representation of the separations. The search for such operational characters is greatly helped by preliminary PCA and FDA studies.

Only scatter diagrams will be reported here: they convey all the necessary evidence and are much more heuristic than PCA or FDA graphs. Numerical results will be reported here only when really needed. Reporting, for instance, the very evident differences separating *O. porphyria* from *O. kaleontina* in numerical terms would be quite superfluous. It would consume space and unnecessarily tax the patience of the reader.

Reading graphs containing hundreds of points is very strenuous. We have therefore preferred to represent the distribution of attributes by plain minimum convex polygons.

3.3. Interpretation of data.

As in nearly all taxonomic studies of Mollusks, the morphospecies approach is adopted here. On the one hand it is evident (but often overlooked) that one can never give a real *demonstration* that two objects (in this case, lots of shells) belong to the same morphospecies. In practice, two specimens belong to the same morphospecies if they are linked by an unbroken chain of intermediate specimens (sympatric or not).

On the other hand, one can present convincing arguments that two (or more) samples belong to separate morphospecies. Two morphospecies are distinct if their representative clouds in the attribute hyperspace are separated by a void region: a morphological gap. To prevent taxonomy from becoming a game of chance, only *full separations* (with no overlap) will be taken into account in this work. If one cannot bring forwards such arguments, then one has no choice: unseparated samples must be considered as belonging to the same morphospecies (awaiting further, objective arguments to the contrary).

Great care should be exercised in the interpretation of the observed separations (see TURSCH & GREIFENEDER 1996). The general problem of detecting separations is much aggravated in multidimensional hyperspaces (where one can get horribly lost). In the bidimensional graphs used in this work, interpretation is much safer but caution is neverteless required. First, one has to consider the size of the samples. In scatter diagrams, weak separations and separations obtained on small samples (from our experience, $N<6$) might be indicative but must be considered with caution. Small gaps observed between small samples should be interpreted with great prudence. All separations accepted in this work are supported by additional evidence: the observed gaps correspond to discontinuities in the distribution of other characters, unrelated to the nature of the axes of the graph (other

metric characters, colour pattern features, distributional data, etc.).

In contrast, observed *overlaps are always significant*, as these overlaps will persist if the size of the sample is increased. Even one single specimen can be legitimately tested by comparison with a large sample. This allows the demonstration of overlaps in the case of type material.

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). Only in these conditions can morphological gaps be safely interpreted in terms of reproductive barriers.

It has been shown (TURSCH 1994) that *Oliva* species consist of a mosaic of distinct populations, each being quite homogeneous. When a large enough number of such local, conspecific populations are compared, they invariably show considerable character overlap. The species is thus represented by a ***morphological continuum*** in the attribute hyperspace. This is a set in which no population (or groups of populations) can be separated from *all* the others. Even if two (or more) of the populations forming the continuum can be easily separated from each other, the gap is invariably bridged by another conspecific population (or an unbroken chain of intermediate populations). The boundaries of the morphological continuum are the limits of the phenetic variability of a species.

Completely separable populations belonging to the same *Oliva* species can occur even within very short geographic distances (TURSCH 1994). Separations between pairs of conspecific populations are thus fully expected (see MAYR & ASHLOCK 1991 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 *Oliva* shells from different localities include much more of the total variability of the species. Clear separations of such samples are more probably significant.

Other problems can occur within the population level. Sexual dimorphism can fortunately be neglected in the genus *Oliva*. In contrast, some *Oliva* species have a non-isometric growth (TURSCH 1997) and in such instances, unless adequate precautions are taken, artificial segregation of young and aged individuals can easily occur.
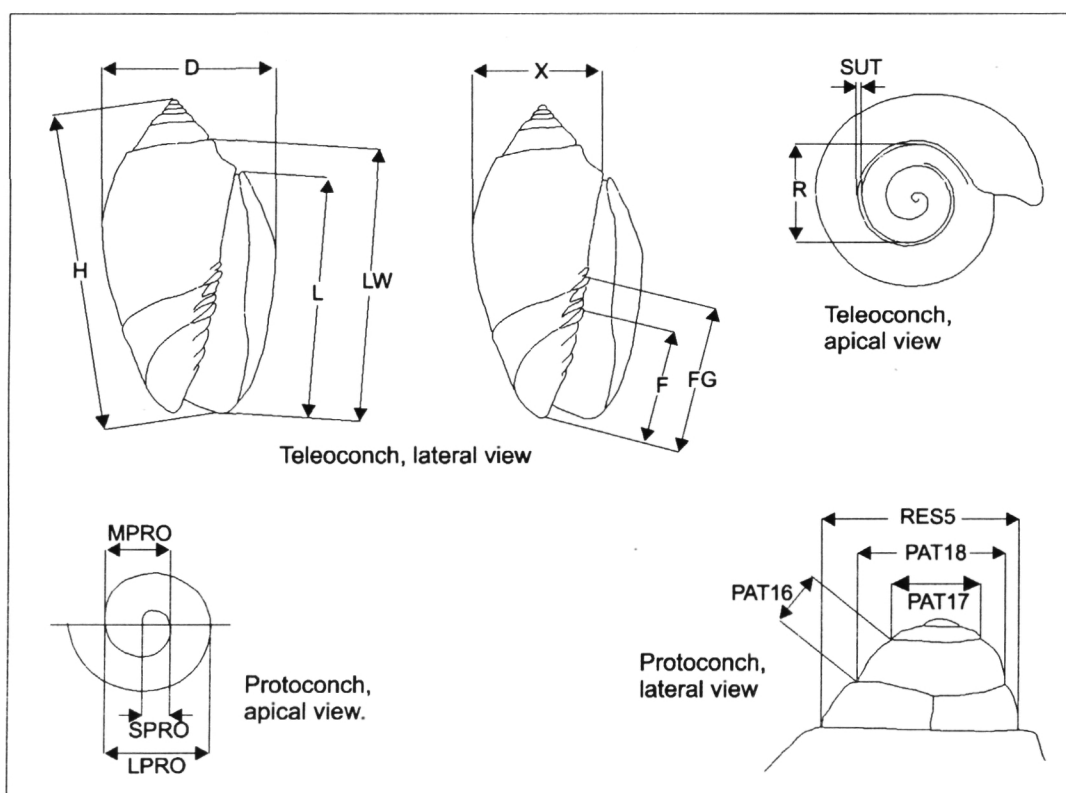

Fig. 2. Sketch of shell measurements used in this work.

In theory, the objective approach advocated here could either increase the number of species (by detecting previously overlooked gaps) or reduce it (by demonstrating previously overlooked overlaps). In practice, it does lead to a sharp diminution of the number of admitted species. This is frequently called *'lumping'* by collectors who 'know' their shells. Please note that *'splitters'* and *'lumpers'* can exist only when taxonomic decisions are a matter of personal opinion. This can certainly be the case at the supraspecific level, where one can disagree on where to 'cut the branches' of a phylogenetic tree. But the species is (or at least should be) the most objective of all taxonomic categories. At the species level, we should not even have the choice between *'splitting'* and *'lumping'*. These two attitudes can, at best, be provisional strategies for handling unsolved cases.

In summary, the method used in this work is very simple. A large number of purposely unidentified specimens are first shown to be separated into distinct morphological groups. By careful selection of characters (using PCA and FDA), the separations of the groups could be demonstrated in bidimensional representations. In spite of all efforts, these groups could not be split any further (even when submitted to PCA and FDA tests on all variables). We consider these groups as separate morphospecies, a conclusion supported by the fact that all additional specimens fall into these clusters. If the type material of other taxa cannot be separated from these groups, synonymy is demonstrated

The species so defined can now be visually identified with a rather high degree of confidence because the distribution of morphometric characters is correlated to the distribution of some (mostly undescribed) visual clues. But these clues could be found only after morphometric analysis. Many 'intuitive species' erected only on other, uncorrelated visual clues are listed in a specially long synonymy (see Index to names).

4. RESULTS AND OBSERVATIONS

4.1. Species delimitation.

The inclusion of many additional specimens in the morphometric analysis did not fundamentally modify the conclusions previously drawn by TURSCH & HUART (1990). For instance, all the Atlantic and Eastern Pacific *Oliva* species are included in the scatter diagram of Fig. 3, where many species are objectively separated in one single operation. *O. foxi* Stingley, 1984 (not considered in TURSCH & HUART 1990) is completely separated from *O. spicata* and *O. polpasta*. The species *O. incrassata*, *O. julieta* and *O. peruviana* (also not considered in TURSCH & HUART 1990) are clearly separated from cognate species and will not be treated here anymore, except for comparison.

All the Atlantic *Oliva* taxa still fall into four objective groups, clearly separated even on one single scatter diagram (see Fig. 4). One of these groups is *O. flammulata* Lamarck, 1811, confined to the West African coast, with a subspecies *O. flammulata dolicha* Locard, 1896 in Cabo Verde (see TURSCH & HUART, 1988). It will not be treated here anymore, except for comparison. The three others live in the warm waters of the Western Atlantic. Two of these objective groups correspond to the species *O. scripta* Lamarck, 1811 and *O. sayana* Ravenel, 1834. These groups are quite homogeneous and could not be split into smaller, objective units.
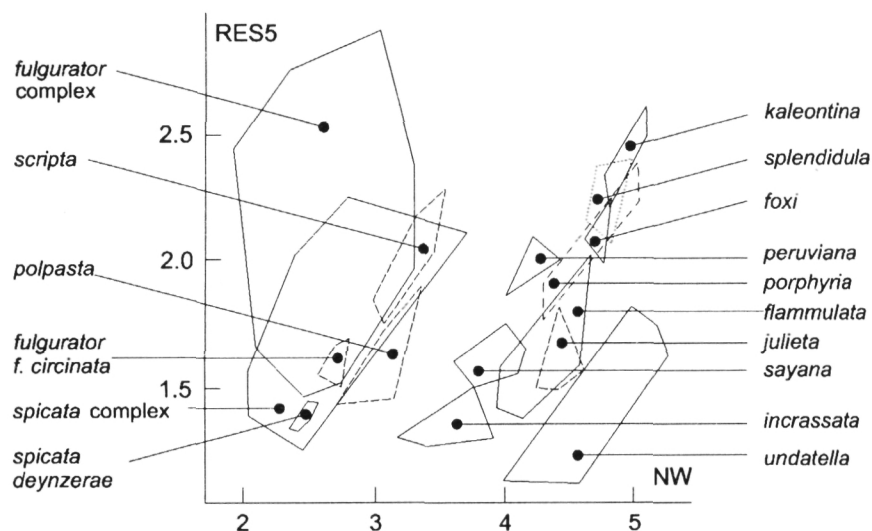

Fig. 3. All Atlantic and Pacific species. Scatter diagram: RES5 *vs.* NW. Minimum convex polygons. Every group is well separated with other variables, with the exception of the "*O. fulgurator* complex" not separated from the "*O. spicata* complex".
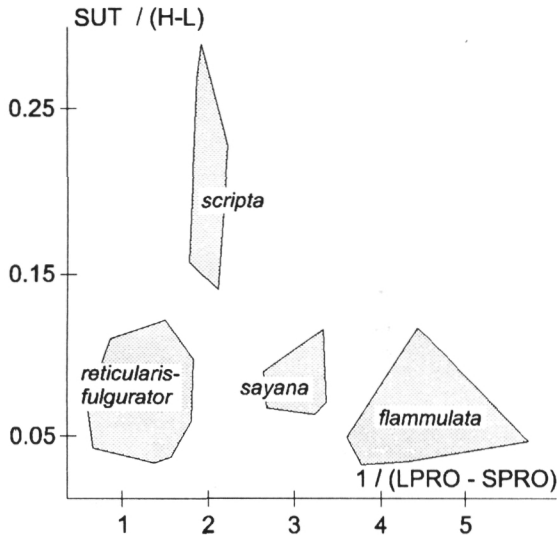
Fig. 4. Separation of Atlantic *Oliva* species. Scatter diagram: SUT/(H-L) *vs.* 1/(LPRO-SPRO). Minimum convex polygons.

The third Western Atlantic group, the "*O. fulgurator-reticularis* complex", has a much higher variability, as attested by the relative dimensions of its representative cloud of points in most dimensions of the attribute hyperspace. Some of the populations that it contains are indeed very dissimilar in aspect. In spite of much effort spent to that end, this "complex" could not be objectively split into smaller units. Inclusion of additional specimens now established that *O. oblonga* Marrat, 1870, formerly thought by us to be a possible candidate for separation (see TURSCH & HUART 1990), does considerably overlap with the complex.

In the Eastern Pacific, all the separations previously observed persisted, with only one exception. A scatter diagram of R/L vs. NW/(LPRO-SPRO) (Fig. 5) clearly separated *O. porphyria* and *O. splendidula* from two large, distinct, but not homogeneous groups

These two unresolved groups (NH) were then analysed in a scatter diagram of PAT18/NW vs. LPRO (Fig. 6) yielding four groups corresponding to *O. kaleontina*, *O. undatella*, *O. polpasta* and the "*O. spicata* complex". None of these final groups could be objectively split into smaller units. One result differed from the previous ones: with the inclusion of additional, allopatric specimens, *O. polpasta* Duclos,1833 could not anymore be separated from *O. kerstitchi* da Motta, 1985 [this separation was suggested in Tursch & Huart (1990) as a working hypothesis awaiting further confirmation].

In spite of much effort to that end, no quantitative discrimination of the "*O. fulgurator-reticularis* complex" from the "*O. spicata* complex" could be established, as already observed in TURSCH & HUART (1990). A very large number of separation attempts (including frequency histograms, scatter diagrams, principal factor analysis, discriminant factorial analysis and UPGMA clustering) invariably resulted in considerable overlap between the two groups, as in the example of Fig. 7. There is nothing really new in this observation:

> "The discrimination of... [*O. melchersi* and *O. venulata*] ... from each other and from *O. reticularis* is a matter of extreme difficulty; which Mr. Reeve escapes by uniting them all together."
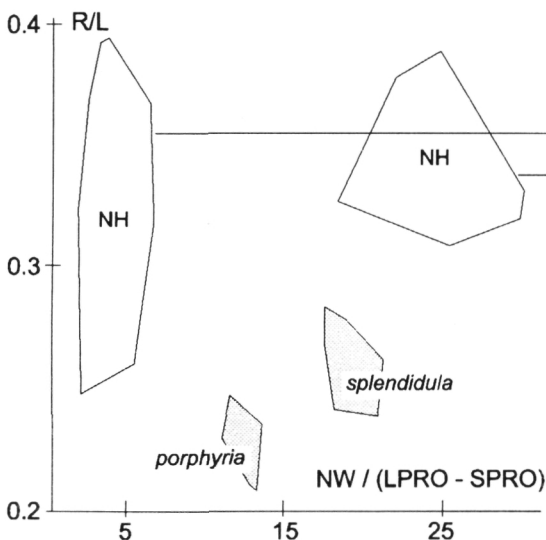>
> CARPENTER (1855: 464).

Fig. 5. Separation of Eastern Pacific *Oliva* species. Scatter diagram: R/L vs. NW/(LPRO-SPRO). Minimum convex polygons. The groups marked NH are not homogeneous.
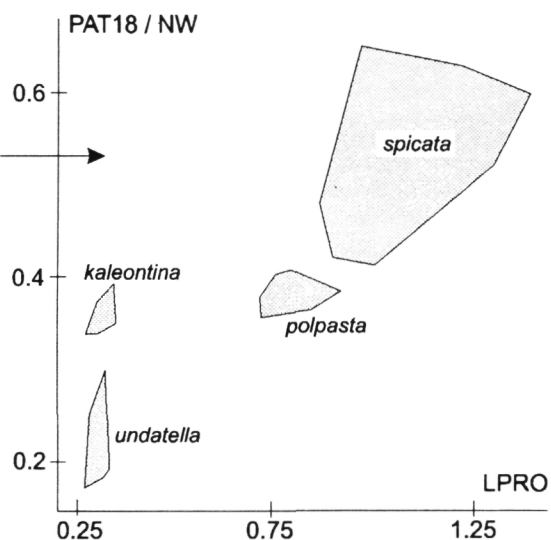

Fig. 6. Separation of Eastern Pacific *Oliva* species. Separations of the groups NH unresolved in Fig. 5. Scatter diagram: PAT18/NW vs. LPRO. Minimum convex polygons.
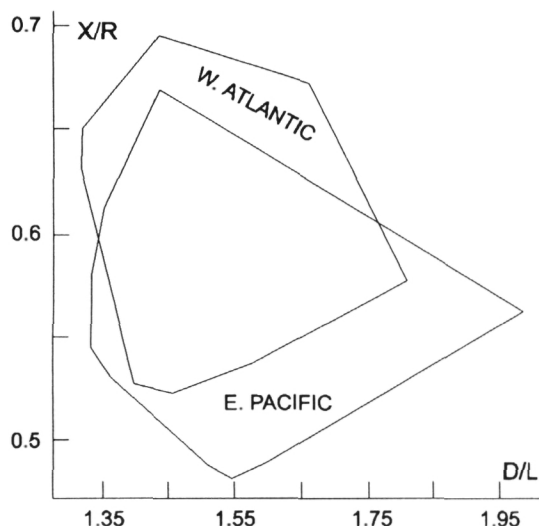
Fig. 7. Attempted separation of the "*O. fulgurator-reticularis* complex" (marked "W. Atlantic") from the "*O. spicata* complex" (marked "E. Pacific"). One example amongst many. Scatter diagram: X/R vs. D/L. Minimum convex polygons.

possible exception of an intermediate pattern found on the Hawaiian, deep water *O. richerti* Kay, 1979 from Hawaii). The presence of this same subchannel pattern in species as different as *O. porphyria* and *O. spicata* could be interpreted as indicating a common, but ancient ancestry.

There is one other shared feature in the colour pattern. Most species of the genus *Oliva* display two more or less diffuse spiral bands of darker colour on the body whorl. It has been shown by GREIFENEDER (1984) that the relative position of these bands in many American *Oliva* species is consistently lower than that observed in their Indo-Pacific congenerics.

Another argument yet could be found in the orientation of the shell microcrystalline layers. The distribution of angular values in both the Western Atlantic and Panamic *Oliva* species has been shown to differ from that of their Indo-Pacific counterparts. This should be interpreted with caution because the phenomenon could possibly be of adaptative nature (TURSCH & MACHBAETE 1995).

Because of their long-standing disjunct geographical distribution (and only for that reason), this constant overlap does not necessarily mean that the two groups are of the same species (see § 5.4).

Many of the groups defined here above have quite characteristic protoconchs. Examples are given in Fig. 8 and Fig. 9. One will note the exceptionally great variation range of the protoconchs of *O. fulgurator* and *O. spicata*. This variation is way larger than for any of the Indo-Pacific species that we have examined. The ranges of variation of all subsamples form an unbroken continuum (see § 4.4).

Two characteristics of the shell colour pattern confirm the close (and expected) relationship of the Western Atlantic and Eastern Pacific *Oliva* faunas, and set a number of species apart from all others. In the genus *Oliva*, the presence on the shell of a peculiar colour pattern located just under the filament channel is a reliable indication that one is dealing with an American species (for details on the filament channel, see VAN OSSELAER & TURSCH 1994). This repeated pattern consists in bundles of divaricate, fasciculated, fine lines meeting at a central point or a small blotch, right at the sharp exterior edge of the channel (see Fig. 10). It is -as expected- very variable but nevertheless highly recognisable. It will be referred here under as the "*fasciculated pattern*", for short. The presence on the shell of this pattern, quite unique in the genus *Oliva,* is a safe indication that one is dealing with either a Western or an Eastern American species. It is indeed present in all American *Oliva* species, except *O. kaleontina, O. peruviana* and *O. undatella* (see Plate 1). It is not clearly present in *O. flammulata* Lam., 1811 (possible intermediates are occasionally met). It is not found in any Indo-Pacific species (with the

4.2. Homogeneous, distinct local populations.

Except for occasional colour variants, the local populations of the members of the "*fulgurator-reticularis* complex" are quite homogeneous in shape and general outline (see DIAZ & PUYANA 1994: 202). Albeit variable (colour polymorphism results in occasional colour variants such as darker or paler individuals) the ground colour of the shell is generally cryptic, matching the substrate, just as for most Indo-Pacific *Oliva* species (see VAN OSSELAER *et al.* 1993). This homogeneity (probably due to the inefficiency of immigration into generally large populations –see § 6.1- and possibly maintained by selection) does restrict even more the intra-population variation.

In contrast, inter-population variation is much greater, considerable differences being often observed between specimens from different localities. This was already clearly perceived by DIAZ & PUYANA (1994: 202), who wrote about *O. bewleyi* Marrat, 1870:

> "Note: this species is very variable in its colour pattern, even within one local population. Variations in the form of the shell (height of the spire, ratio height/width, etc.) are frequent between populations but not so within one same population. Within the abundant material of *O. bewleyi* from different localities of the Colombian and Venezuelan Caribbean examined by us, and applying the criteria of Sargent & Petuch (1986), not less than six different 'species' or 'subspecies' exist in the region..."

> *(translation ours).*

That the distribution of most of the populations is quite restricted, is evidenced by the fact that the experienced collector can often guess the origin of a given specimen.
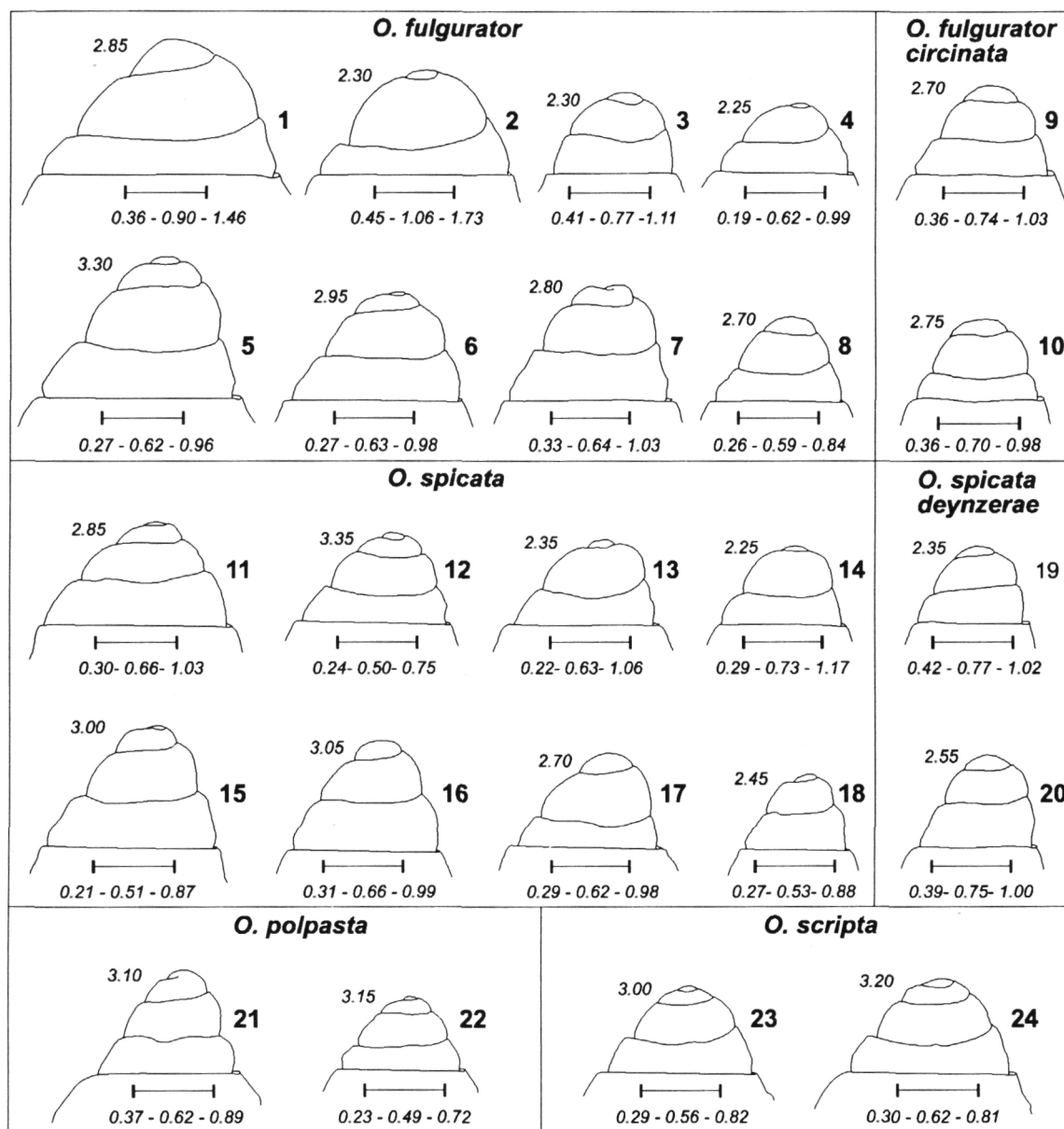
O. fulgurator

2.85 — **1** — 0.36 - 0.90 - 1.46
2.30 — **2** — 0.45 - 1.06 - 1.73
2.30 — **3** — 0.41 - 0.77 -1.11
2.25 — **4** — 0.19 - 0.62 - 0.99

3.30 — **5** — 0.27 - 0.62 - 0.96
2.95 — **6** — 0.27 - 0.63 - 0.98
2.80 — **7** — 0.33 - 0.64 - 1.03
2.70 — **8** — 0.26 - 0.59 - 0.84

O. fulgurator circinata

2.70 — **9** — 0.36 - 0.74 - 1.03
2.75 — **10** — 0.36 - 0.70 - 0.98

O. spicata

2.85 — **11** — 0.30- 0.66- 1.03
3.35 — **12** — 0.24- 0.50- 0.75
2.35 — **13** — 0.22- 0.63- 1.06
2.25 — **14** — 0.29 - 0.73 - 1.17

3.00 — **15** — 0.21 - 0.51 - 0.87
3.05 — **16** — 0.31 - 0.66 - 0.99
2.70 — **17** — 0.29 - 0.62 - 0.98
2.45 — **18** — 0.27- 0.53- 0.88

O. spicata deynzerae

2.35 — **19** — 0.42 - 0.77 - 1.02
2.55 — **20** — 0.39- 0.75- 1.00

O. polpasta

3.10 — **21** — 0.37 - 0.62 - 0.89
3.15 — **22** — 0.23 - 0.49 - 0.72

O. scripta

3.00 — **23** — 0.29 - 0.56 - 0.82
3.20 — **24** — 0.30 - 0.62 - 0.81

Fig. 8. Protoconchs (Atlantic). Scale bars: 1 mm. Figures to the left of apex: number of nuclear whorls (NW). Figures below scale bar: measurements SPRO, MPRO and LPRO of first protoconch volutions (see Fig. 2).

1-10: *O. fulgurator* (Röding, 1798). **1**: Isla Boracha, Venezuela (BT-0984); **2**: Aruba (BT-4964); **3**: Bahamas (BT-3418); **4**: Guantanamo, Cuba (BT-2668); **5**: Lac Bay, Bonaire (BT-3872); **6**: Guantanamo, Cuba (BT-2669); **7**: Lac Bay, Bonaire (BT-3874); **8**: Brevard County, Florida (BT-2764). **9-10**: *O. fulgurator* forma *circinata* Marrat, 1871. **9**: Alagoas, Brazil (BT-2114); **10**: Rio de Janeiro, Brazil (BT-2113). **11-18**: *O. spicata* (Röding, 1798).

11: Baja California, Mexico (AB-b207); **12**: Cebaco I., Panama (BT-3755); **13**: Baja California, Mexico (BT-4289);

14: Guerrero, Mexico (BT-5335); **15**: Baja California, Mexico (BT-0346); **16**: Baja California, Mexico (RF-b06);

17: Baja California, Mexico (BT-4123); **18**: Baja California, Mexico (AB-b384). **19-20**: *O.spicata deynzerae* Petuch & Sargent,1986. **19**: Cocos Is., Costa Rica (BT-5447); **20**: Cocos Is., Costa Rica (BT-5446).

21-22: *O. polpasta* Duclos, 1840. **21**: Oaxaca, Mexico (BT-4613, forma *kerstitchi*); **22**: Cebaco I., Panama (BT-3781). **23-24**: *O. scripta* Lamarck, 1811. **23**: Honduras (BT-2756); **24**: Haiti (BT-2379).
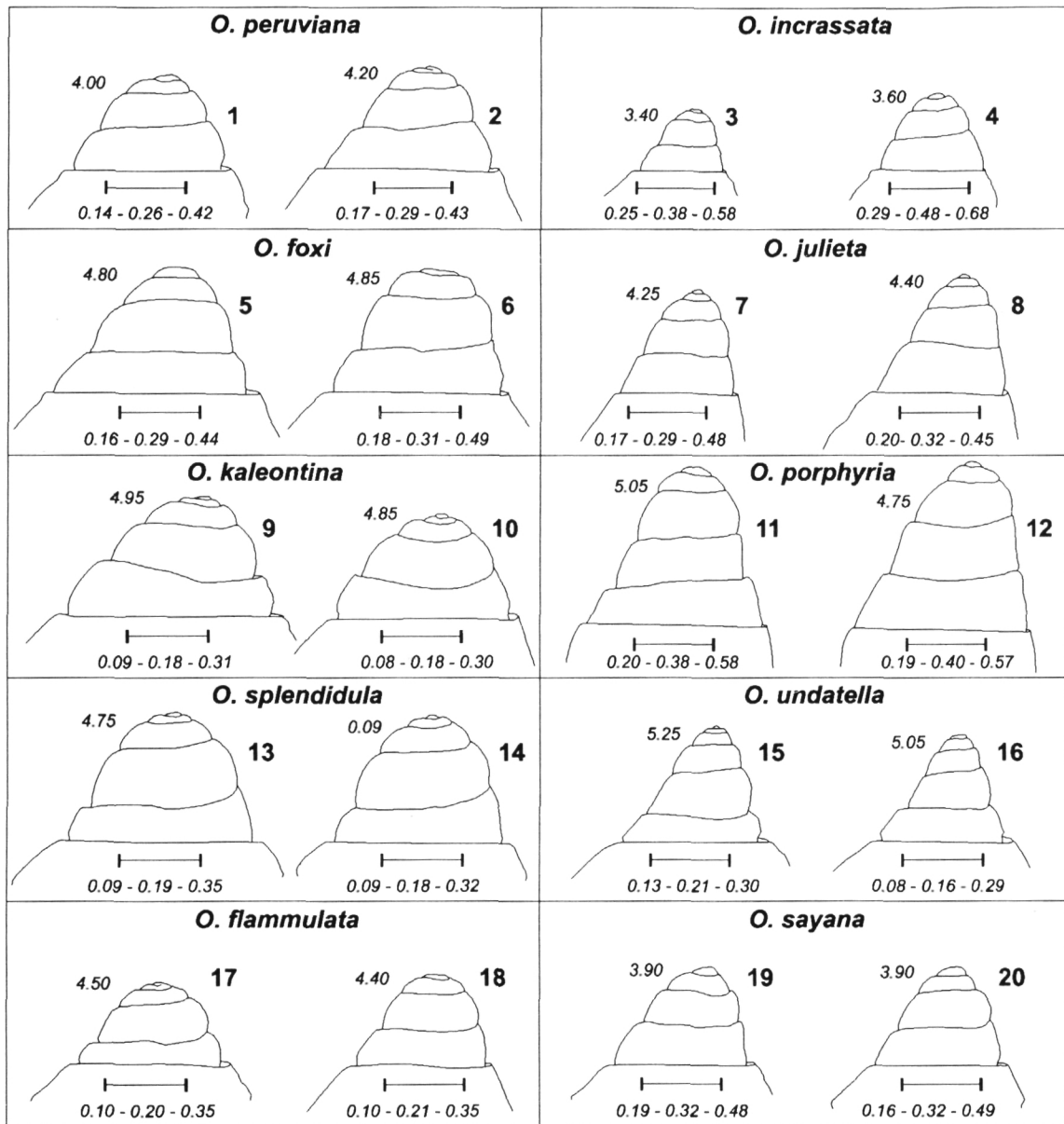
Fig. 9. Protoconchs (Eastern Pacific). Scale bars: 1 mm. Figures to the left of apex: number of nuclear whorls (NW). Figures below scale bar: measurements SPRO, MPRO and LPRO of first protoconch volutions (see Fig. 2). **1-2: O. peruviana** Lamarck, 1811. **1**: Iquique, CHILE (BT-5785); **2**: Iquique, CHILE (BT-5784). **3-4: O. incrassata** (Lightfoot in Solander, 1786). **3**: Puerto Penasco, MEXICO (DG-4224/3);**4**: Michoacan, MEXICO (DG-4224/2).

5-6: O. foxi Stingley, 1984. **5**: Cocos Is., COSTA RICA (BT-3326); **6**: Cocos Is., COSTA RICA (BP-b07).

7-8: O. julieta Duclos, 1840. **7**: Michoacan, MEXICO (DG-4224/3); **8**: Michoacan, MEXICO (DG-4224/3).

9-10: O. kaleontina Duclos, 1835. **9**: Cebaco I., PANAMA (BT-3751); **10**: St. James I., GALAPAGOS (BT-4275).

11-12: O. porphyria (Röding, 1798). **11**: Gubernadora I., PANAMA (BT-4464); **12**: Sonora, MEXICO (BT-0346).

12-13: O. splendidula Sowerby, 1825. **13**: Perlas Is., PANAMA (BT-3731); **14**: Manzanillo, MEXICO (BT-4023).

15-16: O. undatella Lamarck, 1811. **15**: Colima, MEXICO (BT-0331); **16**: Venado I., PANAMA (BT-1666).

17-18: O. flammulata Lamarck, 1811. **17**: Port Gentil, GABON (BT-2087); **18**: Gorée, SÉNÉGAL (BT-2127).

19-20: O. sayana Ravenel, 1834. **19**: Indian River, FLORIDA (BT-4064); **20**: Marco Beach, FLORIDA (BT-3108).
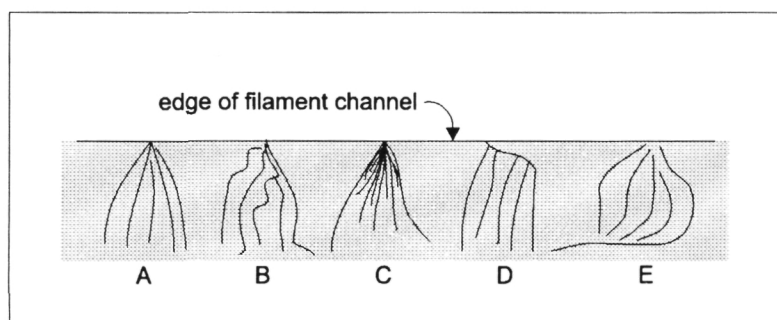
Fig. 10. Some examples of "fasciculated" subchannel colour markings (see § 4.1).

Although some general geographical trends can be noted (see § 4.5), neighbouring populations do not necessarily resemble each other very much. The general distribution of many single characters shows chaotic interdeme variation [like the *"crazy quilt"* distribution observed for *Cerion* by GOULD & WOODRUFF (1978)] and would seem to fairly reflect habitat discontinuities.

4.3. Systematic allotopy.

4.3.1. The *"O. fulgurator-reticularis* complex"
Much time has been spent in interviewing many experienced local collectors (ranging from professional malacologists to fishermen collecting molluscs for the shell trade). All were unanimous in reporting that within the *"fulgurator-reticularis* complex", shells of different forms ('species' ?) are never found living together. This has also been our personal experience during collecting trips in Brazil, Colombia, Mexico, Venezuela and the Virgin Islands. The populations of shells with different forms are invariably *allotopic*.

It is important to stress the restricted meaning of "living together". One could indeed object that some distinct populations can live within short distance (for instance, at least two forms have been reported from Gonave, Haiti, by PETUCH 1986, and at least three different forms live in Aruba. Detailed field studies in the Southern Pacific have demonstrated that completely distinct, conspecific populations of several species have been observed to be separated by only a few hundred meters (VAN OSSELAER *et al.* 1993). The scale of sympatry in the genus *Oliva* is thus much smaller than generally thought (TURSCH 1994) and it should, for safety, be reduced to the scale of *syntopy* (i.e. found living in the same microbiotope, within a distance of meters).

4.3.2. The *"O. spicata* complex"
From all the information we could gather, the same situation is met for the *"O. spicata* complex" in the Eastern Pacific. The only exception known to us is the report by BURCH & BURCH (1962) on the coexistence of the "species" *O. rejecta* Burch & Burch, 1962 (see

Section 7, Systematics, under *O. spicata*) with *O. venulata* Lamarck, 1811. The authors wrote: *"Both forms are found on the same tide flats at La Paz, Baja California, Mexico, with no intergrades in many hundreds of specimens"*. One will notice the use of the word *"forms"* to designate what the authors consider distinct species. Nevertheless, this had to be taken seriously because, if this coexistence were factual, it could falsify the very premises upon which the conclusions of the present work do rest.

One of us (BT) recently went to La Paz for an *in situ* check of the situation. Large numbers of live specimens were observed at eleven tide flats in Bahia La Paz (see map, Pl. 2) (*e.g.* 78 specimens at Punta de Leon, 129 at Herendira, 318 at Balandra). The previous observations made in the Caribbean and in the South Pacific were fully verified: all the *Oliva spicata* populations that were seen were local morphs, with cryptic colouration (matching that of the substrate), and quite homogeneous in characters. No form absolutely identical to the "real" *O. rejecta* was not found (although the Herendira population is quite similar, see Pl. 2). It might live in another of the very numerous isolated bays of the region (their systematical study would take very considerable time). Or its habitat may have been destroyed (the original beaches of La Paz City are said to have been washed away after the construction of the Malecón, many years ago; the sand of the present beaches is imported).

Around La Paz, *Oliva spicata* is collected (overcollected?) in large quantities for the tourist trade. So the conclusions from our field observations were fully confirmed by the examination of well over 100 kilos of specimens in the possession of local fishermen (one single person had a lot of 60 kilos -estimated at over 8000 specimens). None of the local collectors (some gathering *O. spicata* for over 25 years) could remember a single case of co-occurrence of different forms.

It would thus seem that BURCH & BURCH were simply given incorrect locality data (as it only too often happens for commercial specimens) and that the case of *O. rejecta* cannot be construed as a counter-example.
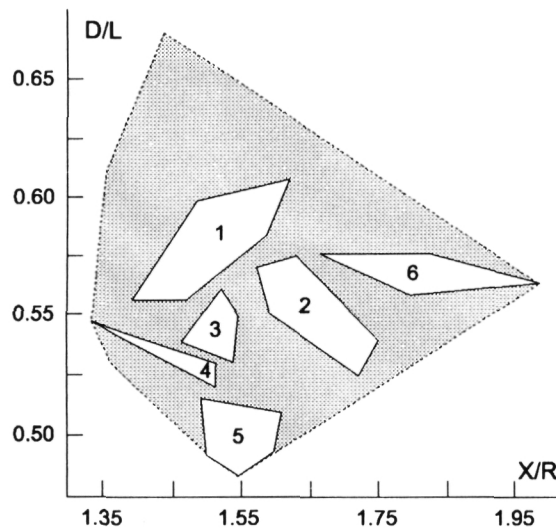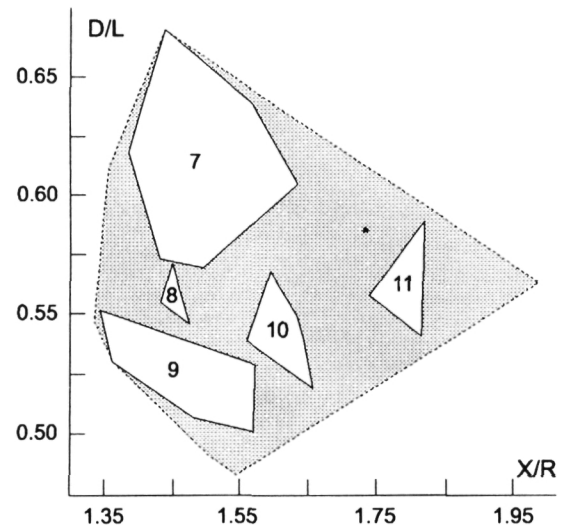
13

Fig. 11. Example of total separation of selected local samples within the "*O. fulgurator-reticularis* complex" (gray zone). Scatter diagram: X/R vs. D/L . Minimum convex polygons. **1.** CURAÇAO, (*O.* cfr. *nivosa* Marrat); **2.** PUERTO RICO (*O. reticularis* Lamarck); **3.** BARBADOS, deep water (*O. barbadensis* Petuch & Sargent); **4.** BERMUDA (*O. bifasciata jenseni* Petuch & Sargent); **5.** BRAZIL, Bahia (*O. circinata* Marrat); **6.** VENEZUELA, Margarita I. [*O. fulgurator* (Röding)].

4.4. Morphological continuum.

Much effort (research on this project started in 1987) has been invested in trying to break the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" into objective subgroups, mainly by using the methods already applied to the Indo-Pacific "*O. miniacea* complex" based upon *O. miniacea* (Röding, 1798) (TURSCH & GREIFENEDER 1996). All these attempts (many combinations of variables were tested) failed consistently.

In the Western Atlantic, all the local populations of the "*O. fulgurator-reticularis* complex" can be objectively separated from some (or even many) others, as illustrated by the scatter diagrams of Figs. 11 and 12. The same situation is met in the Eastern Pacific for the members of the "*O. spicata* complex", as illustrated in the scatter diagrams of Fig. 13.

These separations are invariably obliterated by the inclusion of some additional population(s). As one example amongst many, Fig. 14 groups the populations previously separated in Figs. 11 and 12, with the addition of only four other local samples. Every one of these distinct populations is now linked to every other by an unbroken chain of intermediates, forming a continuum.

Even without any measurement, the existence of a continuum can be sensed just by glancing at Plates 6, 7, 8 and 9, in which the type material of the various taxa constituting the "*O. fulgurator-reticularis* complex"

has been arranged by grouping specimens according to resemblance. These plates, however, give only a limited view of the total variation range because many local forms have not been described.

Fig. 12. Example of total separation of selected local samples within the "*O. fulgurator-reticularis* complex" (gray zone). Scatter diagram: X/R vs. D/L (same variables as in Fig. 11). Minimum convex polygons. **7.** CUBA, Guantanamo (unnamed form); **8.** ST. MARTIN (*O. nivosa* Marrat); **9.** FLORIDA, off Punta Vadra, deep water (*O. bollingi* Clench); **10.** COLOMBIA, Santa Marta (*O. goajira* Petuch & Sargent): **11.** VENEZUELA, Paranaguá Peninsula [*O.* cfr. *fulgurator* (Röding)].
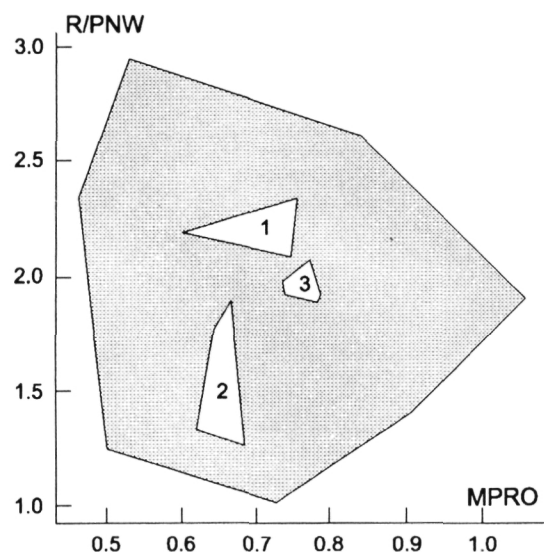
Fig. 13. Example of total separation of selected local samples within the "*O. spicata* complex" (gray zone). Scatter diagram: MPRO vs. R/Pnw. Minimum convex polygons. **1.** PANAMA, Bayarena, 20-30 m. **2.** MEXICO, Baja California, La Paz, shallow water; **3.** COCOS Is., 12-20 m (*O. spicata deynzerae* Petuch & Sargent).
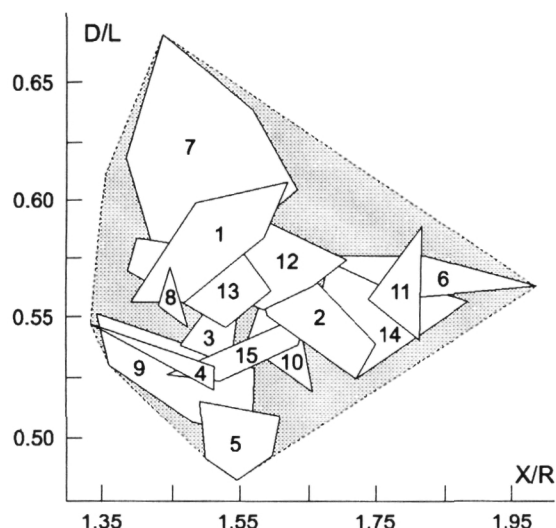
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Fig. 14. Local populations within the "*fulgurator-reticularis* complex" (gray zone) form a morphological continuum: an example. Same variables and populations as in Figs. 11 and 12, 4 populations added: 12 to 15. Scatter diagram: X/R vs. D/L). Minimum convex polygons. **1.** CURAÇAO, (*O.* cfr. *nivosa* Marrat); **2.** PUERTO RICO (*O. reticularis* Lamarck); **3.** BARBADOS, deep water (*O. barbadensis* Petuch & Sargent); **4.** BERMUDA (*O. bifasciata jenseni* Petuch & Sargent); **5.** BRAZIL, Bahia (*O. circinata* Marrat); **6.** VENEZUELA, Margarita I. [*O. fulgurator* (Röding)]; **7.** CUBA, Guantanamo (unnamed form); **8.** ST. MARTIN (*O. nivosa* Marrat); **9.** FLORIDA, off Punta Vadra, deep water (*O. bollingi* Clench); **10.** COLOMBIA, Santa Marta (*O. goajira* Petuch & Sargent): **11.** VENEZUELA, Paranaguá Peninsula [*O. fulgurator* (Röding) variant]; **12.** DOMINICAN REPUBLIC (*O. jamaicensis zombia* Petuch & Sargent); **13.** HONDURAS (*O.* aff. *ernesti* Petuch); **14.** ARUBA (*O.* cfr. *sargenti* Petuch); **15.** ST. VINCENT (unnamed, dark form).

Petuch & Sargent (1986: 119-122) claimed that, "based on shell morphology", the taxa we here place in the "*O. fulgurator-reticularis* complex" break up into groups: the *reticularis* group ("characterized as being ovate shells with rounded outlines and by having variable amounts of triangle net color patterns"), the *bifasciata* group ("slender, cylindrical, elongated shells with fairly straight sides"), the *nivosa* group ("elongated shells with straight or slightly rounded sides ... flattened spires and intricate, fine-netted color patterns") and the *tisiphona* group (said to " ... resemble the Panamic *O. spicata* and *O. incrassata* groups"). We could find no basis whatsoever on which to segregate the above groups.

Exactly the same situation was observed for the "*O. spicata* complex". As one example amongst many, Fig. 15 adds just two other local samples to the populations previously separated in Fig. 13. Here again, one sees the formation of a continuum.

In conclusion: we have found no way of separating any of the populations (or group of populations) from _all_ the others. The "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" each consist of a *morphological continuum* of local forms (see § 3.3).

4.5. Clinal variation.

Although neighbouring populations do not necessarily resemble each other (see § 4.2), the populations of the "*O. fulgurator-reticularis* complex" display a quasi-clinal variation of *some* characters, such as the protoconch size. This can be seen, for instance, in Fig. 16, showing the distribution of the largest local measurements of PAT18 (the diameter of the penultimate nuclear volution, see Fig. 2).

This quasi-clinal variation, from Northern South America outwards, is not restricted to protoconch characters but is also reflected in the general shape of shells. Globose shells (*O. fulgurator s.s.*) are found only around Venezuela and Aruba, whereas more cylindrical, elongated shells are found at both ends of the distribution range, in Brazil (the form *circinata*) and in Florida. Here again, the variation is roughly clinal, as shown in Fig. 17, the distribution of the largest local measurements of D/L (breadth of the body whorl relative to the length of the lip). A quite similar clinal distribution (not illustrated here) is observed for the mean values of D/H.

No such clines have yet been observed for the forms of the "*O. spicata* complex", in the Eastern Pacific.
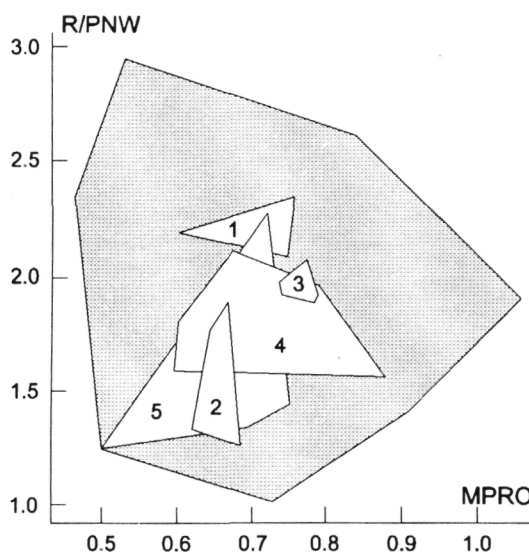

Fig. 15. Local variants within the "*O. spicata* complex" (gray zone) form a morphological continuum: an example. Same variables and populations as in Fig. 13, 2 populations added: 4 and 5. Scatter diagram: X/R vs. D/L). Minimum convex polygons. **1.** PANAMA, Bayarena, 20-30 m. **2.** MEXICO, Baja California, La Paz, shallow water; **3.** COCOS Is., 12-20 m (*O. spicata deynzerae* Petuch & Sargent). **4.** MEXICO, Baja California, Santa Rosalia, shallow water; **5.** PANAMA, Cebaco I., 35-40 m.
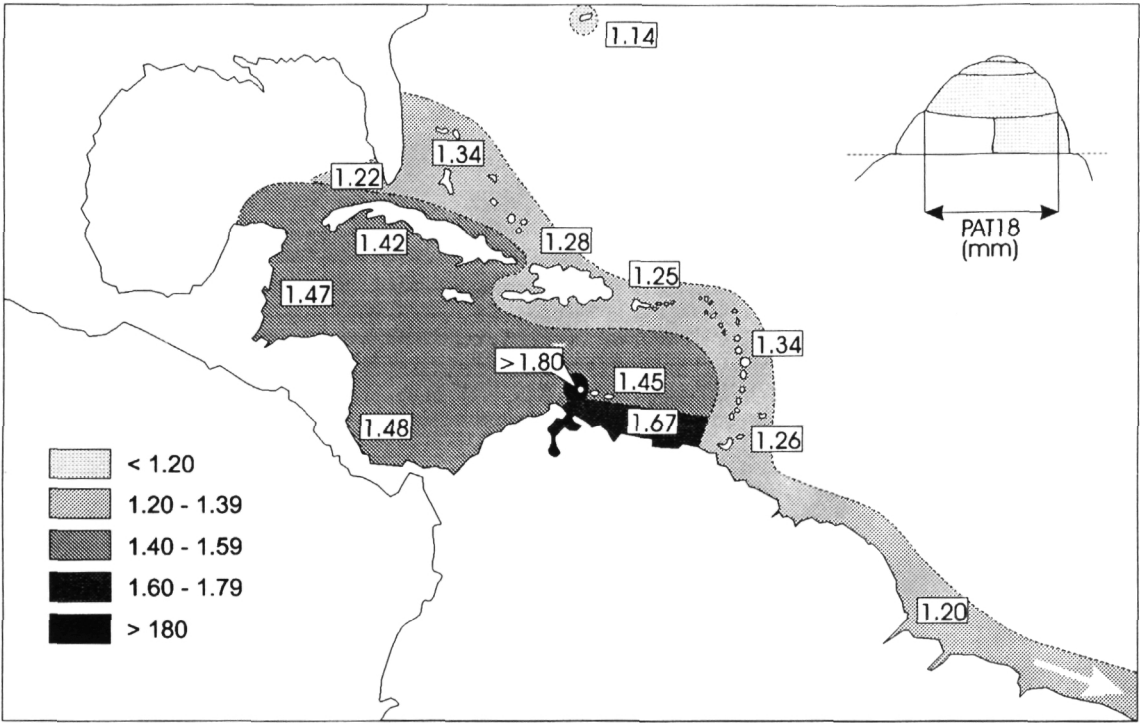
15

Fig. 16. "*O. fulgurator-reticularis* complex". Clinal variation of the protoconch measurement PAT18. Distribution of maximal observed values (see text § 4.5). Only a few values are given, for clarity. The values for isophene lines are arbitrary.
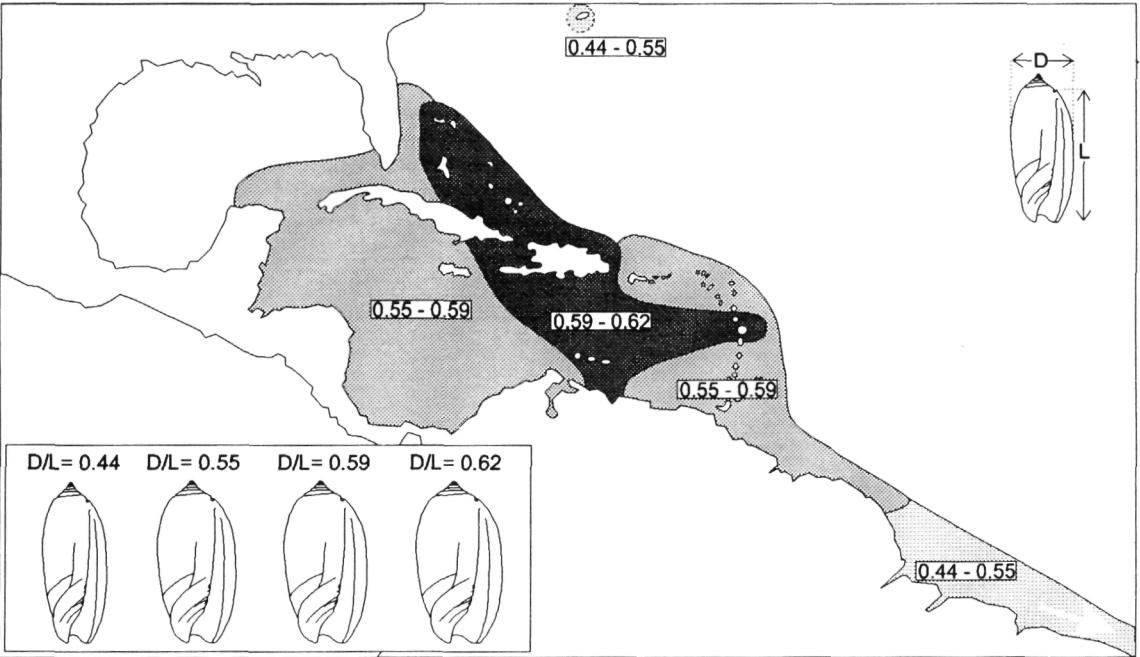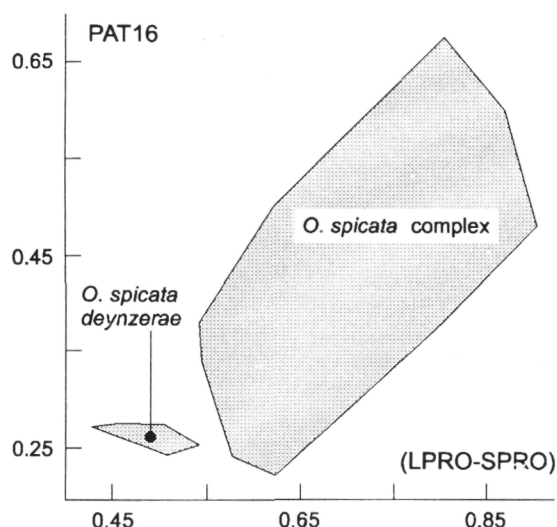
Fig. 17. "*O. fulgurator-reticularis* complex". Clinal variation of the teleoconch character D/L. Distribution of maximal observed values (see text § 4.5). Only a few values are given, for clarity. The values for isophene lines are arbitrary.

Fig. 18. "*O. spicata* complex". Separation of *O. spicata deynzerae*. Scatter diagram: PAT16 vs. (LPRO-SPRO). Minimum convex polygons. See text § 5.3.

5. INTERPRETATION

5.1. *Oliva fulgurator* (Röding, 1798).

Three independent arguments indicate that all the cognate taxa forming the "*O. fulgurator-reticularis* complex" constitute one single, highly variable species. We are certainly not the first to reach this conclusion:

> "*Ol. fusiformis*, Lam. [the former name for *O. fulgurator* (Röding)], is a shell that appears characteristic when one has only *types*, but one finds all possible intermediates and we do not understand why Mr. Reeve did not propose its reunion with *reticularis*, as he has done for others."
>
> DUCROS DE SAINT GERMAIN (1857: 54)
> (*translation ours*)

The first argument is purely phenetic. In spite of much effort to that end, none of the taxa constituting the "*O. fulgurator-reticularis* complex" (cited in the synonymy of *O. fulgurator*) could be separated from *all* the others on the basis of shell measurements. The range of variation of both the teleoconchs and the protoconchs is quite extraordinary for the genus *Oliva*, but all intermediate forms are present. The various populations form a morphological continuum (see § 4.4). Analysis of the colour patterns of the shells fully confirms this view.

The second argument is based on distribution data. All the taxa constituting the "*O. fulgurator-reticularis* complex" are systematically allotopic (see § 4.3). This mutual exclusion of so many *Oliva* 'species' is highly unusual. It is well known to anyone who has collected in the Indo-Pacific that most (if not all) species of *Oliva* are found together with other, congeneric species. Up to 12 species of *Oliva* have been observed to live together in the same microhabitat in Hansa Bay, Papua New Guinea (VAN OSSELAER *et al.* 1993). PETUCH & SARGENT (1986) report that "over twenty"

Oliva species can be found living together in some Indo-Pacific localities. So, one must now ask the question: "How can we explain that the many Caribbean 'species' of the '*O. fulgurator-reticularis* complex' do **never** occur together?" The simplest (and most likely) answer is that they are not different species but only local populations of the same species.

A third, independent argument for the conspecificity of all the populations forming the "*O. fulgurator-reticularis* complex" stems from the quasi-clinal variation of some shell characters over the distribution area (see § 4.5). It is most improbable that the observed pattern of variation reflects an environmental cline. The 1.20-1.39 mm isophene zone in Fig. 16, for instance, stretches over very varied types of sediment, in very diverse physical conditions. An interpretation in terms of clinal gene variation within a same species is much more likely. Note: the observed pattern (of central populations being distinct from Northern and Southern populations which resemble each other) appears to be rather common in other zoological groups. It is familiar to ornithologists under the name of "leapfrog" pattern of geographic variation (see REMSEN 1984).

The differences in protoconch size observed between extreme forms of the "complex" are much greater than in any other *Oliva* species we know of. This does not indicate separate specific status, the range of variation being continuous.

Many of the populations forming the species are today commonly referred to as *O. reticularis* Lamarck, 1811, although the original concept of the species was propably quite different (see the section Systematics). We are nevertheless compelled to use the name *O. fulgurator* (Röding, 1798), which has priority, notwithstanding that it originally designated and is still commonly used for a form which has a restricted distribution and is less common in collections.

5.2. *Oliva spicata* (Röding, 1798).

As in the case of *O. fulgurator* (Röding, 1798), all the examined populations of the "*O. spicata* complex" (save one, see § 5.3) form one single, compact morphological continuum (see § 4.4). We have therefore to consider these populations as members of one same species: *Oliva spicata* (Röding, 1798). Here also, the range of variation of both the shells and the protoconchs is quite extraordinary for the genus *Oliva*, but all forms are linked by intermediates. Analysis of the colour patterns of the shells does again fully confirms this view.

5.3. *Oliva spicata deynzerae* Petuch and Sargent, 1986.

This taxon (see PL. 4, FIG. 5) is restricted to the Cocos Islands and appears to be very closely related to *Oliva spicata* (Röding, 1798). It is nevertheless objectively separated from *all* other forms of the "*O. spicata* complex" in a scatter diagram of LPRO-SPRO *vs.* PAT16 (see Fig. 18). Very similar results are obtained

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with scatter diagrams of SUT/L *vs.* PAT16 and of NW *vs.* PAT16 (not illustrated), the major discriminant being PAT16.

The separation gap is narrow and rests upon a rather small sample (7 only specimens of the Cocos Is. taxon), so it is not impossible that the observed gap could be filled by additional specimens. We shall follow the advise of MAYR & ASQUITH (1991: 37) on such cases (allospecies) and attach the Cocos Is. population as a subspecies (*deynzerae* Petuch and Sargent, 1986) to its closest relative, *O. spicata* (Röding, 1798).

5.4. *O. spicata* and *O. fulgurator*: separate species?

It has been seen (§ 4.1, fig. 7) that the Eastern Pacific "*O. spicata* complex", as a whole, could not be objectively separated on morphometrical grounds from the Western Atlantic "*O. fulgurator-reticularis* complex". Were it not for the existence of the Panama land bridge, one would have little choice but to combine the two complexes into one single morphospecies. This logical step was indeed taken long ago by DUCROS DE SAINT GERMAIN (1857: 52-56), at a time when the locality data of most shells were unreliable. His *O. reticularis* Lamarck, 1811 –which he considered to have a nearly world-wide distribution– included a long list of taxa, known today to be restricted either to the Eastern Pacific or the Western Atlantic faunas.

Within the biological species concept, we cannot anymore take such a simple stand (and we find ourselves in the general problem of species with a discontinuous distribution). The two "complexes" cannot anymore meet to possibly interbreed, and have now been separated by the Panama land barrier for an estimated 1.6 million years (see PETUCH & SARGENT 1986: 119). Therefore, as a working hypothesis until tested by genetic studies, the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" will be here considered as distinct species.

The two complexes certainly share a common ancestry and constitute one more example of the many pairs of 'geminate species', sister taxa of which one element is present in the Panamic region, the other in the Caribbean. In nearly all cases, these 'sister taxa' are considered to now form distinct species. Final closure of the waterway linking the Pacific to the Atlantic occured about 1.6 Ma (millions years ago) according to PETUCH & SARGENT (1986: 119), 3.1-2.8 Ma according to COATES & OBANDO (1996: 21), in any case an acceptable "divergence time " for species separation (see COLLINS 1996). Today, the Caribbean and the Panamic regions are not only geographically separated; they constitute two strikingly different realms. Southern Caribbean waters are in average 2° C warmer and 1.5 $^{o}/_{oo}$ more saline than those of the eastern equatorial Pacific. The latter, in addition, have strong seasonal upwellings causing large increases in primary productivity (see TERANES, GEARY & BEMIS 1996).

The eastern equatorial Pacific also has much stronger tides, is subject to El Niño southern oscillation climate anomalies, more intense predation and a much poorer coral reef development (see JACKSON, JUNG & FORTUNATO 1996).

Populations of the "*O. fulgurator-reticularis* complex" (Western Atlantic) often differ amongst themselves as much as they differ from populations of the "*O. spicata* complex" (Eastern Pacific). But the two "complexes", although not objectively separable by shell measurements, do nevertheless have different trends. In general, Panamic specimens have a more puncticulated colour pattern on the body whorl (the starting point of the chevrons is marked by a dark spot). In addition, the body whorl is often more angular at the lip (this is not detectable by our measurements), the "*bifasciata* colour pattern" with two sharply contrasting dark, spiral bands (see Pl. 99, Fig. 99) is absent (or at least very rare), while all dark (melanistic?) specimens are much more frequent.

So, albeit a few cases could lead to confusion, the experienced *Oliva* student does today rarely err in separating Atlantic from Panamic specimens. In most instances, it is quite possible that we just recognise well-known localities, characterized by familiar forms, instead of using reliable, objective discriminants at the species level. Errors in separation were much more common one century ago. Many kinds of shells were then available (possibly more than today, due to the variety of ports of call of the sailing ships) but their origin was uncertain (see § 1.1.2) and no reliable conclusions could be drawn.

Taxonomic distinction of non objectively separable taxa of on the basis of evident geographic isolation is not restricted to taxa separated by the Central American land barrier and is now widely admitted. For instance, the Panamic *Conus dalli* Stearns, 1873 and the Indo-Pacific *C. textile* L., 1758 are not separable (according to A. KOHN, private communication 1997).

6. DISCUSSION

6.1. Partial isolation of populations.

The most striking characteristic of the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" is the high endemism of mutually exclusive local forms (many of these forms have been named). This has also been recognized by others. For instance, Petuch & Sargent (1986: 120), refering to their "*bifasciata* group" (see $ 4. 4) say that "Many of these species are endemic to isolated seamounts and deep water pockets".

The situation is far from being unique in the genus *Oliva*. Within the distribution limits of the species, and provided the species is present, every isolated little beach of the Indo-Pacific that we have examined appears to have one (and only one) local form of *O. oliva* (L., 1758). Many of these local forms are quite recognisable. Of course, intrapopulation variants are

common, but these are linked by sympatric (syntopic) intergrades. This is the best argument for saying that *O. oliva* is only one species (all populations forming one single morphological continuum). Very similar cases are provided by *O. miniacea* (Röding, 1798), *O. amethystina* (Röding, 1798) and many other *Oliva* species. We are just lucky that many of these local Indo-Pacific forms have not yet been named as species or subspecies.

One possible explanation is genetic. Such a situation can occur if successful, long-distance transport and settlement of the larvae is frequent enough to allow occasional gene flow between conspecific populations but rare enough to allow some genetic drift of the local isolates. The efficiency of larval transport and settlement will of course vary from species to species; if it is highly efficient there will be little local variation. Many *Oliva* species [for instance *O. splendidula*, *O. porphyria*, *O. caerulea* (Röding, 1798)] are indeed very constant over all their distribution range.

Another explanation would be to consider that the different local populations are only ecotypes, arising from the expression of a same genotype in different local environments. In this hypothesis, larval transport should play a secondary role, if any. The great number of local forms within many *Oliva* species would also imply an extraordinary sensitivity to minute environmental changes.

Distribution data support the first, genetic hypothesis. No *Oliva* species has been reported from Clipperton Island (EMERSON, 1994), or from the Revillagigedo Islands (EMERSON, 1995), distant of about 600 and 375 miles from Mexican mainland, respectively. The much larger Galapagos (see FINET 1991) –about 600 miles from the mainland– have two species [*O. porphyria* (Linnaeus, 1758) and *O. kaleontina* Duclos, none belonging to the "*O. spicata* complex"]. The somewhat less isolated Cocos islands (about 300 miles from the mainland) have one endemic species (*O. foxi* Stingley, 1984) and one endemic subspecies (*O. spicata deynzerae* Petuch & Sargent,

1986). This indicates a weak efficiency of successful, long-distance transport and settlement of larvae in the "*O. spicata* complex". Established populations generally contain large numbers of individuals, so the effect of ocasional larvae immigration can be expected to be rapidly diluted in a large gene pool.

Dr. P. E. PENCHASZADEH (private communication) together with Dr. Juan DIAZ, observed and collected in small islands off Venezuela several specimens of a form of "*Oliva circinata*" laying long ribbons of eggs, anchored in the substrate. This phenomenon (not reported yet for other *Oliva* species) could explain the great endemism of local forms, larval development of *Oliva* being known to occur within the egg capsule (OLSSON & CROVO 1968).

The "crazy-quilt" distribution pattern of local populations is not unique to *Oliva* species. A similar pattern is observed for many taxa of *Conus* in the Cabo Verde region and for many forms of *Cymbiola (Cymbiolacca) pulchra* in Quensland, Australia (POPPE & GOTO, 1992). Stable differences between allopatric populations were reported by PARTH (1995) for taxa of the muricid genus *Haustellum* .

6.2. Dynamic environment.

One can quite safely assume that speciation in the genus *Oliva* follows the normal, allopatric (or vicariant) process (see Fig. 19, a, b). This starts by the advent of a geographical barrier restricting the gene flow between populations of a same species. These populations (now partially or totally isolated) will then undergo divergent evolution, possibly to the point where they cannot interbreed any more when brought back into contact. Once started, the speciation process is not irreversible. It might abort for a variety of causes (see Fig. 19, c), for instance if the geographical barrier does not persist long enough (which is precisely the case advocated here above). In any case, speciation is not a sudden event. The process takes place over a large number of generations and there is necessarily a period in time during which the speciation issue is undecided.
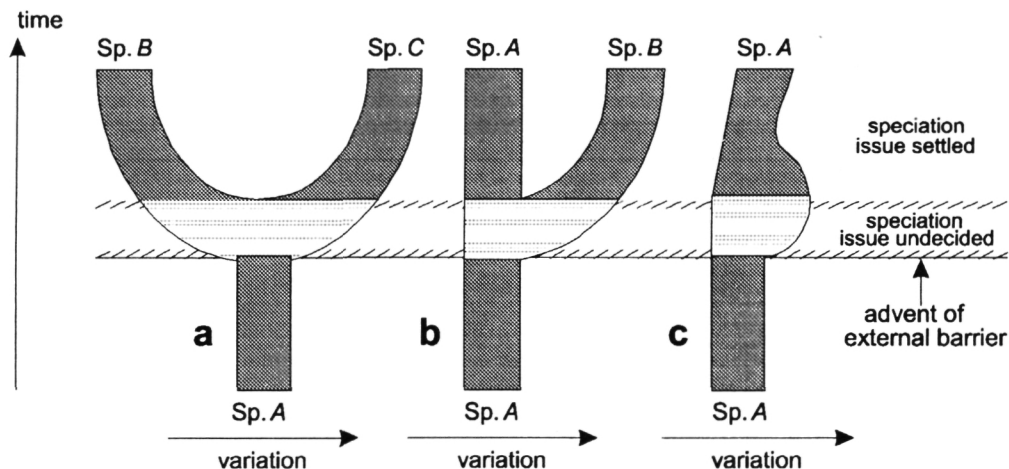

Fig. **19**. The problem of incipient species. **a**: speciation by splitting (allopatric speciation by vicariance). **b**: speciation by budding (peripatric speciation). **c**: aborted speciation. See text § 6.2.

The recent geological history of the Caribbean region is one of many important variations of the sea-level, resulting in huge modifications of the coastlines. The Western Atlantic and the Eastern Pacific regions were repeatedly linked by seaways, then isolated again by emergences of the Panama Isthmus. Many Caribbean islands were also repeatedly separated, then reunited, sometimes into new combinations [see maps figs. 3 (p. 61), fig. 5 (p. 65), fig. 11 (p. 109), fig. 12 (p. 111), fig. 13 (p. 113), fig. 14 (p. 125) in PETUCH 1988; also maps 2.9 and 2.10 in COATES & OBANDO, 1996)].

These geological circumstances provided an ideal stage for a scenario of repeated isolations of populations, reflected in morphological changes (due to genetic drift or/and ecological factors). These episodes of isolation were followed by reunions (and aborted speciations and introgressions). This history also allowed geographical heterochrony –the persistence of Neogene faunas in "relict pockets" into the Recent fauna, [PETUCH 1982, PETUCH 1988: 149-200, map fig. 19 (p. 168)]. In response to such a dynamic geography, *Oliva* species in which succesful, long-distance larval transport and settlement of larva is of weak efficiency (see above, § 6.1), can become highly dynamic in their morphological evolution. It is known that changes can be rapid: one example has been reported of a small isolate of an *Oliva* species [*O. amethystina* (Röding, 1798)] undergoing detectable morphological modifications within the time span of a few decades (TURSCH 1994).

6.3. Nomenclature: fixed names for dynamic species.

It could be argued that populations between which the gene flow is restricted are *incipient species* and should therefore be named. It is of course conceivable that some pairs of such populations, if brought into contact, could not interbreed anymore but we have yet no factual evidence to that point.

An apparent paradox is that, when the speciation issue is undecided, the nomenclatural situation is not. As said by DAWKINS (1996: 96): "*In a way, our naming procedures are set up for a pre-evolutionary age when divides were everything and we did not expect to find intermediates*". In any case, the Code of Nomenclature simply has no provision for *hypothetical*, future species. If one wishes to draw attention to such cases, the best one can do is using infrasubspecific (form) names, which have no nomenclatural standing.

7. SYSTEMATICS

In this 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. The abbreviation "*q.v.*" (*quod vide*) means "*see under that name*".

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).

The taxonomical status of every name has been discussed separately. This entails much repetition but allows the reader to inquire about a particular taxon without having to read all the text.

In deference to conchological tradition, the following "Description" paragraphs are largely based upon shell ornamentation, which is notoriously variable in the genus *Oliva*. So, these sections can serve *only* for quick identification. The species have *not* been delimited on these characters but on morphometrics (see § 4 and 5). This exploratory task being accomplished, detailed measurements are generally not indispensable any more for identification of individual specimens. All characters common to the genus (shell smooth, shiny, etc.) have been 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. *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.

Family OLIVIDAE Latreille, 1825

Subfamily OLIVINAE Latreille, 1825

Genus *Oliva* Bruguière, 1789

Oliva foxi Stingley, 1984.

Oliva foxi Stingley, 1984: 28.

Description.
SIZE: up to about 40 mm.
SHAPE: fusiform-elongated.
SPIRE: conical, elevated, with large spire callus, uniformly purple-gray to beige, covering ½ to 4/5 of the whorl.
CHANNEL: rather narrow.
SUBCHANNEL PATTERN: fasciculated, of short brown stokes.
SHELL BACKGROUND: pale cream to whitish.
COLOUR PATTERN: Faint pink tent pattern overlaid with distinct dark brown triangular areas, speckled

with white tents, and heavy brown lines, formed of rows of small isoscele triangles.

COLUMELLA: white, with faint purple base.

SUPRAFASCIOLAR BAND: lower half with chevron-like brown marks.

APERTURE: suffused with orange-saffron. Inner margin of lip milky white.

PROTOCONCH: pink to bright purple-pink.

Diagnosis. Distinguished from all other American *Oliva* by its unmistakable, outstanding colour pattern, saffron aperture and small size.

Distribution. Known only from 18 m, white sand, Cocos Islands, Costa Rica.

Oliva foxi Stingley, 1984. This taxon, broadly sympatric with *O. spicata deynzerae* is easily separated from all members of the "*O. spicata* complex" (see fig. 3) and is an **objective species** (see § 4.1), in agreement with the conclusions of P. & S. (1986). No synonyms. The holotype (see PL. 4, FIG. 1) has been previously illustrated by KAICHER 1988 (Part III, card no. 5249). Three paratypes are illustrated (see PL. 4, FIGS. 2-4). This species has been placed by PETUCH & SARGENT (1986: 123) in their "*splendidula* group", the argument being: "Both shells exhibit a very hig gloss and colour patterns that include bright pinks and purples and wide bands of dark brown. Both species also have yellow or orange apertures".

Oliva fulgurator (Röding, 1798).

Porphyria fulgurator Röding, 1798: 36, sp. no. 453.

> *Oliva ispida* (Link) (not Röding, 1798), 1807: 96:
> *Oliva fusiformis* Lamarck, 1811: 318, sp. no. 30; Encycl. Pl. 367, figs. 1a, 1b.
> *Oliva reticularis* Lamarck, 1811: 314, sp. no. 16. Encycl. Pl. 361, figs. 1a,b.
> *Oliva olorinella* Duclos, 1835: Pl. 6, figs. 15-16; text in *Illustr. Conch.*: 14 (*pars*).
> *Oliva obesina* Duclos, 1840: Pl. 16, figs. 9-11, text in *Illustr. Conch.*: 26.
> *Oliva timoria* Duclos, 1840: Pl. 17, figs. 11-13; *Illustr. Conch.*: 19 (*pars*).
> *Oliva aldinia* Duclos, 1845: 25, Pl .26, figs. 6-7.
> *Oliva broderipi* Ducros de St.Germain, 1857: 62, sp. no. 39, Pl. 2, 39,a,b.
> *Oliva jamaicensis* Marrat, 1867: 213-15.
> *Oliva oblonga* Marrat, 1867: 215.
> *Oliva pallida* Marrat, 1867: 215.
> *Oliva bewleyi* Marrat, 1870: 7, sp. no. 25, fig. 44.
> *Oliva figura* Marrat, 1870: sp. no. 26, fig. 45.
> *Oliva formosa* Marrat, 1870: sp. no. 16, figs. 29, 30.
> *Oliva graphica* Marrat, 1870: sp. no. 18, Pl. 3, fig. 36.
> "*Oliva oblongata* Marrat, 1870" (auct).
> *Oliva porcea* Marrat, 1870: 6, sp. no. 19, Pl. 3, fig. 35.

> *Oliva olivacea* Marrat, 1870: 7, sp. no. 28, Pl. 4, figs. 46-47, 51-53.
> *Oliva hepatica* ; Marrat (not Lamarck, 1811), 1871: sp. no. 14, Pl. 3, figs. 27-28.
> *Oliva bullata* Marrat, 1871: 40, sp. no..215, Pl. 24, fig. 448.
> *Oliva circinata* Marrat, 1871: sp. no. 109, Pl. 17, fig. 277.
> *Oliva mercatoria* Marrat, 1871: sp. no. 111, Pl. 17, figs. 268-269.
> *Oliva nivosa* Marrat, 1871: sp. no. 112, Pl.17, fig. 276; Pl. 25, fig. 472.
> *Oliva reclusa* Marrat, 1871: sp. no. 27, Pl. 17, fig. 264.
> *Oliva bifasciata* Küster in Weinkauff, 1878: 38, sp. no. 35, Pl. 5, fig. 11; Pl. 10, figs. 10, 11.
> *Oliva cribraria* Marrat, 1883?. Published in ... ?
> *Oliva reticularis bollingi* Clench, 1934: 142, Pl. 7, figs. 3, 4.
> *Oliva reticularis greenwayae* Clench, 1937: 17-26.
> *Oliva pattersoni,* Clench, 1945 4: 49.
> *Oliva drangai* Schwengel, 1951: 117, Pl. 8, figs. 2-3.
> *Oliva antillensis* Petuch & Sargent, 1986: 124, Pl. 20, figs. 11, 12.
> *Oliva bahamasensis* Petuch & Sargent, 1986: 125, pl. 20, figs. 15-18.
> *Oliva barbadensis* Petuch & Sargent, 1986: 126, pl. 20, figs. 19-22.
> *Oliva bifasciata jenseni* Petuch & Sargent, 1986: 128, Pl. 21, figs. 16, 17.
> *Oliva finlayi* Petuch & Sargent, 1986: 129, Pl. 22, figs. 5-7.
> *Oliva goajira* Petuch & Sargent, 1986: 133, Pl. 23, figs. 1 2, 13.
> *Oliva jamaicensis zombia* Petuch & Sargent, 1986: 136, Pl. 24, figs. 17, 18.
> *Oliva magdae* Petuch & Sargent, 1986: 138, Pl. 25, figs. 1-3.
> *Oliva bifasciata sunderlandi* Petuch, 1987: 28, Pl. 3, figs. 13, 14.
> *Oliva circinata tostesi* Petuch, 1987: 141.
> *Oliva sargenti* Petuch, 1987: 105, Pl. 17, figs. 2, 3.
> *Oliva maya* Petuch & Sargent, 1986: 139, Pl. 25, figs. 4, 5, 8, 9.
> *Oliva contoyensis* Petuch, 1988: 54, Pl. 32, figs. 12, 13.
> *Oliva ernesti* Petuch 1990: 63, figs. 19, 20.

Description. Within local populations the shells are quite homogeneous. The ranges of variations here under refer to differences *between* populations.

SIZE: from about 25 mm to over 70 mm.

SHAPE: very variable, from elongated-fusiform to nearly cylindrical, to globose.

SPIRE: conical to telescopic. Relative height very variable. Spire callus covering from one half to nearly all of whorl; shape from flat to convex; colour from white, beige, purplish to brown, often darker at upper margin. Callus without distinct colour strokes.

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CHANNEL: of medium width.

SUBCHANNEL PATTERN: fasciculated, very variable. Not seen in albinistic, melanistic and in rare, unicoloured specimens.

SHELL BACKGROUND: from white to cream, to yellow, to gray.

COLOUR PATTERN: tents and chevrons of very variable size, width and intensity, sometimes arranged into vertical series. Colour of markings varies from pink to reddish, brown or black. In some populations, markings are diffuse in the direction of growth. The angle of chevrons is large and does not vary appreciably with growth (see Plate 3, fig. 2). Two large spiral bands are formed by local reinforcement of the pattern. Overlay of additional uniform brown colour may cover the whole shell (the so-called "*pattersoni* pattern", see PL. 8, FIG. 6), or may appear in two or more sharply delimited spiral bands (the so-called "*bifasciata* pattern", occurring in widely separated populations, from Colombia to Florida).

COLUMELLA: from nearly smooth, overlaid with thick enamel, to heavily plaited. Colour from white to greyish, to pale purple.

FASCIOLE: mostly uniform white to greyish, base can be suffused with colour. Ridges brown in some populations.

SUPRAFASCIOLAR BAND: very variable.

APERTURE: from white to beige, to faint lilac and greyish blue. Inner margin of lip: variable, from aperture colour to row of darker markings. Aspect depends much on age.

PROTOCONCH: large to extremely large.

Diagnosis. The large values of the protoconch character RES5 and the small NW (number of nuclear volutions) (see Fig. 8, 1-8) set *O. fulgurator* apart from all other *Oliva* species, excepted *O. spicata*. Distinguished from *sayana* by constant angle of chevrons. Distinguished from *O. scripta* by a much narrower channel.

Distribution. Very widely distributed in the Western Atlantic, from Bermudas to Southern Brazil.

SYNONYMY.

O. fulgurator (Röding, 1798), based upon the unambiguous figure 562 of MARTINI (see PL. 6, FIG. 10), is the **valid name** (see TURSCH, DUCHAMPS & GREIFENEDER 1994) for an **objective species** (see § 5.1, 5.4). This is agreement with the conclusions of Z. & P. (1969), W. & A. (1978) and P. & S. (1986). This species is very close (or identical) to the fossil *O. schepmani* Weissbord, 1962 (not treated here).

The following names are synonyms or designate local forms:

Oliva ispida (Link) (not Röding, 1798), 1807. This taxon (being based upon the same figure 562 of MARTINI) is an **objective junior synonym of** *O. fulgurator* (Röding, 1798). It was *O. spicata* (Röding, 1798) for B. & B. (1960); *O. fulgurator* (Röding, 1798) for Z. & P. (1969).

Oliva fusiformis Lamarck, 1811. For original illustration, see PL. 6, FIG. 5. This has been demonstrated (see GREIFENEDER, DUCHAMPS & TURSCH, 1995) to be an **objective junior synonym of** *O. fulgurator* (Röding, 1798), in agreement with B. & B. (1960), Z .& P. (1969), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). It was *O. reticularis* Lamarck, 1811 for DUCROS de St. GERMAIN (1857).

Oliva reticularis Lamarck, 1811. For the availability of this name, see GREIFENEDER, DUCHAMPS & TURSCH (1995). No type material could be located. The original description is:

"16. Olive réticulaire. *Oliva reticularis*.

O. Cylindracea, alba, subbifasciata; lineis fulvis, subpunctatis flexuoso-angulatis; spirâ acutâ.

Mus., n.12. Encycl., Pl. 361, f. 1.

Martini, Conch. 2, t. 51, f. 561.

Habite... Sur un fond blanc, cette olive offre quantité de lignes en zigzags, rousses, subponctuées. Dans les espaces qu'embrassent deux bandes transverses, ces lignes, plus épaissies et plus colorées, imitent en quelque sorte des caractères d'écriture. Cette olive est peu bombée, a une spire pointue, et ne présente qu'une couleur blanche à son ouverture. Sa longueur est d'environ 45 millimètres. Le bord supérieur du dernier tour est comme dentelé par des taches d'un brun violet, composé de lignes repliées en faisceau."

The illustration in the *Encyclopédie* (Pl. 361, fig. 1, a, b) depicts a specimen inclined at an angle, as evidenced by the aspect of the shoulder, the aperture, and the lower part of the columella. Several other *Oliva* in the *Encyclopédie* are represented in a similar perspective, which, of course, makes a shell appear more globose. So the illustration (see PL. 8, FIG. 9) represents a rather elongated shell, with a peculiar, very concave lip. The large size (45 mm) and the straight sides ("*peu bombée*") indicates that the shell is not the *O. reticularis* of recent authors ("ovate with rounded sides" in P. & S. 1986).

A shell reasonably matching the original illustration has been found in the Récluz collection, at the MHNG, and could possibly be the figured specimen. Shells of this general type are not uncommon in some central Caribbean localities. These forms are linked to the "typical" *O. fulgurator* by an unbroken chain of many intergrading populations. Considerable efforts invested in attempting objective separation, by many different methods and over many years, have always been completely unsuccessful. Much to our regret (for the stability of nomenclature) we are compelled to consider *O. reticularis* Lamarck, 1811 as a local form and a **subjective junior synonym of** *O. fulgurator* (Röding, 1798) (see § 5.1). It was a valid species for Z. & P. (1969), W. & A. (1978) P. & S. (1986) and many other authors.

Oliva olorinella Duclos, 1835. The heterogeneous lot of 8 dirty-white syntypes at MNHN contains specimens of *O. oliva* (L., 1758) (as correctly inferred by KAICHER 1989, who illustrated one such syntype on her card Part IV, no. 5516) as well as

shells of Caribbean origin (see PL. 9, FIG. 2). These could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, *Oliva olorinella* Duclos, 1835 (*pars*) is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). This name is often utilised to designate a whitish, small form from the Bahamas.

Oliva obesina Duclos, 1840. The type material (figured syntype, out of three, see PL. 6, FIG. 1) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). It is very close to *O. aldinia* Duclos, 1845, and to the semi-fossil *O. schepmani* Weissbord, 1962. Three further specimens have been found in the Duclos collection, at Clermont-Ferrand, under the unpublished name "*O. opisia*". *O. obesina* Duclos, 1840 was *O. spicata* Röding for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978); a valid species for P. & S. (1986). Shells very similar to the type material are found in Venezuela, in the province of Nueva Esparta.

Oliva timoria Duclos, 1840. The type material is heterogeneous. One of the syntypes (see PL. 7, FIG. 1) is very similar to a brown *O. obesina* Duclos, 1840 (*q.v.*), so *O. timoria* Duclos, 1840 is (*pars*) a **subjective junior synonym** of *O. fulgurator* (Röding, 1798), in agreement with Ducros, 1857 (as *O. reticularis* Lamarck, 1811).

Oliva aldinia Duclos, 1845. The type series (see PL. 6, FIG. 2) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This is in agreement with B. & B. (1960), W. & A. (1978, as "*aldina*", misspelling) and P. & S. (1986). Very similar specimens are found in Venezuela, in the province of Nueva Esparta.

Oliva broderipi Ducros de St. Germain, 1857. The holotype (illustrated by KAICHER 1989, PART IV, card no. 5560, and rightly said not to be *O. oliva*) is very badly worn (see PL. 7, FIG. 3) but nevertheless recognisable shell. It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). It is very close to (if not identical with) *O. (Strephona) contoyensis* Petuch, 1988 (*q.v.*). *O. broderipi* is *O. ispidula* for B. & B.

(1960), a colour form of *O. oliva taeniata* Link for P. & S. (1986), a form of *O. oliva* (L., 1758) for Z. & .P (1969) and W. & A.. (1978). *O. broderipi* ; Petuch & Sargent (not Duclos,1857), 1986 (p. 108, Pl. 18, figs. 1, 2) bears no resemblance with the type material and is an *O. oliva* (L., 1758), probably from the Indian Ocean.

Oliva jamaicensis Marrat, 1867. This taxon was re-described in the *Thesaurus*: sp. no. 17, Pl. 4, fig. 26. The holotype (illustrated by KAICHER 1988, Part III, card no. 5187) (see PL. 6, FIG. 6) resembles *O. bewleyi* Marrat, 1870 and could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), *O. scripta* Lamarck, 1811 for ABBOTT (1974), possibly *O. scripta* Lamarck, 1811 for W. & A. (1978) and a valid species for P. & S. (1986).

Oliva oblonga Marrat, 1867. This taxon was re-described in 1870 in the *Thesaurus* (sp. no. 11, Pl. 2, fig. 14). The large holotype (illustrated by KAICHER 1989, Part IV, card no. 5484) (see PL. 6, FIG. 7) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. spicata* (Röding, 1798) for B. & B. (1960), KEEN (1971) and W. & A. (1978); a colour form of *O. tisiphona* Duclos, 1845 for P. & S. (1986) and PETUCH (1987); *O. bewleyi* Marrat, 1870 for DIAZ & PUYANA (1994).

Oliva pallida Marrat, 1867. The taxon was re-described in the *Thesaurus*: 27, sp. no. 138, Pl. 21, figs. 341-343. The type material is missing, as already reported by McMILLAN (1985). But the identity of the taxon leaves little doubt because Marrat himself considers it as a synonym of his own *O. nivosa* (*q.v.*). His label for the type material of *O. nivosa* Marrat, 1871 reads: "*O. nivosa* 112 Marrat *pallida* Marrat in Annals & Mag. of N. History". In the Index of the *Thesaurus* one also reads: "*pallida* Marr., nivosa, *Marr.*" It follows that *Oliva pallida* Marrat, 1867 is a **local variety of *O. fulgurator*** (Röding, 1798), linked to all other conspecific forms by many intergrading populations. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and P. & S. (1986); *O. olorinella* Duclos, 1835 for W. & A. (1978). Note: the name *pallida* has been also used by SWAINSON (1831: 78, Pl. 3, fig. 2) for a species of *Agaronia*, by DAUTZENBERG (1910) for a variety of *Oliva flammulata* Lamarck, 1811 and by DAUTZENBERG (1927: 71: 110) for a colour form of *Oliva reticulata* (Röding, 1798).

Oliva bewleyi Marrat, 1870. The holotype (illustrated by KAICHER 1989, Part IV, card no. 5557) (see PL. 7,

FIG. 10) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This is *O. reticularis* Lamarck, 1811 for B. & B. (1960) and W. & A. (1978), a valid species for P. & S. (1986) and DIAZ & PUYANA (1994) who insisted on the extreme variation of this taxon.

Oliva figura Marrat, 1870. The holotype (see PL. 8, FIG. 3) (illustrated by KAICHER 1988, Part III, card no. 5186) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960) and W. & A. (1978). It was a colour form of "*O. jamaicensis brunnea* Marrat" for P. & S. (1986).

Oliva formosa Marrat, 1870. The slim holotype, with several brown spiral stripes (illustrated by KAICHER 1989, Part IV, card no. 5566) (see PL. 9, FIG. 6), could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960) and Z. & P. (1969), a form of the same for ABBOTT (1974), W. & A. (1978) and a colour form of *O. bewleyi* Marrat, 1870 for P & S (1986).

Oliva graphica Marrat, 1870. The swollen, worn holotype (see PL. 6, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5561) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. obesina* Duclos, 1840 for TOMLIN (in FORD 1953); *O. spicata* (Röding, 1798) for B. & B. (1960); *O. scripta* Lamarck, 1811 for OLD (cited in Z & P, 1969), Abbott (1974) and W. & A. (1978); *O. julieta* Duclos, 1840 for Z. & P. (1969) and Keen (1971). It was a valid species for P. & S. (1986: 134, Pl. 23, figs. 7, 8) but their illustration does not at all match the type material.

"***Oliva oblongata*** Marrat, 1870" (auct). This is a misspelling (and a date error) for *O. oblonga* Marrat, 1867 (q.v.). It was *O. spicata* (Röding, 1798) for Z. & P. (1969), W. & A. (1978), Abbott (1974) and P. & S. (1986).

Oliva olivacea Marrat, 1870. This name is available, as *O. olivaceus* Meuschen, 1787 is a nomen nudum (in a rejected work) as noted by W. & A. (1978). The same would apply for *O. olivacea* Karsten, 1789, should the work of that author be rejected by the Commission. Marrat's taxon (illustrated by KAICHER 1988, Part III, card no. 5163), reported as *Oliva olivacea* Meuschen, is certainly a **local variety of *O. fulgurator*** (Röding, 1798), linked to all other conspecific forms by many intergrading populations. It was indeed *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978); *O. bewleyi* Marrat, 1870 for DIAZ & PUYANA (1994). It was a valid species for P & S (1986). Marrat himself wrote "*olivaceus* Meuschen; *reticularis* Lamk." in his caption to Plate IV.

Oliva porcea Marrat, 1870. The very fat holotype (see PL. 6, FIG. 3) is quite similar to *O. obesina* Duclos, 1840, as already stated by TOMLIN (in FORD 1953). It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. spicata* (Röding, 1798) for B. & B. (1960); *O. scripta* Lamarck, 1811 for ABBOTT (1974) and W. & A. (1978); *O. julieta* Duclos, 1840 for Z. & P. (1969) and KEEN (1971).

Oliva hepatica ; Marrat (not Lamarck, 1811), 1871. The shell described in Marrat as *O. hepatica* Lamarck does not correspond to the original, very vague description of Lamarck. Marrat's figures leave little doubt that this is the same as *O. bifasciata* Küster 1878, as already suggested by Z. & P. (1969) and W. & A. (1978). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), possibly a form of the same for Z. & P. (1969), a colour form of *O. tisiphona* Duclos, 1845 for P. & S. (1986). It is in any case a **local variety of *O. fulgurator*** (Röding, 1798). *O. hepatica* Lamarck, 1811 is a nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH 1995).

Oliva bullata Marrat, 1871. The holotype (illustrated by KAICHER 1988, Part III, card no. 5172) (see PL. 9, FIG. 3) is a **local variety of *O. fulgurator*** (Röding, 1798) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. fulgurator* (Röding, 1798) for B. & B. (1960) and W. & A. (1978), a subspecies of the same for P. & S. (1986).

Oliva circinata Marrat, 1871. The holotype (see PL. 9, FIG. 8) (illustrated by KAICHER 1988, Part III, card no. 5526), the four paratypes at MCM, and a probable paratype at AMNH form an homogeneous series that could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. This rather distinctive form very often occupies a peripheral position in scatter diagrams. It also occupies a large, peripheral

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geographic range all along the coast of Brazil, South of the possible geographical barrier formed by the Amazon River. All populations in this region share the same characteristics, with very little variation save that some (for instance one found in 30 m off Recife) are smaller in size. The temptation to consider this as a subspecies was resisted because extremely similar forms occur in deep water off Florida, in Venezuela and in Colombia. So this taxon is here considered to be a **local variety of** *O. fulgurator* (Röding, 1798). *O. circinata* Marrat, 1871 was *O. sayana* Ravenel, 1834 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A. (1978); a colour form of *O. graphica* Marrat, 1870 for P. & S. (1986); *O. figura* Marrat, 1870 for DIAZ & PUYANA (1994). *O. circinata* Martyn, 1789, a *nomen nudum* (in a rejected work) was *O. lignaria* Marrat, 1868 for W. & A. (1978).

Oliva mercatoria Marrat, 1871. The two syntypes at MCM (one figured PL. 6, FIG. 9) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of** *O. fulgurator* (Röding, 1798). This was also the interpretation of B. & B. (1960), Z. & .P (1969), W. & A. (1978) and P. & S. (1986).

Oliva nivosa Marrat, 1871. The holotype at MCM (illustrated by KAICHER 1988, Part III, cards no. 5158, 5159) (see PL. 7, FIG. 9) and one possible paratype could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of** *O. fulgurator* (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & .P (1969), ABBOTT (1974) and W. & A. (1978); a valid species for P. & S. (1986).

Oliva reclusa Marrat, 1871. The holotype (see PL. 9, FIG. 7), illustrated as "syntype" by KAICHER 1988, Part III, (card no. 5247) was correctly described by TOMLIN (in FORD 1953) as "a pale *reticularis* Lam. It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of** *O. fulgurator* (Röding, 1798). Very similar specimens are found in Aruba (see HEMMEN 1981). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A. (1978); a valid species for P. & S. (1986) and PETUCH (1987).

Oliva bifasciata Küster in Weinkauff, 1878. The locality given is "South coast of America (Marrat), probably Brazil and Guyana". The reference "Pl. 10, figs. 8,9" in the text is wrong and is corrected to " Pl. 10, Figs. 10, 11" in the "Erklärung der Tafeln". The

figured specimen (H: 61.39 mm, D: 26.73 mm) (see PL. 8, FIG. 4) SMF no. 9353 represents a striking, but common colour variant, encountered in many Caribbean populations. It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **colour form of** *O. fulgurator* (Röding, 1798). *O. bifasciata* Küster in Weinkauff, 1878 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978); a separate, valid species for P. & S. (1986).

Oliva cribraria Marrat, 1883? This taxon is represented by a properly labelled holotype in MCM. The work in which the publication appeared is unknown. According to McMILLAN (1985) "Description and col. fig. of this species exist in print (two copies); possibly ex Marrat's privately printed *Notebook of a Liverpool Naturalist* (1833)". The upper edge of the fasciole of the beautiful holotype (see PL. 9, FIG. 10) is delimited by a thin, bright purple zone (more vivid than in *O. circinata* Marrat, 1871, to which the shell is very closely related). The type (with a purple protoconch) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of** *O. fulgurator* (Röding, 1798). Locality unknown. This was *O. oblonga* Marrat for TOMLIN in FORD (1953).

Oliva reticularis bollingi Clench, 1934. The heavy holotype (see PL. 7, FIG. 8) (illustrated by KAICHER 1989, Part IV, card no. 5543) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of** *O. fulgurator* (Röding, 1798). *O. bollingi* Clench, 1934 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A. (1978); a subspecies of *O. bifasciata* Küster, 1878 for P. & S. (1986). This form comes from crab traps, off Miami, Florida.

Oliva reticularis greenwayae Clench, 1937. The holotype (see PL. 8, FIG. 5) (illustrated by KAICHER 1989, Part IV, card no. 5562) is extremely similar to the figured specimen of *O. bifasciata* Küster in Weinkauff, 1878 (see PL. 8, FIG. 4). It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** (and colour form) **of** *O. fulgurator* (Röding, 1798). *O. reticularis greenwayae* Clench, 1937 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969) and ABBOTT (1974); *O. bifasciata* Küster,

1878 for W & A (1978) and P. & S. (1986). This form comes from Smith Point, Grand Bahama Island, Bahamas.

Oliva reticularis pattersoni*,** Clench, 1945. The dark, heavy holotype (see PL. 8, FIG. 6) (illustrated by KAICHER 1989, Part IV, card no. 5568) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** (and colour form) **of *O. fulgurator (Röding, 1798). *O. pattersoni* Clench, 1945 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969) and ABBOTT (1974); *O. formosa* Marrat, 1870 for W. & A. (1978) and KAICHER (1989); a colour form of *O. bifasciata bollingi* Clench, 1937 (sic) for P. & S. (1986). This form comes from 5 miles E of Crabbing Point, Great Bahama Island, Bahamas.

Oliva drangai Schwengel, 1951. The light-coloured holotype (see PL. 7, FIG. 7) (previously illustrated by KAICHER 1988, Part III, card no. 5165, as "*O. drangae*") could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). *O. drangai* Schwengel, 1951 was probably *O. scripta* Lamarck, 1811 for W. & A .(1978); a valid species for P. & S. (1986). This form comes from Pigeon Pt., Tobago. Note: the holotype (ANSP 247107) has an abnormal, tilted protoconch. The protoconch of the smaller (H: 18.56 mm; D: 8.46 mm) paratype (ANSP 247093) is normal.

Oliva antillensis Petuch & Sargent, 1986. The holotype (see PL. 9, FIG. 1) (illustrated by KAICHER 1988, Part III, card no. 5245) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form comes from the Southern coast of Gonave Island, HAITI. This was *O. bewleyi* Marrat for DIAZ & PUYANA (1994).

Oliva bahamasensis Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 10) (illustrated by KAICHER 1989, Part IV, 5575) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was caught in a lobster pot, in 200 m off Grand Bahama I.

Oliva barbadensis Petuch & Sargent, 1986. The holotype (see PL. 9, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5531) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form comes from deep water (200 m) off St. James, Barbados. Other deep water specimens from close neighbouring localities have a very different colour pattern.

Oliva bifasciata jenseni Petuch & Sargent, 1986. The holotype (see PL. 7, FIG. 6) (illustrated by KAICHER 1988, Part III, card no. 5202) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected in shallow water (0.5 m), in Bermuda.

Oliva finlayi Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 8) (illustrated by KAICHER 1988, Part III, card no. 5184) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This is a deep water form, from 200 m, Matanzas Bay, Cuba.

Oliva goajira Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 2) (illustrated by KAICHER, 1988, Part III, card no. 5189) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form comes from 60 m off Cabo La Vela, Colombia. It falls within the range of variation of *O. circinata* Marrat, 1871 for DIAZ & PUYANA (1994). An extremely similar form lives in 5-6 m, coarse sand, Tayrona, Colombia.

Oliva jamaicensis zombia Petuch & Sargent, 1986. The holotype (see PL. 7, FIG. 2) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected on sand flats, Southern side of Gonave I., Haiti.

Oliva magdae Petuch & Sargent, 1986. The holotype (see PL. 6, FIG. 8) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was caught in a fish trap, 300 m, off Matanzas Bay, Cuba.

Oliva maya Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 1) (illustrated by KAICHER 5186) could not be separated from the *"fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was trawled by a shrimper in 35 m. off Contoy Is., Yucatan, Mexico. It is broadly sympatric with *Oliva contoyensis* Petuch, 1988, but there is no clear indication that the two taxa are syntopic. For reasons unknown to us, *O. maya* was considered by PETUCH & SARGENT (1986: 121) to belong to their "*sayana* group".

Oliva bifasciata sunderlandi Petuch, 1987. The holotype (see PL. 9, FIG. 5) could not be separated from the *"fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was trawled from 150 m West of Cedar Key, Florida.

Oliva circinata tostesi Petuch, 1987. The holotype (see PL. 9, FIG. 9) (illustrated by KAICHER 1989, Part IV, card no. 5530) and several topotypes could not be separated from a large sample of *O. fulgurator circinata* Marrat, 1871, encompassing several populations. This, being described from a single population, does hardly qualify as a subspecies and is (at best) a **local variety of *O. fulgurator*** (Röding, 1798).

Oliva sargenti Petuch, 1987. The holotype (see PL. 7, FIG. 5) could not be separated from the *"fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected in 5 m, Malmok, Aruba.

Oliva contoyensis Petuch, 1988. The holotype (see PL. 7, FIG. 4) is very similar to that of *O. broderipi* Ducros de St. Germain, 1857 (*q.v.*). It could not be separated from the *"fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected in 35 m. off Contoy I., Yucatan, Mexico. It is broadly sympatric with *Oliva maya* Petuch & Sargent, 1986, but there is no clear indication that the two taxa are syntopic.

Oliva ernesti Petuch 1990. The holotype (see PL. 8, FIG. 7) could not be separated from the *"fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid

arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was trawled in 40 m, silty sand, off Portobello, Panama (East Coast).

The following names have been mistakenly (or very questionably) considered as synonyms:

Oliva oriola ; Duclos (not Lamarck, 1811), 1835: Pl. 10, figs. 1, 2, text in *Illustr. Conch.*: 15. This was *O. spicata* (Röding, 1798) and *O. reticularis* Lamarck, 1811 for W & A (1978). It was *O. spicata* (Röding, 1798) for B. & B. (1960), Z. & P. (1969) and KEEN (1971). Duclos' illustrations of *O. oriola* Lamarck, 1811 are somewhat ambiguous and, in the absence of specimens in the Duclos collection, attribution is most uncertain. It would be better to consider this as a **nomen dubium**. In any case, this is a junior homonym of *O. oriola* Lamarck, 1811 (see GREIFENEDER, DUCHAMPS & TURSCH 1995).

Oliva quersolina Duclos, 1835: Pl. 10, figs.7-8. This is *O. olorinella* Duclos, 1835 for W. & A. (1978) and *O. reticularis* Lamarck, 1811 for Z. & P. (1969), ABBOTT (1974) and P. & S. (1986). *O. quersolina* has been demonstrated to be a **subjective junior synonym** of the Indian Ocean species *O. atalina* Duclos, 1835 (see TURSCH & GREIFENEDER 1996).

Oliva memnonia Duclos, 1845: 15, Pl. 17, figs. 19-20. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A .(1978). The original figures (illustrated by KAICHER 1989, Part IV, card no. 5497) are not recognisable with any certainty. In the absence of type material, it is much safer to consider this name as a **nomen dubium**.

Oliva tisiphona Duclos, 1845. No type material has been located. The characteristic sub-channel pattern of the *"fulgurator-reticularis* complex" is not apparent on the illustrations of DUCLOS and is not mentioned in the original description. Although DUCLOS says this taxon is rather close to *O. oniska* Duclos, 1845, his illustrations are quite problematic and it is certainly safer to consider this as a **nomen dubium**. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A .(1978). P. & S. (1986) consider this to be a valid species, but it is not at all evident that the specimen they illustrate (Pl. 29, figs. 11-12) matches the original figure.

"*Oliva alba* Lamarck" was listed, without a word of clarification, by GRAY (1858: 44) in the synonymy of *Strephona reticularis*. This is a **misquotation**, as there is no *O. alba* Lamarck (see GREIFENEDER, DUCHAMPS & TURSCH 1995). Gray refers to sp. no. 42 (*O. candida*) of Lamarck for which "*alba*" is part of the Latin description (see B. & B. 1960).

"*Oliva vermiculata* Lamarck" was listed, without a word of clarification, by GRAY (1858: 44) in the synonymy of *Strephona reticularis*. This is a **misquotation**, as there is no *O. vermiculata* Lamarck (see GREIFENEDER, DUCHAMPS & TURSCH 1995).

"*Oliva diaphana* Duclos 1835" (auct.) was *O. reticularis* Lam. for B & B (1960), W & A (1978) and P. & S. (1986). This is a **misquotation**, as there is no *Oliva diaphana* described by Duclos.

"*Oliva vermiculata* Gray, 1858" (auct.) constitutes a fine example of sequential taxonomic hallucinations in the genus *Oliva*. This non-existent taxon was *O. reticularis* Lamarck, 1811 for B. & B. (1960) and W. & A. (1978). It was considered to be a valid species by P. & S. (1986: 155). PETUCH (1987: 105) even described an *Oliva* from Haiti as "closely resembling Gray's type of *O. vermiculata*". One wonders where this type material could be seen. "*Oliva vermiculata* Gray, 1858" is a **misquotation** because there is no *O. vermiculata* Gray. One finds a citation of "*vermiculata* Lamarck" in Gray (1858: 44), in the synonymy of *Strephona reticularis*). But this is yet another misquotation, as there is no such thing as a "*O. vermiculata* Lamarck" (*q.v.*).

Oliva sowerbyi Marrat, 1870: 13, sp. no. 61, Pl. 8, figs. 114,115. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). *Oliva sowerbyi* Marrat, 1870 (not illustrated here) has been demonstrated to be a **subjective junior synonym** of the very different Indian Ocean species *O. atalina* Duclos, 1835 (see TURSCH & GREIFENEDER, 1996). *Oliva sowerbyi* Anton, 1839: 102 is does not to the genus *Oliva* but is a small fossil, possibly an *Ancilla*. (see TURSCH & GREIFENEDER, 1996). Likewise, *Oliva sowerbyi* Ducros de St-Germain, 1857: 105, sp. no. 103 is not an *Oliva* but an *Olivella*.

Oliva polpasta Duclos, 1833.

Oliva polpasta Duclos, 1833: Pl. 20; 1840: Pl. 16, figs. 1-2; 1844: 26.

> *Oliva truncata* Marrat, 1867: 215.
> *Oliva kerstitchi* da Motta, 1985: 8-9.
> *Oliva olssoni* Petuch & Sargent, 1986: 140, Pl. 25, figs. 17, 18.

Description.
SIZE: to over 50 mm.
SHAPE: ovate to biconic.
SPIRE: flat conical. Spire callus covers from 1/2 to nearly all the whorl. Colour of callus from bluish grey to yellow, beige and brown, often darker in upper zone; occasional dark strokes or points.
CHANNEL: medium.
SUBCHANNEL PATTERN: fasciculated, forming a regular, narrow zone of black triangles pointing upwards alternating with whitish triangles of equal size, pointing downwards. When seen in apical view, this produces a characteristic "cogwheel pattern" (see PL. 3, FIG. 6).
SHELL BACKGROUND: yellowish brown to olive gray to bluish gray.
COLOUR PATTERN: network of chevrons of variable thickness (mostly blurred to produce nearly homogeneous backdrop), overlaid with a pattern of single dark blotches, sometimes forming strokes, chevrons or ziczacs. Two faint large spiral bands (not always present) are formed by local reinforcement of the pattern. Some specimens have one or two wide spiral white bands ("*kerstitchi* pattern").
COLUMELLA: rather smooth, mostly white, with very faint yellow to green shadow only at the base.
FASCIOLE: uniform white.
SUPRAFASCIOLAR BAND: lower part often with nearly axial, sharp strokelets.
APERTURE: white to pale greyish or yellowish. Inner margin of lip: like aperture; dark brown or grey only in shells with a sharp lip.
PROTOCONCH: medium large.

Diagnosis. Differs from *O. spicata* by the all-white fasciole, the "cogwheel pattern" (see PL. 3, FIG. 6) and a protoconch generally smaller.

SYNONYMY.

Oliva polpasta Duclos, 1833. This taxon (of which the figured syntype is illustrated PL. 4, FIG. 6), although closely related to *O. spicata* (Röding, 1798), is easily and totally separated from that species (see TURSCH & HUART, 1990) by quantitative characters. Both are syntopic (for instance at Cebaco I., Panama) and *Oliva polpasta* Duclos, 1833 thus is the **valid name** for a separate, **objective species**, in agreement with Z. & P. (1969), W. & A. (1978) and P. & S. (1986). It was a variety of *O. spicata* (Röding, 1798) for B. & B. (1960). This species is very close (or identical) to the fossils *O. davisae* Durham, 1950 and *O. callosa* Li, 1930 (not treated here).

The following names are synonyms or designate local forms:

Oliva truncata Marrat, 1867. The holotype (see PL. 4, FIG. 7) could not be separated from *O. polpasta* Duclos, 1833. In the absence of valid arguments to the contrary, this is here considered as a **subjective junior synonym** of *O. polpasta* Duclos, 1833. This was a valid species for P. & S. (1986). It was *O. elegans* Lamarck, 1811 (a completely different Indo-Pacific species, see GREIFENEDER, DUCHAMPS & TURSCH 1995) for B. & B. (1960) Z. & P. (1969) and W. & A. (1978).

Oliva kerstitchi da Motta, 1985. The holotype (see PL. 4, FIG. 8) (with the label "*kirstitchi*") could not be separated from *O. polpasta* Duclos, 1833, except for the presence of a white spiral band on the body whorl. TURSCH & HUART (1990) considered this as having specific status, as a working hypothesis, awaiting further confirmation (see § 1.1.3). Further work (see § 4.1) established that *O. kerstitchi* da Motta, 1985 is consistently syntopic with *O. polpasta* Duclos, 1833, to which it is linked by an unbroken chain of intergrades (KOCH 1992). In the absence of valid arguments to the contrary, this is here considered as a **colour form of *O. polpasta*** Duclos, 1833. This was a valid species for P. & S. (1986).

Oliva olssoni Petuch & Sargent, 1986. The faded, bulging holotype (see PL. 4, FIG. 9) presents the characteristic sub-channel "cogwheel pattern" and could not be separated from *O. polpasta* Duclos, 1833, to which it is linked by an unbroken chain of intergrades (bulging forms of *O. polpasta* are not uncommon, for instance in Panama). In the absence of valid arguments to the contrary, this is here considered as a **local variety of** *O. polpasta* Duclos, 1833.

Oliva sayana Ravenel, 1834.

Oliva sayana Ravenel, 1834: 19.

> *Oliva litterata* Lamarck (not Röding, 1798), 1811: 315, sp. no. 20.
> *Oliva circinata* var. *citrina* Johnson, 1911: 23.
> *Oliva (Strephona) sayana sarasotensis* Petuch & Sargent, 1986: 146, Pl. 28, figs. 4, 5.
> *Oliva (Strephona) sayana texana* Petuch & Sargent, 1986: 147, Pl. 38, figs. 3, 4.

Description.

SIZE: to over 70 mm.

SHAPE: elongated fusiform to cylindrical. In old specimens, anterior part of lower lip very heavy and extended outwards.

SPIRE: conical and distinctly telescopic. Spire callus covering only 1/3 or 1/2 of the whorl. Colour of callus beige or gray to orange, with no markings.

CHANNEL: medium.

SUBCHANNEL PATTERN: coarsely fasciculated, very rapidly shifting to tent pattern.

SHELL BACKGROUND: whitish-grey to yellow.

COLOUR PATTERN: tents and chevrons of variable size, sometimes arranged into vertical series. Very large white tents are common. Two large spiral bands are formed by local reinforcement of the pattern. The angle of chevrons starts small and does appreciably increase with growth (see PL. 3, FIG. 1). Golden forms occur, with overall yellow appearance and reduction of the pattern.

COLUMELLA: with very strong coarse plaits, often smoothed by enamel. Colour white.

SUPRAFASCIOLAR BAND: very variable.

APERTURE: inner part often lilac to pink, changing to whitish grey or cream towards the lip. Inner margin of lip: dark (interrupted or not) in shells with sharp lip.

PROTOCONCH: small.

Diagnosis. Differs from *O. fulgurator* and *O. scripta* by a marked increase of the angle of chevrons during growth (see PL. 3, FIGS. 1, 2), a much smaller protoconch, a telescopic spire. Differs from *O. scripta* by a much narrower channel.

Distribution. Southeastern coast ud U.S. and Gulf of Mexico. According to P. & S. (1986: 121), *O. sayana* "cannot tolerate the tropical carbonate environment of the southern tip of Florida ... [which] acts as a barrier to dispersal"

SYNONYMY.

Oliva sayana Ravenel, 1834. The type is missing in the Ravenel collection, housed at the Charleston Museum (*fide* Dr. Harry D. LEE, *in litt*). There is no original figure, nor any actual description. Comparing this shell to *O. litterata* (described by Lamarck as being 66 to 68 mm -about 2.75 inches- long), Ravenel writes:

> "These Shells are certainly distinct, and therefore should be distinguished by different names. The O. sayana, sometimes exceeds 3 inches in length –fine specimens are rare– worn specimens are not uncommon on the coast of South Carolina."

With so little information, this widely used name should normally be a *nomen dubium*. Nomenclatural stability can nevertheless be preserved by an unusual (but good) argument: no other *Oliva* species is found on the coast of South Carolina (a very intensively prospected area). This species is easily and completely separated by quantitative criteria from all other Atlantic *Oliva* species (see TURSCH & HUART, 1990), so one can consider that *Oliva sayana* Ravenel, 1834 is the **valid name** for an **objective species**, in agreement with Z. & P. (1969), W. & A. (1978) and P. & S. (1986).

The following names are synonyms or designate local forms:

Oliva litterata Lamarck, 1811. This (see original illustration PL. 5, FIG. 1) is the former name of *O. sayana* Ravenel, 1834, in agreement with B. & B. (1960), Z. & P. (1969), W. & A. (1978) and .P & S. (1986). It is a **junior homonym of** *O. litterata* (Röding, 1798) (see TURSCH & al., 1994), a synonym of *O. spicata* (Röding, 1798) for KEEN (1971), a nomen dubium for TURSCH, DUCHAMPS & GREIFENEDER, 1994.

Oliva circinata var. *citrina* Johnson, 1911. Examination of the paratype MCZ 6267 (figured here PL. 5, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5482) confirms this is a **colour form of** *O. sayana* Ravenel, 1834, in agreement with B. & B. (1960), Z. & P. (1969), W. & A. (1978) and .P & S. (1986). This conclusion is supported by the characteristic small, intact protoconch.

Oliva sayana sarasotensis Petuch & Sargent, 1986. The rather small (40 mm) holotype (see PL. 5, FIG. 3) (previously illustrated by KAICHER 1989, Part IV, card no. 5493) could not be separated from a large sample of *O. sayana* Ravenel, 1834, containing many populations. This, being described from a single population (15 km West of Lido Beach, Sarasota, Florida), does hardly qualify as a subspecies. In the absence of valid arguments to the contrary, it is here considered as a **local variety of** *O. sayana* Ravenel, 1834.

Oliva sayana texana Petuch & Sargent, 1986. The holotype (see PL. 5, FIG. 2) (previously illustrated by KAICHER 1989, Part IV, card no. 5487) could not be

separated from a large sample of *O. sayana* Ravenel, 1834, containing many populations. This, being described from a single population (shallow water, Padre I., off South Texas), does hardly qualify as a subspecies. In the absence of valid arguments to the contrary, it is here considered as a **local variety of *O. sayana*** Ravenel, 1834.

The following names have been mistakenly considered as synonyms:

Oliva polita Marrat, 1867. The two small, dark syntypes (with no locality data) at MCM (one illustrated by Kaicher 1988, Part III, card no. 5190) do not at all resemble *O. sayana* Ravenel, 1834 and are most probably the Polynesian form of *O panniculata* Duclos, 1835, an extremely different, well-known Indo-Pacific shell. This was *O. sayana* Ravenel, 1834 for B. & B. (1960), Z. & P. (1969) and ABBOTT (1974).

Oliva circinata Marrat, 1871 (*q.v.*, under *O. fulgurator*) was *O. sayana* Ravenel, 1834 for ABBOTT (1974).

Oliva scripta Lamarck, 1811.

Oliva scripta Lamarck, 1811: 315, sp. no. 21; *Encycl.* Pl. 362, fig .4.

> *Oliva caribaeensis* Dall & Simpson, 1901: 391, Pl. 56, fig. 9.
>
> *Oliva trujilloi* Clench, 1938: 109-113, Pl. 9.
>
> *Oliva (Cariboliva) scripta venezuelana* Petuch & Sargent, 1986: 71, Pl. 4, figs. 20, 21.

.

SIZE: to over 50 mm.
SHAPE: cylindrical.
SPIRE: low conical, telescopic. Spire callus semi-convex to convex, covering from half to whole whorl. Colour beige, without ornamentation.
CHANNEL: extremely wide.
SUBCHANNEL PATTERN: fasciculated, variable.
SHELL BACKGROUND: pale beige, occasionally whitish.
COLOUR PATTERN: network of fine strokes, forming tents and triangles of variable size. This is overlaid by fine dark brown markings sometimes arranged in axial series, concentrated in two spiral bands. These often contain long fine strokes or chevrons. Near the shoulder, the angle of these dark chevrons coincides with that of the fine strokes pattern. In many specimens, the angle of the fine strokes pattern becomes progressively larger as one goes towards the base, while the angle of the dark chevrons remains nearly constant (see PL. 3, FIG. 3).
COLUMELLA: mostly with coarse plaits over all the length, often with white enamel.
FASCIOLE: white to faint beige.
SUPRAFASCIOLAR BAND: lower zone with parallel fine strokes of variable shape; upper zone with parallel, axial strokes.

APERTURE: greyish white, sometimes faint purplish, rarely violet. Inner lip margin dark in specimens with sharp lip.
PROTOCONCH: medium large.
Diagnosis. Readily distinguished from all other *Oliva* species by its extremely wide channel.
Distribution: From Florida to Brazil.

SYNONYMY.

Oliva scripta Lamarck, 1811. As for all Lamarck's *Oliva* species, the type material could not be located. The original figure is reproduced in PL. 5, FIG. 5. *O. scripta* Lamarck, 1811 is the **valid name** (see GREIFENEDER, DUCHAMPS & TURSCH 1995) of an **objective species** (see TURSCH & HUART 1990), in agreement with the conclusions of ABBOTT (1974) and P. & S. (1986). This name has been applied by Z. & P. (1969) and W. & A. (1978) to another species with an Indo-Pacific distribution.

The following names are synonyms or designate local forms:

Oliva caribaeensis Dall & Simpson, 1901. The holotype (see PL. 5, FIG. 6) (previously illustrated by KAICHER 1989, Part IV, card no. 5526) could in no way be distinguished from *O. scripta* Lamarck, 1811, of which it is a **subjective junior synonym**. This is in agreement with the conclusions of W. & A. (1978), OLD (cited in Z. & P. 1969), ABBOTT (1974) and DIAZ & PUYANO (1994). It was a valid species for Z. & P. (1969), who state that in Puerto Rico, solid color intergrades link this taxon with *O. reticularis* Lamarck, 1811 –not confirmed on the solid coloured Portorican specimens examined by us.

Oliva trujilloi Clench, 1938. The holotype (see PL. 5, FIG. 7) (previously illustrated by KAICHER 1988, Part III, card no. 5200) and the six paratypes examined (see PL. 5, FIG. 8 and FIG. 9) are dead shells that could not be distinguished from *O. scripta* Lamarck, 1811 except for their reddish colouration, commonly seen in old shells that have been long exposed to sunlight. *O. trujilloi* Clench, 1938 is a **subjective junior synonym of *O. scripta*** Lamarck, 1811, in agreement with the conclusions of B. & B. (1960, as *O. caribaeensis*), W. & A. (1978), OLD cited in Z. & P. (1969), ABBOTT (1974), P. & S. (1986) and DIAZ & PUYANO (1994).

Oliva scripta venezuelana Petuch & Sargent, 1986. The holotype (see PL. 5, FIG. 10) (previously illustrated by KAICHER 1988, Part III, card no. 5199) is linked by an unbroken series of intergrading specimens (Shells with very similar, nebulose colour pattern are found in Honduras) to other populations of *O. scripta* Lamarck, 1811. It is, at best, a **local form of *O. scripta*** Lamarck, 1811, in agreement with the conclusions of DIAZ & PUYANO (1994).

The following names have been mistakenly or questionably considered as synonyms:

Oliva leucostoma d'Orbigny, 1842 (belonging to the genus *Olivancillaria* according to B. & B., 1960) was

considered by W. & A. (1978) to be a probable synonym of *O. scripta* Lamarck, 1811. Even if *O. leucostoma* d'Orbigny, 1842 belonged to the genus *Oliva*, it would be a younger homonym of *O. leucostoma* Duclos, 1840.

Oliva jamaicensis Marrat, 1867, [a local variety of *O. fulgurator* (Röding, 1798)] was considered by Z. & P. (1969) to be a possible synonym, and by Abbott (1974) to be a synonym of *O. caribaeensis* Dall & Simpson, 1901.

Oliva graphica Marrat, 1870 [a local variety of *O. fulgurator* (Röding, 1798)] was considered by Abbott (1974) to be a possible synonym of *O. scripta* Lamarck, 1811.

Oliva porcea Marrat, 1870 [a local variety of *O. fulgurator* (Röding, 1798)] was considered by Abbott (1974) to be a possible synonym of *O. scripta* Lamarck, 1811.

Oliva spicata (Röding, 1798).

Porphyria spicata Röding, 1798: 35, sp. no. 423.

> *Porphyria arachnoidea* (Röding, 1798): 36, sp. no. 450.
> *Oliva araneosa* Lamarck, 1811: 315, sp. no. 19.
> *Oliva venulata* Lamarck, 1811: 313, sp. no. 13; Encycl. Pl. 361, fig. 5.
> *Oliva oniska* Duclos, 1845: 19, Pl. 32, figs. 7-9.
> *Oliva pindarina* Duclos, 1840: Pl. 16, figs. 7-8; 1845: 19.
> *Oliva timoria* Duclos, 1840: Pl. 17, figs. 11-13; Illustr. Conch.: 19 (*pars*).
> *Oliva subangulata* Philippi, 1848: Pl. 1, fig. 2.
> *Oliva cumingii* Reeve, 1850: Pl. 11, figs. 19, a, b.
> *Oliva ligneola* Reeve, 1850: sp. no. 57, Pl. 21, fig. 57.
> *Oliva melchersi* Menke, 1851: 24.
> *Oliva intertincta* Carpenter, 1857: 465.
> *Oliva violacea* Marrat, 1867: 213.
> *Oliva brunnea* Marrat, 1870: 7, sp. no. 24, figs. 54, 55.
> *Oliva punctata* Marrat, 1870: sp. n° 6, Pl.2, figs. 12-13.
> *Oliva fuscata* Marrat, 1870: sp. n° 8, figs. 20-22.
> *Oliva spicata* var. *hemphilli* Ford in Johnson, 1911: 122.
> *Oliva spicata* var. *perfecta* Johnson, 1911: 122.
> *Oliva rejecta* Burch & Burch, 1962: 165.
> *Oliva ionopsis* Berry, 1969: 163-64.
> *Oliva (Strephona) radix* Petuch & Sargent, 1986: 143, Pl.26, figs.20-23.
> *Oliva subangulata corteziana* Petuch & Sargent, 1986: 150, Pl. 29, figs. 7-10.

Description.

Local populations are very homogeneous. The ranges of variations here under describe differences *between* populations.

Size: from about 25 mm to over 65 mm.

Shape: very variable, from elongated fusiform to inflated fusiform. Cylindrical forms do not seem to occur. Strong tendency to inflated, angular shoulders (biconical appearance).

Spire: conical, rather elevated. Spire callus rarely covering more than half of whorl, colour from white, beige, purplish to brown, often darker at upper margin. Callus often presents oblique dark strokes.

Channel: of medium width.

Subchannel pattern: fasciculated, very variable. Not seen in albinistic, melanistic and in unicoloured specimens.

Shell background: from white to cream, to yellow, to gray.

Colour pattern: tents and chevrons of very variable size, width and intensity. Colour of markings varies from reddish to brown or black. Start of chevrons often marked with small blotch. Two faint large spiral bands are formed by local reinforcement of the pattern. Some populations are nearly devoid of colour pattern and have overall golden or whitish appearance. Overlay of additional uniform brown colour often covers the whole shell, but the Caribbean "*bifasciata* pattern" is absent (or very rare).

Columella: very variable. Colour from white to greyish, to pale purple.

Fasciole: mostly uniform white to greyish, purplish or brownish. Lower part often suffused with colour. Ridges often marked with light brown to dark purplish brown.

Suprafasciolar band: very variable.

Aperture: from white to beige, to greyish blue and purple. Inner margin of lip: variable, from aperture colour to continuous or interrupted darker markings.

Protoconch: large to very large.

Diagnosis. The large values of the protoconch character RES5 and the small NW (number of nuclear volutions) (see Fig. 8, 11-18) set *O. spicata* (Röding, 1798) apart from all other *Oliva* species, excepted *O. fulgurator* (Röding, 1798). In most cases, it differs from *O. fulgurator* (Röding, 1798) by much weaker spiral bands, (the Caribbean "*bifasciata* pattern" is absent or very rare), by the presence of oblique strokes on the spire callus and by the presence of coloured fasciolar ridges.

Distribution. Widely distributed in the Panamic region, from the Gulf of California to Ecuador.

Synonymy.

Oliva spicata (Röding, 1798), based upon the acceptable figures 509 and 510 of Martini (see Pl. 10, fig. 5), is the **valid name** (see Tursch, Duchamps & Greifeneder 1994) for an **objective species** (see § 4.1) . This is agreement with the conclusions of Z. & P. (1969), W. & A .(1978), P. & S. (1986) and. For a colour variation see Jackson (1991).

The following names are synonyms or designate local forms:

"*Oliva arachmoidea*" (Röding, 1798) in W. & A. (1978) is a **printing error** for *O. arachnoidea* (Röding, 1798) (*q.v.*).

Oliva arachnoidea (Röding, 1798) is an **objective junior synonym** of *O. spicata* (Röding, 1798) (see TURSCH, DUCHAMPS & GREIFENEDER 1994), in agreement with B. & B. (1960), Z. & .P (1969), KEEN (1971), ABBOTT (1974), W. & A. (1978) and P. & S. (1986).

Oliva araneosa Lamarck, 1811. This is an **objective junior synonym** of *O. spicata* (Röding, 1798) (see TURSCH, DUCHAMPS & GREIFENEDER 1994), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). It was a colour form of the same for TERZER (1996).

"*Oliva aranersa* Lamarck, 1811" (auct) in W. & A. (1978) is a **printing error** for *O. araneosa* Lamarck, 1811.

Oliva venulata Lamarck, 1811. This is an **objective junior synonym** of *O. litterata* (Röding, 1798) (see GREIFENEDER, DUCHAMPS & TURSCH 1995), which is itself a nomen dubium (see TURSCH, DUCHAMPS & GREIFENEDER 1994). This was a valid species for DUCLOS (1845: 25; Pl. 17, figs. 5, 6; Pl. 22, figs. 19, 20; Pl. 33, fig.11, illustrating rather dissimilar shells) and for P. & S. (1986). It was a form of *O. spicata* (Röding, 1798) for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). It was a separate species for TERZER (1996).

Oliva timoria Duclos, 1840. The type material is heterogeneous. One of the syntypes (see PL. 10, FIG. 1) is very similar to *O. radix* Petuch & Sargent, 1986, so *O. timoria* Duclos, 1840 is (*pars*) a **subjective junior synonym** of *O. spicata* (Röding, 1798).

"*Oliva onisca* Duclos, 1844" (auct) is a **misspelling** for *O. oniska* Duclos, 1845. This was *O. fulgurator* (Röding, 1798) for B. & B. (1960).

Oliva oniska Duclos, 1845. The type series consists in 6 mottled specimens and 3 brown specimens, including the figured syntype (see PL. 11, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5473). The type material could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **subjective junior synonym** of *O. spicata* (Röding, 1798), in agreement with Z. & P. (1969). This was *O. fulgurator* (Röding, 1798) for W. & A. (1978); a subspecies of *O. tisiphona* Duclos, 1845 (a nomen dubium) for P. & S. (1986).

Oliva pindarina Duclos, 1840. The type material, including the figured syntype (see PL. 10, FIG. 2) (illustrated by KAICHER 1989, Part IV, card no. 5523), could not be separated from the "*spicata* complex" morphological continuum, being linked to

all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **local form of** *O. spicata* (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This was a colour form of *O. venulata* Lamarck, 1811 for P. & S. (1986) and for TERZER (1996). Similar to some forms of *O. fulgurator*

Oliva subangulata Philippi, 1848. This is represented in BM(NH) by two specimens, with the label "type" fallen off. One of the specimens bears traces of glue and is most probably the holotype. This shell (see PL. 11, FIG. 6), with a slight shoulder bulge, could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **local form of** *O. spicata* (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This was a valid species for P. & S. (1986) and for TERZER (1996).

Oliva cumingii Reeve, 1850. The three syntypes (see PL. 11, FIG. 1) (one is illustrated by KAICHER 1989, Part IV, card no. 5551) with the label "Gulf of California. H. Cuming colln." have a banded colour pattern and are somewhat bulging. The type material could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of** *O. spicata* (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). It was a subspecies of *O. venulata* Lamarck, 1811 for P. & S. (1986); a form of the same for TERZER (1996).

Oliva ligneola Reeve, 1850. One of the two heterogeneous syntypes (see PL. 10, FIG. 3) is a specimen of *O. tigrina fallax* Johnson, 1910, for which *ligneola* Reeve, 1850 would thus be an earlier name. The other one is a bleached shell that could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, *O. ligneola* Reeve, 1850 (*pars*) is here considered as yet another **subjective junior synonym** of *O. spicata* (Röding, 1798). This was a nomen dubium for W. & A. (1978).

Oliva melchersi Menke, 1851. There is no type material and no original illustration. The original description says that the shell is angular, ash and flesh in colour, with yellowish ("*ochroleucus*"), triangular blotches and brown dots. The shoulder presents a pattern of lines in bundles("American pattern"). Lower whorls of spire uniformly flesh coloured, with brown spots above; lip sharp, with black maculations. The above description, together with the type locality (Mazatlan, Mexico) and the

mention by the author that it could be a freak of *O. venulata* Lamarck, 1811, indicates this is a **subjective junior synonym** of *O. spicata* (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974), and W. & A. (1978). It was a subspecies of *O. spicata* (Röding, 1798) for P. & S. (1986) and for TERZER (1996).

Oliva intertincta Carpenter, 1857. The two homogeneous syntypes USNM 716187 (see PL. 11, FIG. 9) are dead, discoloured, juvenile specimens of *O. spicata* (Röding, 1798). So are the three additional syntypes at BM(NH) (see KEEN 1968). All have a brown fasciole and the second whorl of the protoconch is more inflated than usual, both characters intergrading with *O. spicata* (Röding, 1798), of which this is here considered to be a **subjective junior synonym**. This is in agreement with the conclusions of B & B (1960), Z & P (1969), KEEN (1971) ABBOTT (1974) W & A (1978), P & S (1986) and TERZER (1996).

Oliva violacea Marrat, 1867. The holotype (see PL. 11, FIG. 8) (illustrated by KAICHER 1989, Part IV, card no. 5479) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), KEEN (1971), ABBOTT (1974), Z. & P. (1969) and W. & A. (1978). This was a valid species for TERZER (1996) and for P. & S. (1986), but *O. violacea* ; Petuch & Sargent (not Marrat, 1867), 1986, depicted in the *Atlas*, Pl. 30, figs. 20, 21 differs very much from the type specimen.

Oliva brunnea Marrat, 1870. The brown holotype (see PL. 11, FIG. 3) (illustrated by KAICHER 1989, Part IV, card no. 5573) is nearly identical to one of the syntypes of *Oliva fuscata* Marrat, 1870 (*q.v.*, see PL. 11, FIG. 2). It could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** (and colour form) **of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960) and W. & A. (1978). It was a subspecies of the Atlantic taxon *O. jamaicensis* Marrat, 1870 for P. & S. (1986). This taxon is indeed one of the cases of striking resemblance between populations of *O. fulgurator* (Röding, 1798) and populations of *O. spicata* (Röding, 1798) (see § 5.4). Some specimens from Paranagua, Venezuela are extremely similar to their Pacific counterparts.

Oliva punctata Marrat, 1870. This name is available because *O. punctata* (Röding, 1798) is a nomen nudum (see TURSCH, DUCHAMPS & GREIFENEDER 1994). According to TOMLIN (in FORD, 1953) the 8 specimens at MCM are not types because the largest specimen (said to be 33 mm x 16 mm) is not large enough. But according to McMILLAN (1985), the two syntypes are the originals of Marrat's figures. In any

case, these specimens (see PL. 10, FIG. 4) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971) and ABBOTT (1974). This was *O. spicata* var. *venulata* Lamarck, 1811 for B. & B. (1960); *O. rejecta* Burch & Burch, 1962 for P. & S. (1986) and for TERZER (1996). "*punctulata* Johnson, 1911" is a misquotation in B & B (1960) and W & A (1978) for *punctata* Marrat, cited in Johnson (1911: 122) under *spicata*.

Oliva fuscata Marrat, 1870. The type material consists of three syntypes [Note: TOMLIN (in FORD, 1953) mentions six syntypes]. Two are mottled (one is figured PL. 11, FIG. 7); the last (see PL. 11, FIG. 2) is brown and nearly identical with the type of *O. brunnea* Marrat, 1870. The type material could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974), W. & A. (1978), P. & S. (1986) and TERZER (1996).

Oliva spicata var. **hemphilli** Ford in Johnson, 1911. The five syntypes (see PL. 10, FIG. 8) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This was a colour form of *O. venulata* Lamarck, 1811 for P. & S. (1986) and for TERZER (1996).

Oliva spicata var. **perfecta** Johnson, 1911. The three homogeneous, dark syntypes (the largest is figured here PL. 11, FIG. 5) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **colour form of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969) and KEEN (1971). This was *O. fuscata* Marrat, 1870 for W. & A. (1978); *O. venulata* Lamarck, 1811 for P & S (1986) and TERZER (1996).

Oliva rejecta Burch & Burch, 1962 is a specially interesting case, as this is the only report known to us of syntopic coexistence of two forms within the "*spicata* complex" (an information contradicted by recent field observations, see § 4.3.2). The examined paratypes at USNM (see PL. 10, FIG. 10) (illustrated by KAICHER 1989, Part IV, card no. 5527) and MNHN (see PL. 10, FIG. 9) could not be separated

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from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. The reported differences -base of columella light purple instead of white, D/H 0.42 (calculated from reported measurements of two specimens only; 0.43 measured on paratypes) instead of 0.49- fall well within the variation range of the "*spicata* complex". The other reported difference -brittleness of the shell, making it unsuitable for producing Indian artifacts- and reported differences in the X-Ray diffraction pattern of the shell (DONOHUE & HARDCASTLE 1962) could not be tested by us, as this would entail destruction of type material. These could certainly represent interpopulation variation. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** of *O. spicata* (Röding, 1798), in agreement with the conclusions of Z & P (1969) KEEN (1971) ABBOTT (1974). It was a valid species (*Oliva punctata* Marrat, 1870) for P. & S. (1986) and for TERZER (1996). This form comes from La Paz, Baja California, Mexico, on tide flats.

Oliva ionopsis Berry, 1969: 163-64. The holotype (see PL. 11, FIG. 10) (previously illustrated in HERTZ (1984: 37, Fig. 89) and the seven paratypes could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. For instance, the blue aperture (to which the name refers) is also found in the varieties *violacea* Marrat, 1867, *rejecta* Burch and Burch, 1962 as well as in many unnamed forms. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** of *O. spicata* (Röding, 1798), in agreement with KEEN (1971) and TERZER (1996). It was considered a valid species by ABBOTT (1974), W. & A. (1978) and P. & S. (1986). The type locality is Bahia de las Palmas, Baja California, in 10-33 fms.

Oliva radix Petuch & Sargent, 1986. The holotype (see PL. 10, FIG. 6) (previously illustrated by KAICHER 1989, Part IV, card no. 5486) has an angulose shape that somewhat reminds of some bulgy forms of *O. polpasta* Duclos (a species broadly co-occurring in Ecuador, see KEEN, 1971) but lacks the characteristic subchannel "cogwheel" pattern of this species (see under *O. polpasta*). Shells of *O. spicata* (Röding, 1798) with rather similar shapes (but less bulgy) occur in Western Mexico. The protoconch measurements (RES5= 1.58, NW=2.50, see Fig. 3) and (PAT18/NW = 0.4, lpro = 0.82, see Fig. 6) also indicate it is a **local variety** of *O. spicata* (Röding, 1798).

Oliva subangulata corteziana Petuch & Sargent, 1986. In spite of its more bulging body whorl (see PL. 10, FIG. 7), the holotype could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** of *O. spicata* (Röding,

1798). This form comes from the Northern end of the Gulf of California. This was a valid subspecies of *O. subangulata* Philippi, 1848 for TERZER (1996).

The following names have been mistakenly (or very questionably) considered as synonyms:

Oliva harpularia Lamarck, 1811 is a nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH 1995). This was *O. spicata* (Röding, 1798) for B. & B. (1960) and W. & A. (1978); a colour form of *O. venulata* Lamarck,1811 for P. & S. (1986); a possible synonym of *O. pindarina* Duclos, "1835" for TERZER (1996).

Oliva ustulata Lamarck, 1811 is another nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH 1995). This was a synonym of *O. reticularis* Lamarck, 1811 for DUCLOS (1845, p. 16); *O. spicata* (Röding, 1798) for B. & B. (1960); a form of *O. spicata* (Röding, 1798) for Z. & P. (1969); possibly *O. fuscata* Marrat, 1870 for W. & A. (1978); a colour form of *O. venulata* Lamarck,1811 for P. & S. (1986) and for TERZER (1996).

Oliva oriola ; Duclos (not Lamarck, 1811), 1835: Pl. 10, figs. 1, 2, text in *Illustr. Conch.*: 15. This was *O. spicata* (Röding, 1798) for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva obesina Duclos, 1840. This was *O. spicata* Röding for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978); a separate Panamic species for TERZER (1996). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva ispida (Link) (not Röding, 1798), 1807. This was *O. spicata* (Röding, 1798) for B. & B. (1960). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva oblonga Marrat, 1867. This was *O. spicata* (Röding, 1798) for B. & B. (1960), KEEN (1971) and W. & A. (1978). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva graphica Marrat, 1870. This was *O. spicata* (Röding, 1798) for B. & B. (1960). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

"*Oliva oblongata* Marrat, 1870" (auct). This was *O. spicata* (Röding, 1798) for Z. & P. (1969), W. & A. (1978), ABBOTT (1974) and P. & S. (1986). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva porcea Marrat, 1870. This was *O. spicata* (Röding, 1798) for B. & B. (1960). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

One name is still unsolved:

Oliva schumacheriana Beck in Gray (1858: 46) (original name: *Strephona schumacheriana*), cited by B. & B. (1960) as "Beck 1858 Cal. Proc. 1858, p.46")

could not be tracked. The only indication in Gray is "Front of pillar lip brown. *Hab.* California". This possibly refers to the ridges of the fasciole, often marked with brown in *O. spicata* (Röding, 1798).

Oliva spicata deynzerae Petuch & Sargent, 1986.

Oliva (Strephona) spicata deynzerae Petuch & Sargent, 1986: 149, Pl. 28, figs. 12, 13.

Description.
SIZE: to over 55 mm.
SHAPE: elongated fusiform.
SPIRE: conical, slightly telescopic. Spire callus gray brown to purple, covering up to 2/3 of whorl, with dark brown oblique strokes.
CHANNEL: medium.
SUBCHANNEL PATTERN: fasciculated, of variable intensity.
SHELL BACKGROUND: whitish.
COLOUR PATTERN: Network of fine tent marks (giving bluish-gray aspect) is overlaid with dark brown little blotches, especially concentrated to form two large spiral bands, in which are found strokes, chevrons and ziczacs.
COLUMELLA: with sharp plaits over all the length. Colour purplish white.
FASCIOLE: same colour as columella, with smoky base and upper margin purple.
SUPRAFASCIOLAR BAND: two similar zones of puncticulated brown marks.
APERTURE: beige-cream.
PROTOCONCH: medium large.

Diagnosis. Spire more telescopic than *O. spicata.* Double spiral band more conspicuous.

Distribution. Known only from the Cocos Islands, Costa Rica.

Oliva spicata deynzerae Petuch & Sargent, 1986. The holotype (see PL. 4, FIG. 5) and the six topotypes that were examined could be separated from all the remainder of the "*O. spicata* complex" (see § 5. 3 and Fig. 18). This is therefore considered as a **subspecies of *Oliva spicata*** (Röding, 1798), in agreement with P. & S. (1986) and TERZER (1996). All specimens examined had a very similar colour pattern, curiously reminiscent of that of the sympatric species *Oliva foxi* Stingley, 1984 (local crypsis pattern?). The subspecies status rests on a rather small sample (see § 5. 3) and would have to be modified if another form of *O. spicata* were to be discovered in the Cocos Is.

8. INDEX TO NAMES (objective species in bold)

"*alba* Lamarck": misquotation in Gray (1858).

"*aldina*" Duclos: misspelling for *O. aldinia* Duclos, 1845.

aldinia Duclos, 1845: subjective junior synonym of *O. fulgurator* (Röding, 1798).

angulata Lamarck, 1811: objective junior synonym of *O. incrassata* (Röding, 1798).

antillensis Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

" *arachmoidea*" (Röding, 1798) (auct.): printing error for *O. arachnoidea* (Röding, 1798).

arachnoidea (Röding, 1798): objective junior synonym of *O. spicata* (Röding, 1798).

araneosa Lamarck, 1811: objective junior synonym of *O. spicata* (Röding, 1798).

"*aranersa*" Lamarck, 1811 (auct.): printing error for *O. araneosa* Lamarck, 1811.

bahamasensis Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

barbadensis Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

bewleyi Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

bifasciata Küster in Weinkauff, 1878: colour form of *O. fulgurator* (Röding, 1798).

bifasciata jenseni Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

bifasciata sunderlandi Petuch, 1987: local variety of *O. fulgurator* (Röding, 1798).

bollingi Clench, 1934: see *reticularis bollingi* Clench, 1934.

broderipi Ducros de St.Germain, 1857: local variety of *O. fulgurator* (Röding, 1798).

brunnea Marrat, 1870: local variety of *O. spicata* (Röding, 1798).

bullata Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

caribaeensis Dall & Simpson, 1901: subjective junior synonym of *O. scripta* Lamarck, 1811.

circinata Martyn, 1789:*nomen nudum* (in a rejected work).

circinata Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

circinata var. *citrina* Johnson, 1911: colour form of *O. sayana* Ravenel, 1834.

circinata tostesi Petuch, 1987: local variety of *O. fulgurator* (Röding, 1798).

citrina Johnson, 1911: see *circinata* var. *citrina* Johnson, 1911

contoyensis Petuch, 1988: local variety of *O. fulgurator* (Röding, 1798).

corteziana Petuch & Sargent, 1986: see *subangulata corteziana* Petuch & Sargent, 1986.

cribraria Marrat, 1833? : local variety of *O. fulgurator* (Röding, 1798).

cumingii Reeve, 1850: local variety of *O. spicata* (Röding, 1798).

deynzerae Petuch & Sargent, 1986: see *spicata deynzerae*.

"*diaphana* Duclos 1835" (auct.): misquotation.

drangai Schwengel, 1951: local variety of *O. fulgurator* (Röding, 1798).

ernesti Petuch 1990: local variety of *O. fulgurator* (Röding, 1798).

figura Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

finlayi Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

formosa Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

foxi Stingley, 1984: valid.

fulgurator (Röding, 1798): valid.

fuscata Marrat, 1870: local variety of *O. spicata* (Röding, 1798).

fusiformis Lamarck, 1811: objective junior synonym of *O. fulgurator* (Röding, 1798).

goajira Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

graphica Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

greenwayae Clench, 1937: see *reticularis greenwayae* Clench, 1937.

harpularia Lamarck, 1811: nomen dubium.

hemphilli Ford in Johnson, 1911: see *spicata* var. *hemphilli* Ford in Johnson, 1911.

hepatica ; Marrat (not Lamarck, 1811), 1871: local variety of *O. fulgurator* (Röding, 1798).

incrassata (Lightfoot in Solander, 1786): valid.

ionopsis Berry, 1969: local variety of *O. spicata* (Röding, 1798).

intertincta Carpenter, 1857: subjective junior synonym of *O. spicata* (Röding, 1798)

ispida (Link) (not Röding, 1798), 1807: objective junior synonym of *O. fulgurator* (Röding, 1798).

jamaicensis Marrat, 1867: local variety of *O. fulgurator* (Röding, 1798).

jamaicensis zombia Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

jenseni Petuch & Sargent, 1986: see *bifasciata jenseni* Petuch & Sargent, 1986.

kerstitchi da Motta, 1985: colour form of *O. polpasta* Duclos, 1833.

ligneola Reeve, 1850 (*pars*): subjective junior synonym of *O. spicata* (Röding, 1798); (pars): earlier name for *tigrina fallax* Johnson, 1910.

litterata (Röding, 1798): nomen dubium.

litterata Lamarck, 1811: junior homonym of *O. litterata* (Röding, 1798).

magdae Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

maya Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

melchersi Menke, 1851: subjective junior synonym of *O. spicata* (Röding, 1798).

memnonia Duclos, 1845: nomen dubium.

mercatoria Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

nivosa Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

obesina Duclos, 1840: local variety of *O. fulgurator* (Röding, 1798).

oblonga Marrat, 1867: local variety of *O. fulgurator* (Röding, 1798).

"*oblongata* Marrat, 1870" (auct): misspelling (and a date error) for *O. oblonga* Marrat, 1867.

olivacea Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

olorinella Duclos, 1835 (*pars*): local variety of *O. fulgurator* (Röding, 1798).

olorinella Duclos, 1835 (*pars*): subjective junior synonym of *O. oliva* (L., 1758).

olssoni Petuch & Sargent, 1986: local variety of *O. polpasta* Duclos, 1833.

"*onisca* Duclos, 1844" (auct): misspelling for *O. oniska* Duclos, 1845.

oniska Duclos, 1845: subjective junior synonym of *O. spicata* (Röding, 1798).

oriola ; Duclos (not Lamarck, 1811), 1835: nomen dubium.

pallida Marrat, 1867: local variety of *O. fulgurator* (Röding, 1798).

pattersoni, Clench, 1945 4: local form and colour variety of *O. fulgurator* (Röding, 1798).

perfecta Johnson, 1911: see *spicata* var. *perfecta* Johnson, 1911.

pindarina Duclos, 1840: local variety of *O. spicata* (Röding, 1798).

polpasta Duclos, 1833: valid.

porcea Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

punctata (Röding, 1798): nomen nudum.

punctata Marrat, 1870: local variety of *O. spicata* (Röding, 1798).

"*punctulata* Johnson, 1911" (auct.): misquotation.

quersolina Duclos, 1835: subjective junior synonym of *O. atalina* Duclos, 1835.

radix Petuch & Sargent, 1986: local variety of *O. spicata* (Röding, 1798).

reclusa Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

rejecta Burch & Burch, 1962: local variety of *O. spicata* (Röding, 1798).

reticularis Lamarck, 1811: subjective junior synonym of *O. fulgurator* (Röding, 1798).

reticularis bollingi Clench, 1934: local variety of *O. fulgurator* (Röding, 1798).

reticularis greenwayae Clench, 1937: local form and colour variety of *O. fulgurator* (Röding, 1798).

sarasotensis Petuch & Sargent, 1986: see *sayana sarasotensis* Petuch & Sargent, 1986.

sargenti Petuch, 1987: local variety of *O. fulgurator* (Röding, 1798).

sayana Ravenel, 1834: valid.

sayana sarasotensis Petuch & Sargent, 1986: local form of *O. sayana* Ravenel, 1834.

sayana texana Petuch & Sargent, 1986: local form of *O. sayana* Ravenel, 1834.

schumacheriana Beck in Gray (1858): unknown to us, possibly *O. spicata* (Röding, 1798).

scripta Lamarck, 1811: valid.

scripta venezuelana Petuch & Sargent, 1986: local form of *O. scripta* Lamarck, 1811.

sowerbyi Marrat, 1870: subjective junior synonym of *O. atalina* Duclos, 1835.

spicata (Röding, 1798): valid.

spicata deynzerae Petuch & Sargent, 1986: subspecies of *O. spicata* (Röding, 1798).

spicata var. *hemphilli* Ford in Johnson, 1911: local variety of *O. spicata* (Röding, 1798).

spicata var. *perfecta* Johnson, 1911: colour form of *O. spicata* (Röding, 1798).

subangulata Philippi, 1848: local variety of *O. spicata* (Röding, 1798).

subangulata corteziana Petuch & Sargent, 1986: local variety of *O. spicata* (Röding, 1798).

sunderlandi Petuch, 1987: see *bifasciata sunderlandi* Petuch, 1987.

texana Petuch & Sargent, 1986: see *sayana texana* Petuch & Sargent, 1986.

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

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

tisiphona Duclos, 1845: nomen dubium.

tostesi Petuch, 1987: see *circinata tostesi* Petuch, 1987.

trujilloi Clench, 1938: subjective junior synonym of *O. scripta* Lamarck, 1811.

truncata Marrat, 1867: subjective junior synonym of *O. polpasta* Duclos, 1833.

ustulata Lamarck, 1811: nomen dubium.

venezuelana Petuch & Sargent, 1986: see *scripta venezuelana* Petuch & Sargent, 1986.

venulata Lamarck, 1811: objective junior synonym of *O. litterata* (Röding, 1798).

"*vermiculata* Gray, 1858" (auct.): misquotation and nomen nudum.

"*vermiculata* Lamarck": misquotation in Gray (1858).

violacea Marrat, 1867: local variety of *O. spicata* (Röding, 1798).

zombia Petuch & Sargent, 1986: see *jamaicensis zombia* Petuch & Sargent, 1986.

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PLATE 1.

Examples of subchannel colour pattern in Atlantic and Eastern Pacific *Oliva* species (see text § 4.1).

1. *O. foxi* Stingley, 1984. Cocos Is., Costa Rica.
2. *O. foxi* Stingley, 1984. Cocos Is., Costa Rica.
3. *O. porphyria* (Linnaeus, 1758). W. Mexico.
4. *O. porphyria* (Linnaeus, 1758). Cebaco I., W. Panama.
5. *O. polpasta* Duclos, 1833. Kobbe Beach, W. Panama.
6. *O. polpasta* Duclos, 1833. Montijo Bay, W. Panama.
7. *O. incrassata* (Lightfoot in Solander, 1786). Baja California, W. Mexico.
8. *O. incrassata* (Lightfoot in Solander, 1786). Baja California, W. Mexico.
9. *O. julieta* Duclos, 1840. Gubernadora I., W. Mexico.
10. *O. julieta* Duclos, 1840. Manzanillo, W. Mexico.
11. *O. splendidula* Sowerby, 1825. W. Panama.
12. *O. splendidula* Sowerby, 1825. W. Panama.
13. *O. spicata* (Röding, 1798). Baja California, W. Mexico.
14. *O. spicata* (Röding, 1798). Baja California, W. Mexico.
15. *O. sayana* Ravenel, 1834. Marco Beach, Florida, USA.
16. *O. sayana* Ravenel, 1834. Morgans Pass, Florida, USA.
17. *O. scripta* Lamarck, 1811. Honduras.
18. *O. scripta* Lamarck, 1811. Honduras.
19. *O. fulgurator* (Röding, 1798) f. *reticularis* Lamarck, 1811. E. Panama.
20. *O. fulgurator* (Röding, 1798). Aruba.
21. *O. fulgurator* (Röding, 1798) f. *circinata* Marrat, 1871. Ilha Bela, Brazil.
22. *O. fulgurator* (Röding, 1798) f. *circinata* Marrat, 1871. Salvador, Brazil.
23. *O. spicata deynzerae* Petuch & Sargent, 1986. Cocos Is., Costa Rica.
24. *O. spicata deynzerae* Petuch & Sargent, 1986. Cocos Is., Costa Rica.
25. *O. kaleontina* Duclos, 1835. Melon I., W. Panama.
26. *O. kaleontina* Duclos, 1835. Cebaco I., W. Panama.
27. *O. undatella* Lamarck, 1811. W. Mexico.
28. *O. undatella* Lamarck, 1811. San Pedro, Ecuador.
29. *O. peruviana* Lamarck, 1811. Iquique, Chile.
30. *O. peruviana* Lamarck, 1811. Iquique, Chile.
31. *O. flammulata* Lamarck, 1811. Luanda, Angola.
32. *O. flammulata* Lamarck, 1811. La Awera, Mauritania.
33. *O. flammulata dolicha* Locard, 1896. S⊕o Vicente, Cabo Verde.
34. *O. flammulata dolicha* Locard, 1896. S⊕o Vicente, Cabo Verde.
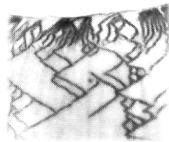
1. *O. foxi*　　2. *O. foxi*　　3. *O. porphyria*　　4. *O. porphyria*　　5. *O. polpasta*　　6. *O. polpasta*
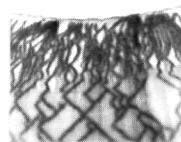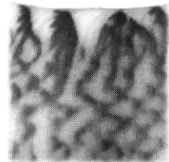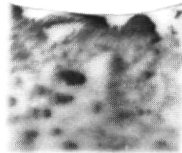
7. *O. incrassata*　　8. *O. incrassata*　　9. *O. julieta*　　10. *O. julieta*　　11. *O. splendidula*　12. *O. splendidula*
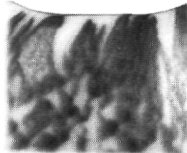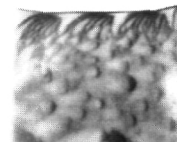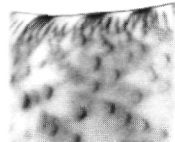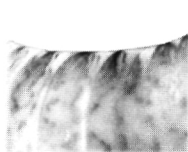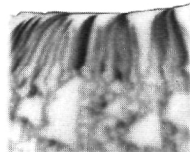
13. *O. spicata*　　14. *O. spicata*　　15. *O. sayana*　　16. *O. sayana*　　17. *O. scripta*　　18. *O. scripta*
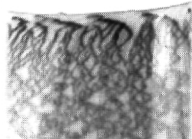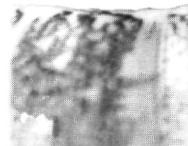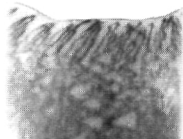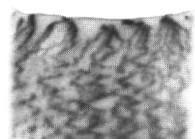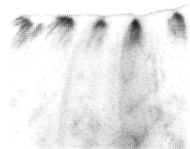
19. *O. fulgurator*　20. *O. fulgurator*　21. *O. fulgurator*　22. *O. fulgurator*　23. *O. spicata*　　24. *O. spicata*
f. *reticularis*　　　　　　　　　　f. *circinata*　　f. *circinata*　　*deynzerae*　　*deynzerae*
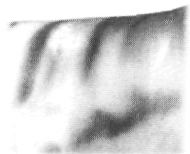
25. *O. kaleontina*　26. *O. kaleontina*　27. *O. undatella*　28. *O. undatella*　29. *O. peruviana*　30. *O. peruviana*
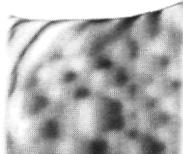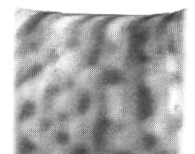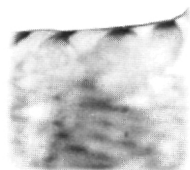
31. *O. flammulata*　32. *O. flammulata*　33. *O. flammulata*　34. *O. flammulata*
dolicha　　　　　*dolicha*
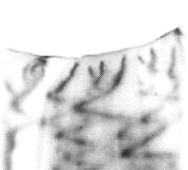
PLATE 2.

An example of occurrence of distinct, conspecific *Oliva* populations in neighbouring localities.

O. spicata (Röding, 1798) in the vicinity of La Paz, Baja California, Mexico.

O. rejecta

SEA OF CORTEZ

N

Tecolote
Balandra

Playa del Tesoro
Bahia Pichilingue
Punta Prieta
Herendira

Punta de Leon

BAHIA
LA PAZ

Costa Baja

El Mogote

C.I.B.
Ensenada de
La Paz
Comitan

LA PAZ

0 1 2 3 4 5
mi.

● collecting stations
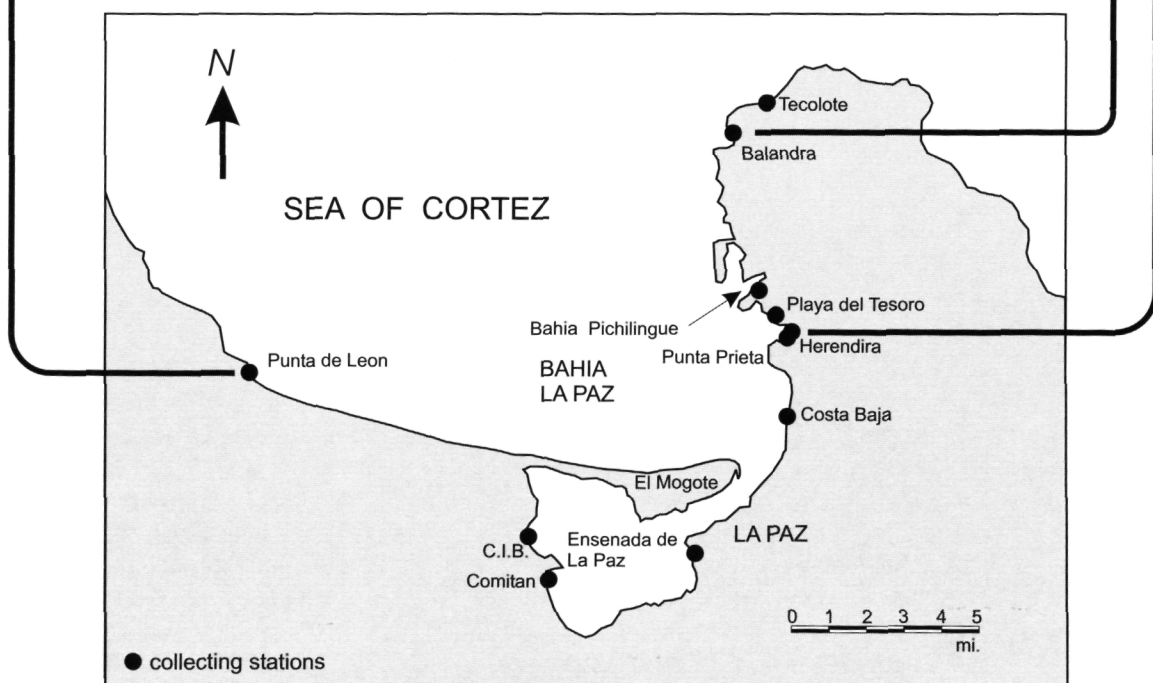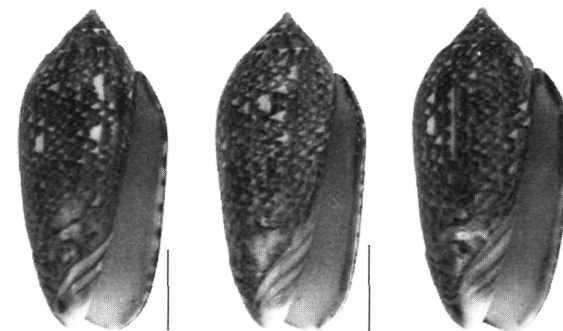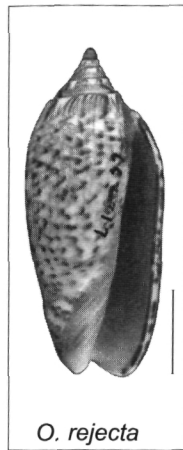
PLATE 3.

Some tips for quick identification.
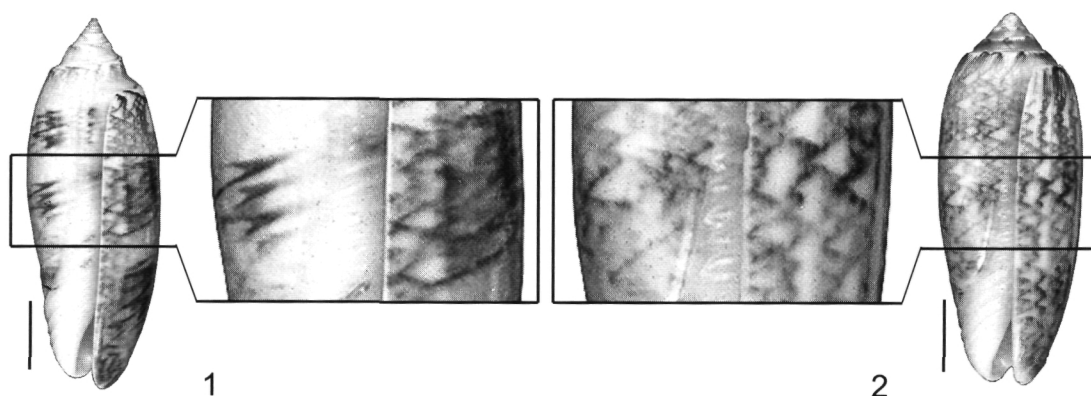
Figs. 1-2. Tip for quick identification of *O. sayana* (**1**). The angle of chevrons increases markedly during growth, while in *O. fulgurator* (**2**) the angle of chevrons stays nearly constant. Scale bars: 10 mm.
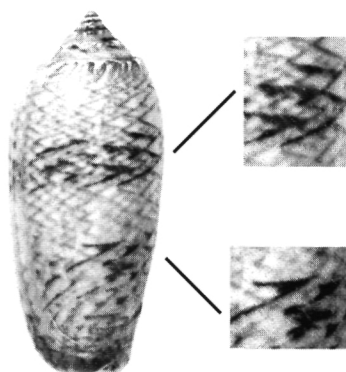
Fig. 3. Tip for quick identification of *O. scripta*. In most specimens, the angle of the fine strokes pattern becomes progressively larger as one goes towards the base, while the angle of the dark chevrons remains nearly constant

5. *O. foxi*
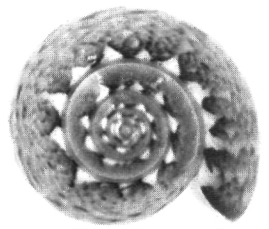
6. *O. polpasta*
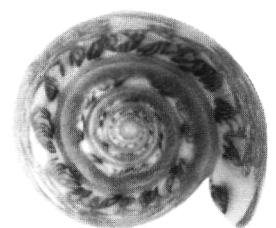
7. *O. spicata*
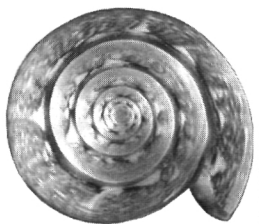
8. *O. sayana*
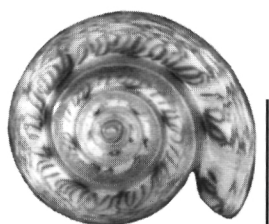
9. *O. fulgurator*
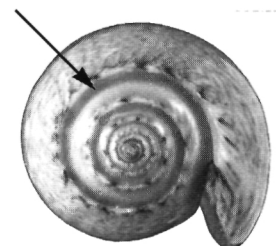
10. *O. scripta*

Figs. 4-10. Tip for quick identification of *O. polpasta* (**6**): characteristic "cogwheel pattern" in apical view, very rarely present in other related species. Note the very wide filament channel of *O. scripta* (**10**). Scale bars: 10 mm.

PLATE 4. Type material.

1-4. *O. foxi* Stingley, 1984.

1. Holotype ANSP 358356. (H: 36.98 mm, D: 14.82 mm). Cocos I., Costa Rica.

2. Paratype ANSP 358357. (H: 37.60 mm, D: 15.17 mm). Cocos I., Costa Rica.

3. Paratype AMNH 264800. (H: 34.9 mm, D: 14.1 mm). Cocos Is., Costa Rica.

4. Paratype AMS C.170890. (H: 33.35 mm; D: 13.36 mm). Cocos Is., Costa Rica. .

5. *O. spicata deynzerae* Petuch & Sargent, 1986.

5. Holotype USNM 841452 (H: 53.19 mm; D: 21.95 mm). Cocos Is., Costa Rica.

6-9. *O. polpasta* Duclos, 1833.

6. *O. polpasta* Duclos, 1833. Figured syntype, MNHN (H: 40.1 mm; D: 21.0 mm).

7. *O. truncata* Marrat, 1867. Holotype, MCM (H: 37 mm, D: 18 mm).

8. *O. kerstitchi* da Motta, 1985. Holotype MHNG 984.631 (H: 24.5, D: 11.2 mm).

9. *O. olssoni* Petuch & Sargent, 1986. Holotype USNM 841444 (H: 35.03 mm; D: 19.57 mm). 60 m off Gulf of Panama (8°7'N, 78°40'W), Panama.

O. foxi   O. foxi par. ANSP   O. foxi par. AMNH   O. foxi par. AMS   O. spicata deynzerae

O. polpasta   O. truncata   O. kerstitchi   O. olssoni
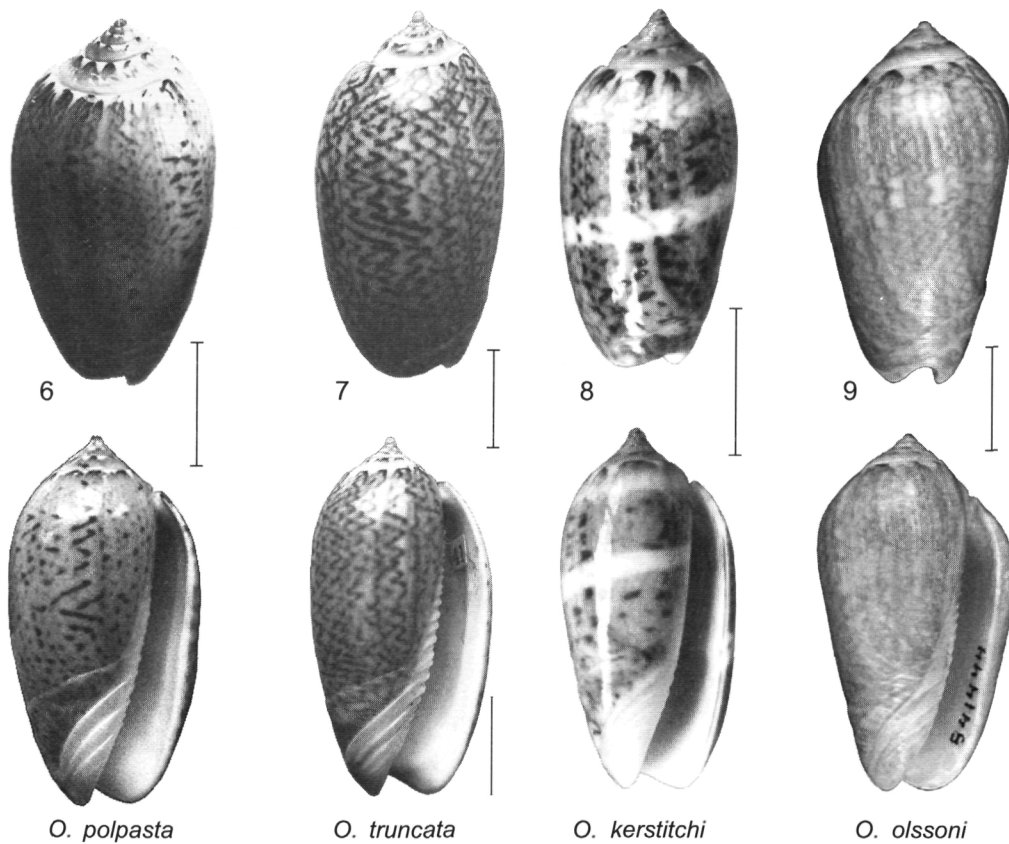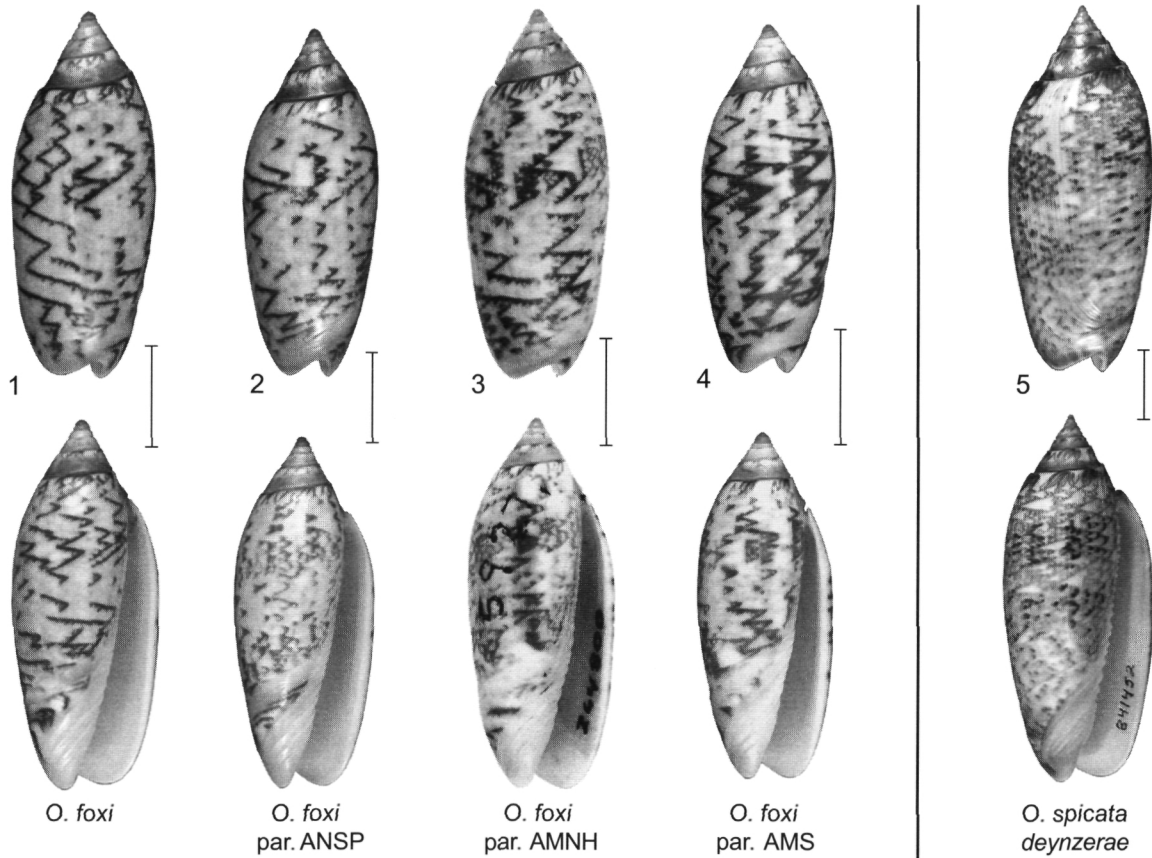
PLATE 5. Type material.

1-4. *O. sayana* Ravenel, 1834.

1. *O. litterata* Lamarck (not Röding, 1798), 1811. *Encycl.*, Pl. 362, Figs. 1a, 1b.

2. *O. sayana texana* Petuch & Sargent, 1986. HOLOTYPE USNM 841465 (H: 43.60 mm; D: 17.54 mm). Shallow water, Padre I., off South Texas.

3. *O. sayana sarasotensis* Petuch & Sargent, 1986. HOLOTYPE USNM 841450 (H: 40.60 mm; D: 17.90 mm). 15 m, sand, SCUBA, 15 km West of Lido Beach, Sarasota, Florida.

4. *O. circinata citrina* Johnson, 1911. HOLOTYPE MCZ 6267 (H: 60.51 mm, D: 23.56 mm). "W. Coast Florida".

5-10. *O. scripta* Lamarck, 1811.

5. *O. scripta* Lamarck (not Röding, 1798), 1811. *Encycl.*, Pl. 362, Figs. 4a, 4b.

6. *O. caribaeensis* Dall & Simpson, 1901. Holotype USNM 159692 (H: 31.61 mm; D: 14.93 mm). Mayaguez, Puerto Rico.

7. *O. trujilloi* Clench, 1938. HOLOTYPE MCZ 57240 (H: 40.52 mm, D: 17.95 mm). "Puerto Plata, Santo Domingo, Dominican Republic. Dredged 30 ft."

8. *O. trujilloi* Clench, 1938. PARATYPE AMNH 79010 (H: 34.8 mm; D: 15.5 mm). "Dredged in 5 fath., Puerto Plata, Santo Domingo".

9. *O. trujilloi* Clench, 1938. PARATYPE (out of five) AMS C.095147, (H: 39.57 mm; D: 18.59 mm). "Suction dredge, 5 m, bluish clay, Puerto Plata, Santo Domingo". Purchased Krause coll., 1972".

10. *O. scripta venezuelana* Petuch & Sargent, 1986. HOLOTYPE USNM 841451 (H: 44.22 mm; D: 22.02 mm). 30 m off Punta Fijo, Paranagua Peninsula, Venezuela.

1   2
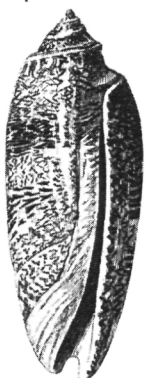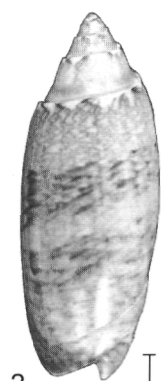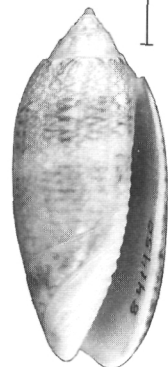
O. litterata   *O. sayana*
texana

5   6   7

O. scripta   *O. caribaeensis*   *O. trujilloi*

3   4

O. sayana
sarasotensis   *O. sayana*
citrina

8   9   10
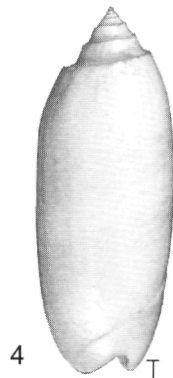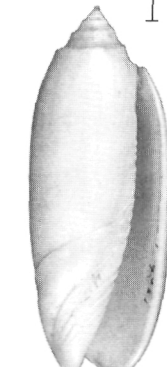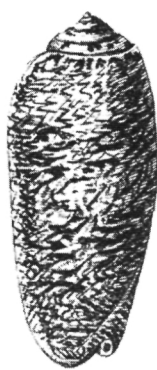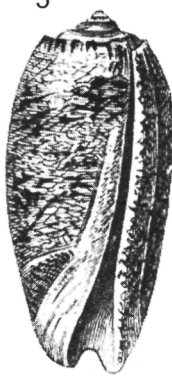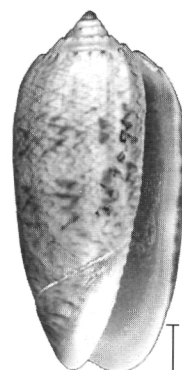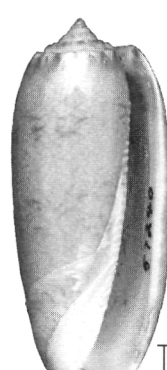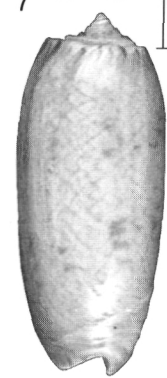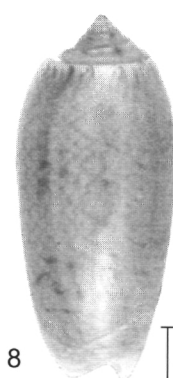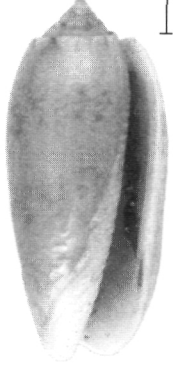
O. trujilloi
par. AMNH   *O. trujilloi*
par. AMS   *O. scripta*
venezuelana

PLATE 6. Type material.

1-10. *O. fulgurator* (Röding, 1798).

1. *O. obesina* Duclos, 1840. FIGURED SYNTYPE MNHN (H: 44.0 mm, D: 26.3 mm).

2. *O. aldinia* Duclos, 1845. FIGURED SYNTYPE MNHN (H: 55.6 mm, D: 30.3 mm).

3. *O. porcea* Marrat, 1870. HOLOTYPE MCM (H: 42 mm, D: 20.8 mm).

4. *O. graphica* Marrat, 1870. HOLOTYPE MCM (H: 44.6 mm, D: 22.2 mm).

5. *O. fusiformis* Lamarck, 1811. *Encycl.*, Pl. 367, Figs. 1a, 1b.

6. *O. jamaicensis* Marrat, 1867. HOLOTYPE MCM (H: 37.7 mm, D: 18.4 mm).

7. *O. oblonga* Marrat, 1867. HOLOTYPE MCM (H: 63.2 mm, D: 29.2 mm).

8. *O. magdae* Petuch & Sargent, 1986. HOLOTYPE USNM 841441 (H: 37.57 mm; D: 18.62 mm). In fish trap, 300 m, off Matanzas Bay, Cuba. C. J. Finlay, coll., 1956.

9. *O. mercatoria* Marrat, 1871. SYNTYPE MCM (H: 41.0 mm, D: 19.5 mm).

10. *O. fulgurator* (Röding, 1798). Martini Fig. 562, rotated.

1

2

3

4

5

O. obesina   *O. aldinia*   *O. porcea*   *O. graphica*   *O. fusiformis*

6

7

8

9

10

O. fulgurator

O. jamaicensis   *O. oblonga*   *O. magdae*   *O. mercatoria*
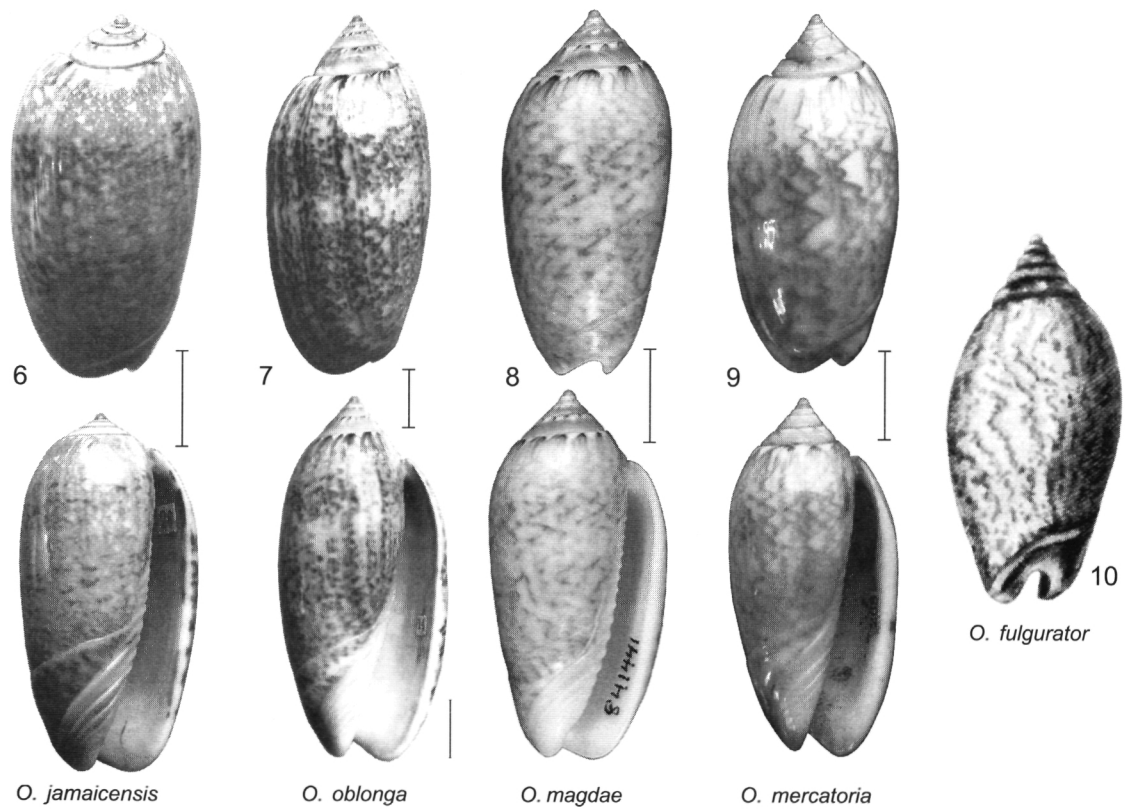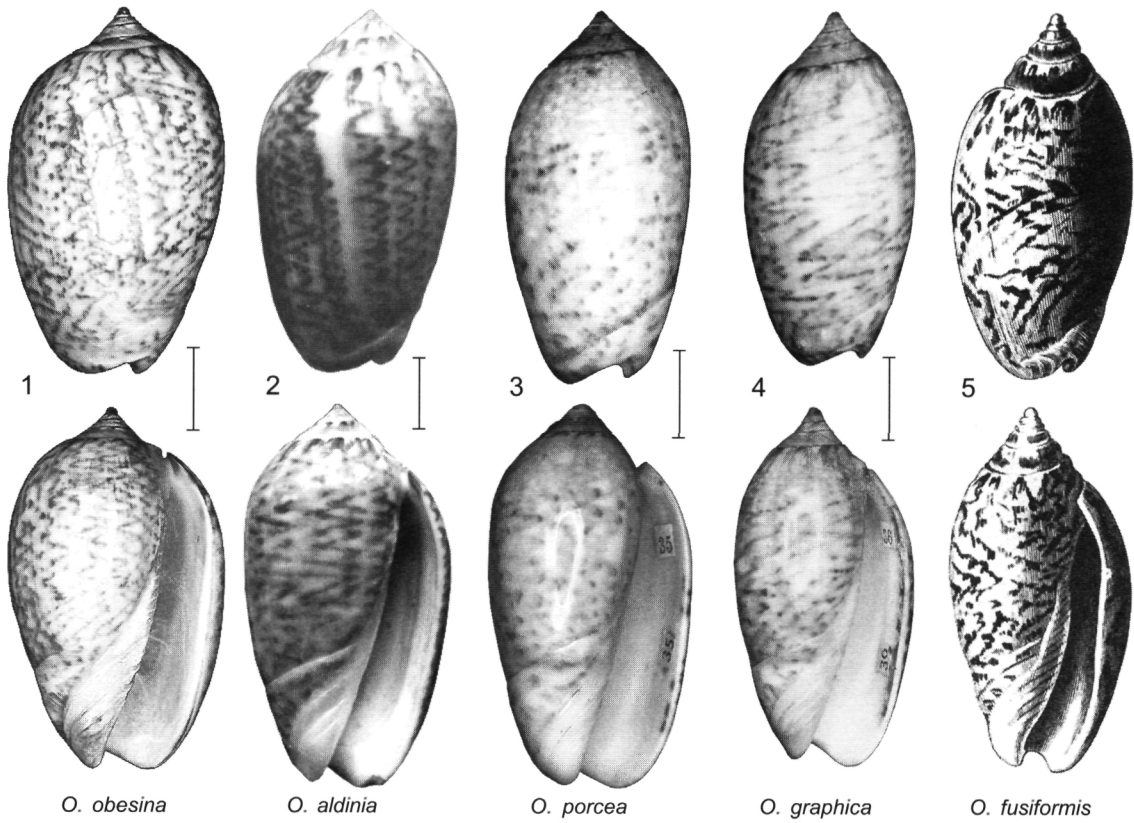
PLATE 7. Type material.

1-9. *O. fulgurator* (Röding, 1798) (continued).

1. *O. timoria* Duclos, 1840. Figured SYNTYPE (out of 3) (H: 62.0 mm; D: 33.1 mm), MNHN.

2. *O. jamaicensis zombia* Petuch & Sargent, 1986. HOLOTYPE USNM 841454. (H: 23.87 mm; D: 12.61 mm). On beach after storm, near sand flats, Southern side of Gonave I. Haiti. 1974.

3. *O. broderipi* Ducros, 1857. HOLOTYPE MNHN (H:27.8 mm; D: 13.4 mm).

4. *O. contoyensis* Petuch, 1988. HOLOTYPE USNM 859945 (H: 36.71 mm; D: 18.42 mm). 35 m. off Contoy I., Yucatan, Mexico.

5. *O. sargenti* Petuch, 1987. Holotype USNM 859864 (H: 28.60 mm; D: 14.03 mm). 5 m, sand, Malmok, Aruba.

6. *O. bifasciata jenseni* Petuch & Sargent, 1986. Holotype USNM 859302 (changed from 841453, Germon *in litt..*) (H: 50.30 mm; D: 24.12 mm). 0.5 m sand, off Blue Horizons Beach, Bermuda, R. Jensen coll. 1963.

7. *O. drangai* Schwengel, 1951. HOLOTYPE ANSP 247107. (H: 40.47 mm, D: 18.62 mm). Pigeon Pt., Tobago.

8. *O. reticularis bollingi* Clench, 1934. HOLOTYPE MCZ 76656 (H: 61.95 mm, D: 28.52 mm). "Crab-trap, Miami, Florida".

9. *O. nivosa* Marrat, 1871. HOLOTYPE MCM (H: 49.2 mm, D: 22.0 mm).

10. *O. bewleyi* Marrat, 1870. HOLOTYPE MCM (H: 41.8, D: 18.1 mm).

1

O. timoria 2

2

*O. jamaicensis
zombia*

3

O. broderipi

4

O. contoyensis

5

O. sargenti

6

*O. bifasciata
jenseni*

7

O. drangai

8

*O. reticularis
bollingi*

9

O. nivosa

10

O. bewleyi
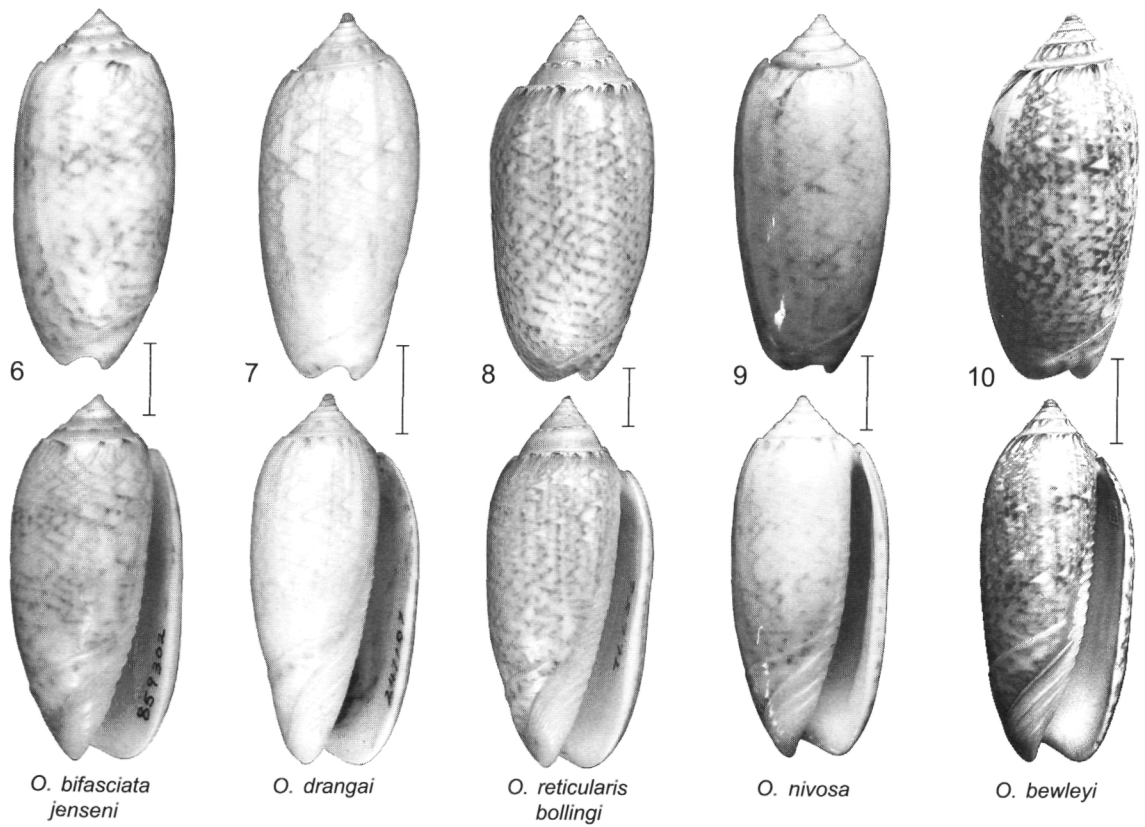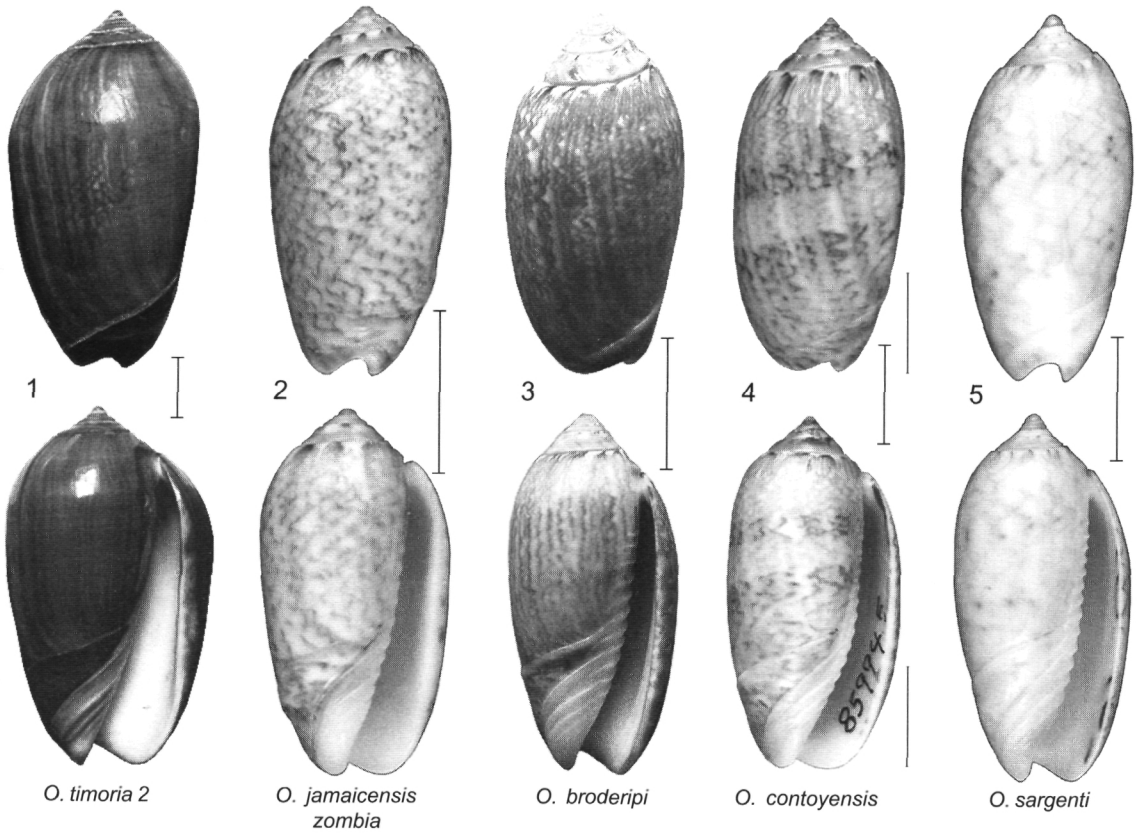
PLATE 8. Type material.

1-10. *O. fulgurator* (Röding, 1798) (continued).

1. *O. maya* Petuch & Sargent, 1986. Holotype USNM 859301 (changed from 841453, Germon *in litt.*) (H: 57.81 mm: D: 24.97 mm). Trawled by shrimper in 35 m. off Contoy Is., Yucatan, Mexico. 1977.

2. *O. goajira* Petuch & Sargent, 1986. Holotype USNM 841433 (H: 36.79 mm; D: 15.49 mm). 60 m off Cabo La Vela, Colombia.

3. *O. figura* Marrat, 1870. Holotype MCM (H: 41.2 mm, D: 18.1 mm).

4. *O. bifasciata* Küster in Weinkauff, 1878. Figured specimen SMF 9353. (H: 61.39 mm, D: 26.73 mm). "Brasilien".

5. *O. reticularis greenwayae* Clench, 1937. Holotype MCZ 115455 (H: 59.65 mm, D: 25.18 mm). "Smith Point, Grand Bahama Island, Bahamas".

6. *O. reticularis pattersoni* Clench, 1945. Holotype MCZ 151166 (H: 62.57 mm, D: 28.29 mm). "5 miles E of Crabbing Point, Great Bahama Island, Bahamas".

7. *O. ernesti* Petuch 1990. Holotype USNM 860535. (H: 33.66 mm, D: 15.45 mm) (not H: 38 mm as in description). Trawled 40m silty sand, off Portobello, Panama (East).

8. *O. finlayi* Petuch & Sargent, 1986. Holotype USNM 841432 (H: 39.98 mm; D: 18.71 mm). 200 m, Matanzas Bay, Cuba.

9. *O. reticularis* Lamarck, 1811. *Encycl.*, Pl. 361, Figs. 1a, 1b.

10. *O. bahamasensis* Petuch & Sargent, 1986. Holotype USNM 841426 (H: 44.58 mm; D: 20.62 mm). In lobster pot, in 200 m off Grand Bahama I., Bahamas.

1   2   3   4   5
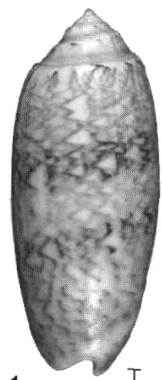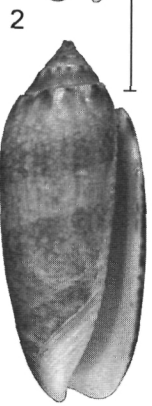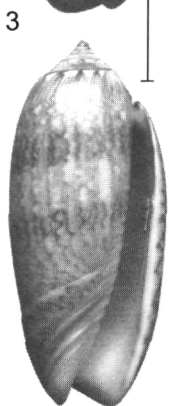
O. maya   O. goajira   O. figura   O. bifasciata   O. reticularis
greenwayae
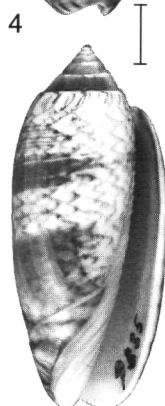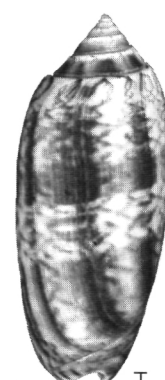
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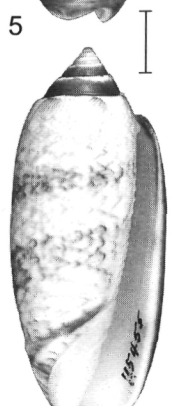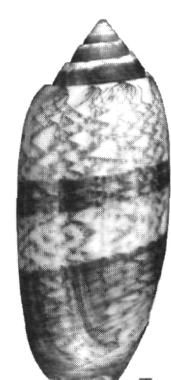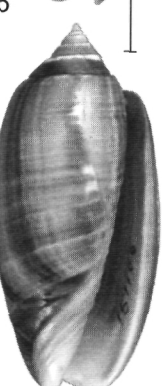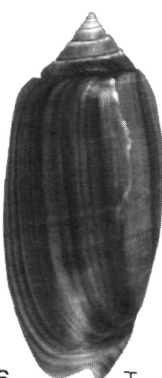
O. pattersoni   O. ernesti   O. finlayi   O. reticularis   O. bahamensis
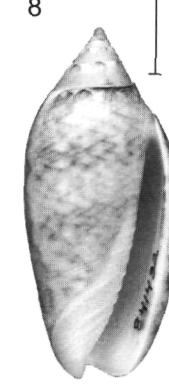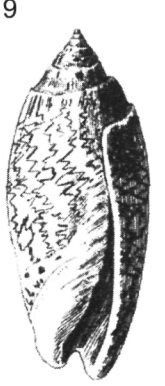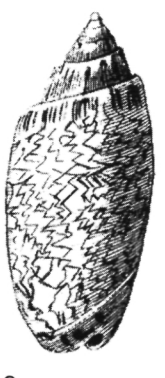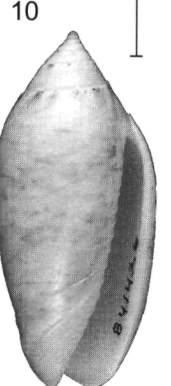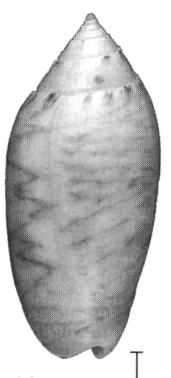
PLATE 9. Type material.

1-10. *O. fulgurator* (Röding, 1798) (continued).

1. *O. antillensis* Petuch & Sargent, 1986. HOLOTYPE USNM n° 841425 (H: 28.05 mm; D: 11.47 mm). On sand flats, low tide, at night, Southern coast of Gonave Island, Haiti.

2. *O. olorinella* Duclos, 1835. SYNTYPE MNHN (H: 28.7 mm; D: 12.1 mm.).

3. *O. bullata* Marrat, 1871. HOLOTYPE MCM (H: 60.83 mm; D: 26.21 mm).

4. *O. barbadensis* Petuch & Sargent, 1986. HOLOTYPE USNM 841427 (H: 47.05 mm; H: 20.32 mm). 200 m off St. James, Barbados.

5. *O. bifasciata sunderlandi* Petuch, 1987. HOLOTYPE USNM 859904 (H: 22.02 mm; D: 9.56 mm). Trawled 150 m West of Cedar Key, Florida.

6. *O. formosa* Marrat, 1870. HOLOTYPE MCM (H: 45.23 mm; D: 19.52 mm).

7. *O. reclusa* Marrat, 1871. HOLOTYPE MCM (H: 43.2 mm, D: 18.1 mm).

8. *O. circinata* Marrat, 1871. HOLOTYPE MCM (H: 55.4, D: 23.4 mm).

9. *O. circinata tostesi* Petuch, 1987. HOLOTYPE USNM 859865 (H: 46.20 mm; D: 21.37 mm) (not H: 41 mm as in description). 1 m, sand, Ilha Cabra, Illhabela, Sao Paulo State, Brazil.

10. *O. cribraria* Marrat, 1883? HOLOTYPE MCM (H: 48.22 mm; D: 22.12 mm).

1 *O. antillensis*

2 *O. olorinella*

3 *O. bullata*

4 *O. barbadensis*

5 *O. bifasciata sunderlandi*

6 *O. formosa*

7 *O. reclusa*

8 *O. circinata*

9 *O. circinata tostesi*

10 *O. cribraria*
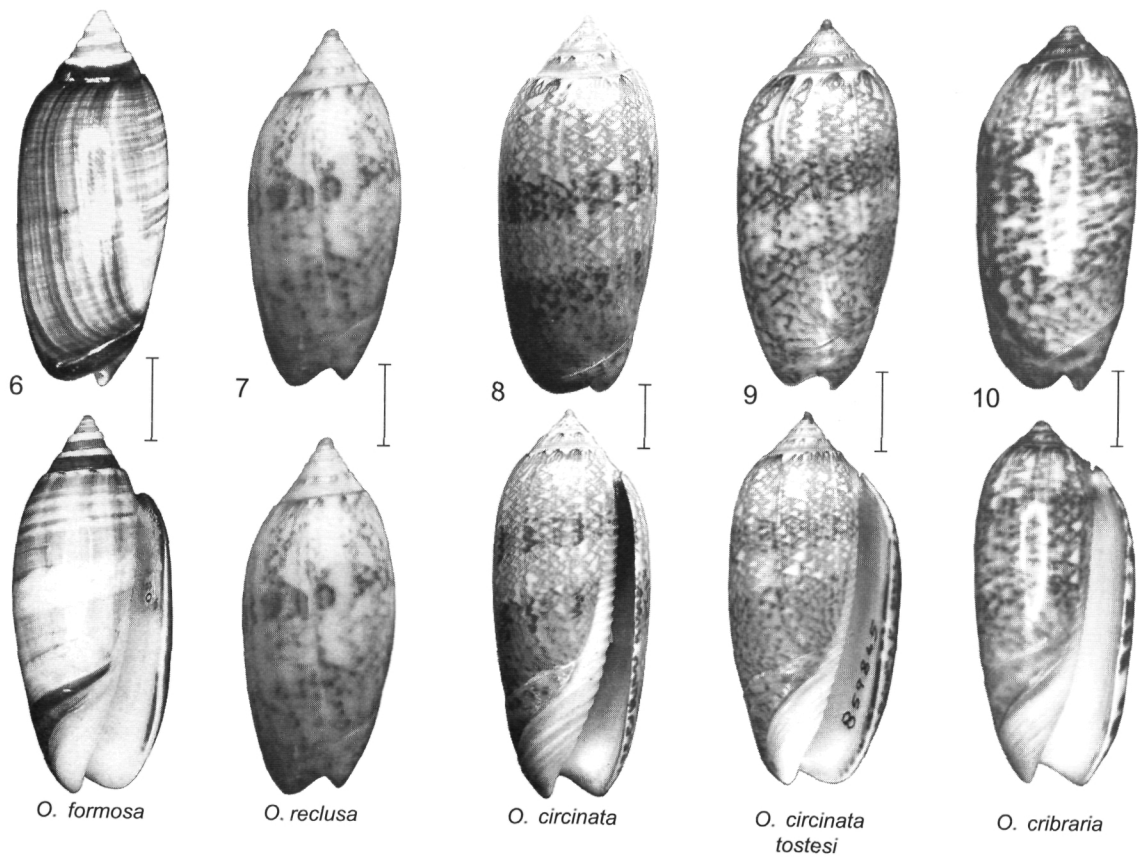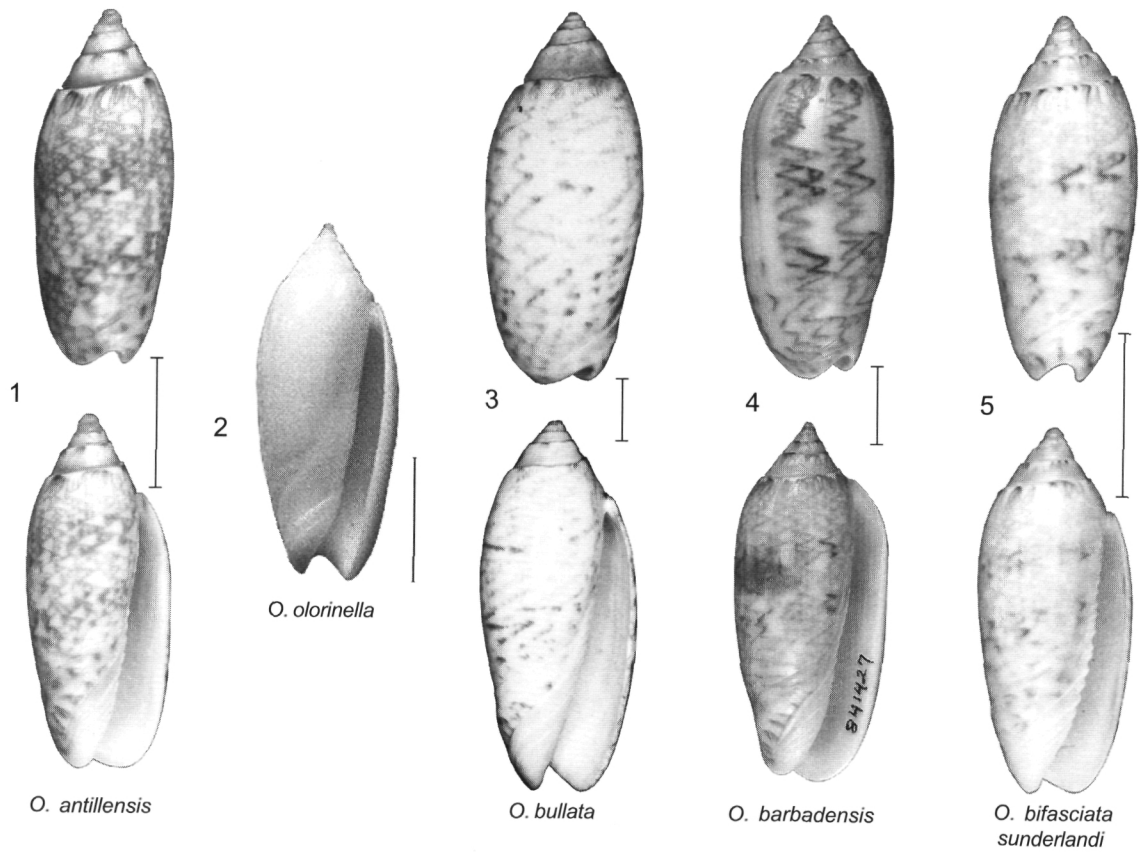
PLATE 10. Type material.

1-10. *O. spicata* (Röding, 1798).

1. *O. timoria* Duclos, 1840. Figured SYNTYPE (out of 3) (H: 55.8 mm; D: 39.1 mm), MNHN.

2. *O. pindarina* Duclos, 1840. FIGURED SYNTYPE MNHN (H: 53.4mm; D: 27.3 mm).

3. *O. ligneola* Reeve, 1850. SYNTYPE (out of 2) BM(NH) 1892.9.24.4-5 (H: 25.60 mm; D: 13.09 mm). "Loc? Purchased of Miss Steere".

4. *O. punctata* Marrat, 1870: SYNTYPE (out of two) MCM (H: 35.35 mm; D: 17.24 mm).

5. *O. spicata* (Röding, 1798). Martini's figures 509 and 510 (rotated, cast shadow removed for better legibility).

6. *O. radix* Petuch & Sargent, 1986. HOLOTYPE USNM 841446 (H: 36.62mm; D: 22.51 mm).. 75m, off Isla la Plata, Ecuador.

7. *O. subangulata corteziana* Petuch & Sargent, 1986. HOLOTYPE USNM 841457 (H: 32.33 mm; D: 16.21 mm). Northern end of the Gulf of California.

8. *O. spicata hemphilli* Johnson, 1911. SYNTYPE (out of five) ANSP 111697 (H: 54.05 mm, D: 23.38 mm). "San Ignacio Lagoon, Lower California. John Ford colln."

9. *O. rejecta* Burch & Burch, 1962. PARATYPE MNHN (H: 31.3, D: 13.6 mm). La Paz, Baja California, Mexico.

10. *O. rejecta* Burch & Burch, 1962. PARATYPE USNM 667317 (H: 37.24 mm; D: 16.01 mm). La Paz, Baja California, Mexico.

O. timoria 1   O. pindarina   O. ligneola   O. punctata   O. spicata

O. radix   O. subangulata   O. spicata   O. rejecta   O. rejecta
           corteziana   var. *hemphilli*   par. MNHN   par. USNM
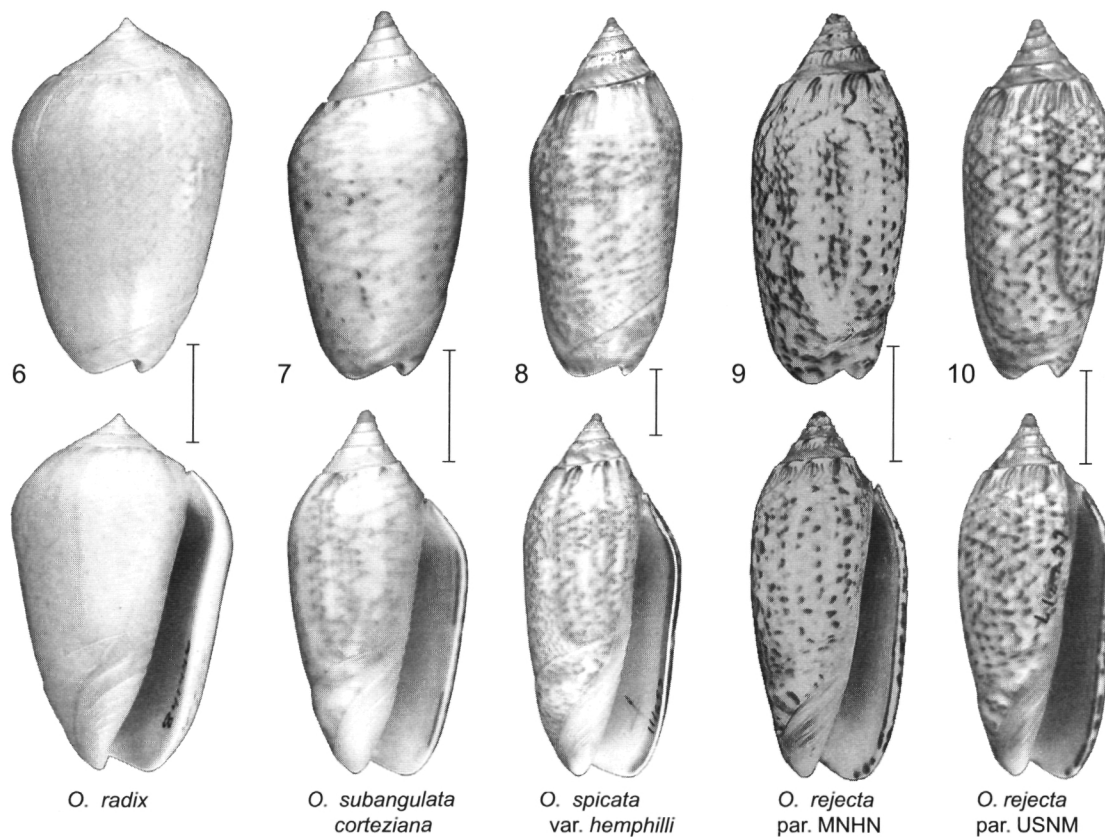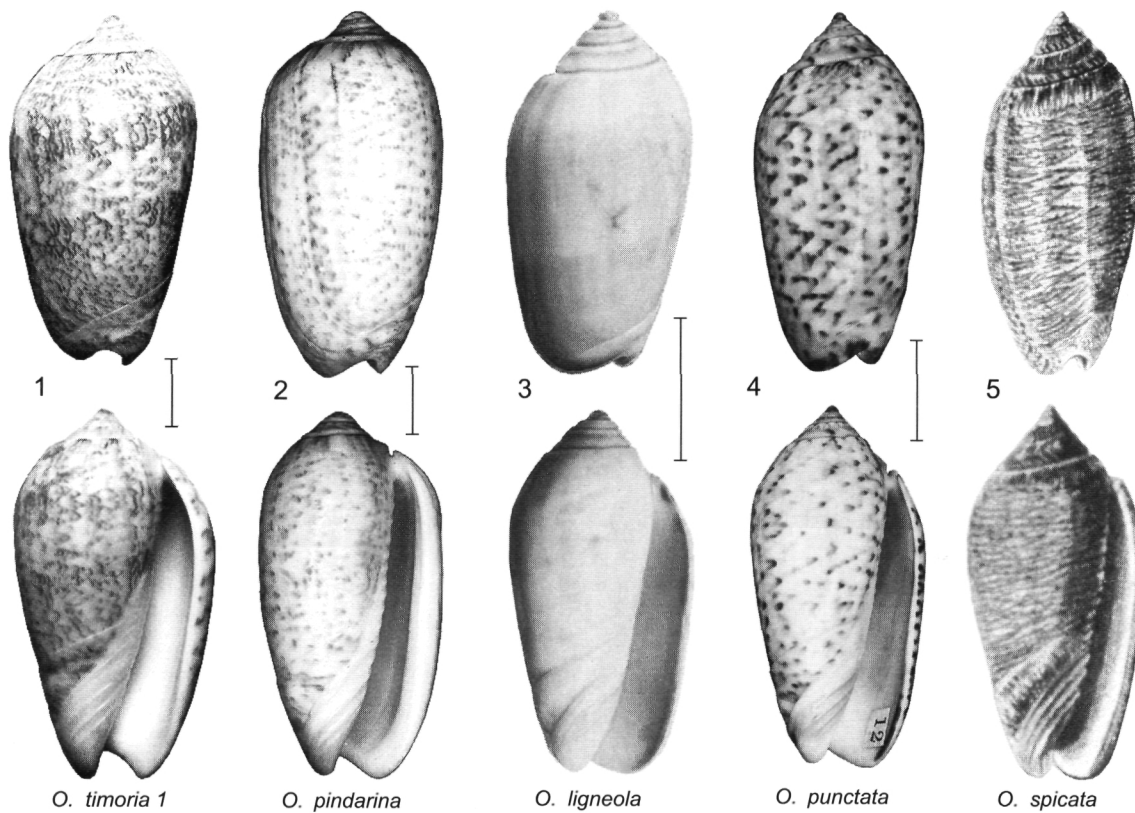
PLATE 11. Type material.

1-8. *O. spicata* (Röding, 1798) (continued).

1. *O. cumingii* Reeve, 1850. SYNTYPE (out of 3) BM(NH) 1987008 (H: 48.4 mm; D: 24.2 mm). "Gulf of California. H. Cuming colln."

2. *O. fuscata* Marrat, 1870. SYNTYPE (out of 3) MCM (H: 42.66 mm; D: 20.30 mm).

3. *O. brunnea* Marrat, 1870. HOLOTYPE MCM (H: 34,0 mm, D: 16.1 mm).

4. *O. oniska* Duclos, 1844. FIGURED SYNTYPE MNHN (H: 61.0 mm; D: 26.2 mm).

5. *O. spicata perfecta* Johnson, 1911. SYNTYPE (out of three) ANSP 111729 (H: 59.06 mm, D: 25.73 mm). "West Coast Central America. John Ford colln."

6. *O. subangulata* Philippi, 1848. SYNTYPE (out of two) BM(NH) 1924.1.5.98-99. (H: 59.62 mm; D: 26.38 mm).

7. *O. fuscata* Marrat, 1870. Another SYNTYPE (out of 3) MCM (H: 39.76 mm; D: 18.62 mm).

8. *O. violacea* Marrat, 1867.

9. *O. intertincta* Carpenter, 1857. SYNTYPE (largest of two) USNM 716187, (both specimens numbered with ink "592/2121") (H: 19.68 mm; D: 9.70 mm). Mazatlan, Sinaloa, Mexico, ex coll. F. REIGEN.

10. *O. ionopsis* Berry, 1969. Holotype SMBNH 34656 (H: 30.54 mm; D: 13.76 mm). 33fms, Bahia de las Palmas, Baja California.
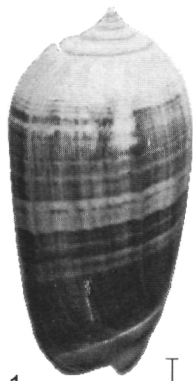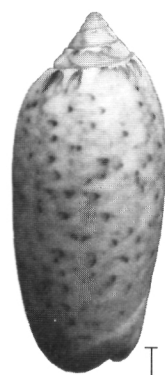
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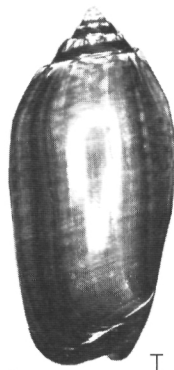
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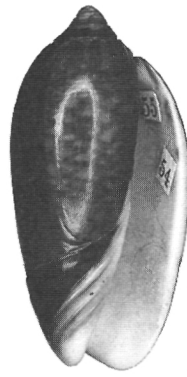
O. brunnea

4
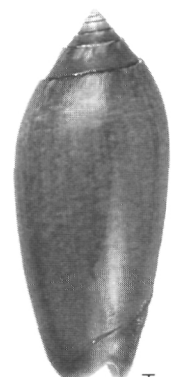
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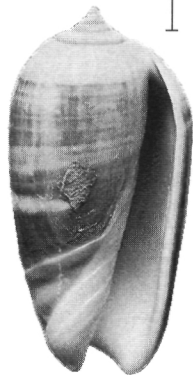
O. cumingi
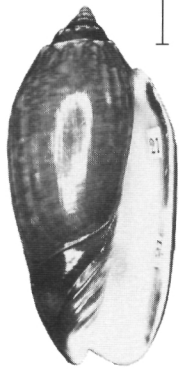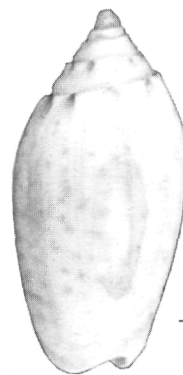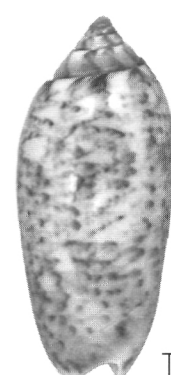
O. fuscata 1
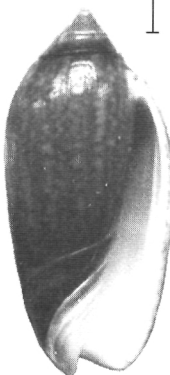
O. oniska
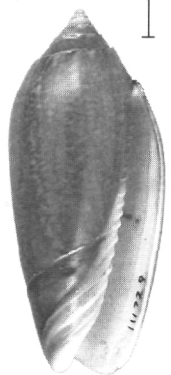
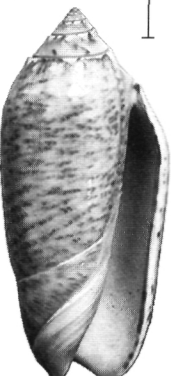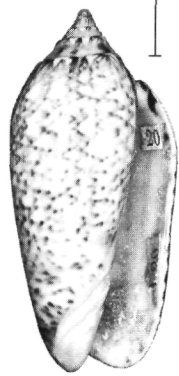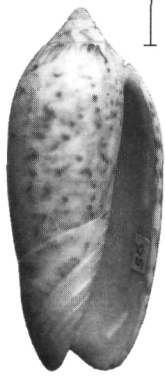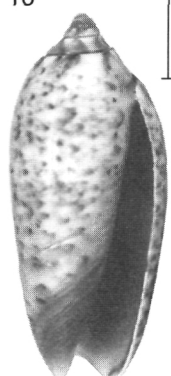*O. spicata* var. perfecta

6
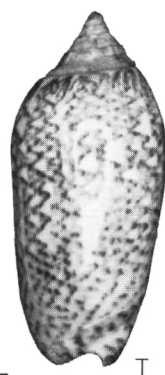
7

8

9

10

O. subangulata

O. fuscata 2

O. violacea

O. intertincta

O. ionopsis