Studies on Olividae. XIV.

The taxonomic structure of ***Oliva oliva*** (auct.).

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KEYWORDS. Mollusca, Gastropoda, Olividae, *Oliva oliva*, quantitative taxonomy, structure.

ABSTRACT. The "*Oliva oliva* complex" appears as a limited, dense cloud in the attribute hyperspace of the genus *Oliva*. Shells of this cluster display a wide variety of shapes, sizes and colour patterns and appear at first sight to be all linked by intergrades. Evidence based upon over 8500 measurements effected on 387 specimens indicates on the contrary that our sample of the "*Oliva oliva* complex" consists of three sibling species and two subspecies.

RESUME. Le "complexe *Oliva oliva*" apparaît comme un nuage limité et dense dans l'hyperespace des attributs du genre *Oliva*. Les coquilles de ce groupe présentent une grande variété de formes, de tailles et de motifs colorés et paraissent à première vue être toutes reliées par des intergrades. L'analyse de plus de 8500 mesures effectuées sur 387 spécimens indique au contraire que notre échantillon du "complexe *Oliva oliva*" se compose de trois espèces jumelles et de deux sous-espèces.

1. INTRODUCTION

Oliva oliva L., (1758) is maybe the commonest Olive in the world and quite logically one of the first species described. Its original description in twelve words (LINNAEUS, 1758) is very vague and refers to illustrations that are ambiguous and even contradictory. There should be no problem about the identity of the nominal species since OLSSON & DANCE (1966) have selected and figured a lectotype amongst a mixed lot in the Linnean collection. Why then bother to devote further study to *Oliva oliva* ?

The problem is that *Oliva oliva* is so variable in size, shape and colour pattern that the limits of the species have never been clearly defined. This extreme variability is reflected in a long list of over 50 names (see for instance BURCH & BURCH, 1960; BURCH & BURCH, 1967; DAUTZENBERG, 1927; DUCROS de SAINT GERMAIN,

1857; GREIFENEDER, 1981; PETUCH & SARGENT, 1986; ZEIGLER & PORRECA, 1969) applied to many closely related shells, that appear at first sight to be linked by intergrades. We have no safe clue so far for deciding if these shells belong to the same species or not.

In practice (and for lack of a better solution) a tacit consensus seems to prevail on the taxonomy of these shells, as evidenced by the perusal of most collections. The name *Oliva oliva* is quite generally applied to many small Indo-Pacific olives that have a darkened aperture and that do not evidently belong to some well known species. At this stage, we deem wiser to refer to that nebulous group of shells as "*Oliva oliva* (auct.)".

The use of the name *Oliva oliva* as some kind of taxonomic dustbin would seem to be a tradition dating back to Linnaeus himself *fide* DUCROS de SAINT GERMAIN (1857: 9) and HANLEY (1855). This situation is all the more embarrassing since *Oliva oliva* L., (1758) is the type species of the genus *Oliva*.

The purpose of the present work is to gather enough information for answering two questions:

1. Is "*Oliva oliva* (auct.)" (or part of it) a real, limited entity ?
2. Is "*Oliva oliva* (auct.)" an amalgam of several related species or is it just one species endowed with an extraordinary variability ?

Answering these questions is an obligate prerequisite to any serious taxonomic study of the group.

2. METHODS

2.1. GENERAL APPROACH.

The taxonomical approach of a group as difficult as "*Oliva oliva* (auct.)" will be operational only if it consist in separate, sequential steps.

a. decisions on the existence of separable phena, based upon objective characters.

b. decisions on the taxonomical rank of these phena, principally on zoogeographical data (sympatry or allopatry).

It is only when the phena are delimited and their rank established that one is entitled to take nomenclatural decisions, estimate affinities and eventually establish identification keys.

2.2. CHOICE OF CHARACTERS.

In the case of *Oliva*:

- one has no direct data on reproductive barriers,
- anatomical data (including radulae) are very homogeneous and offer scant prospects at the specific level,
- colour patterns are very variable and often so complex that they defy accurate verbal description.

It has been suggested (TURSCH & GERMAIN, 1985) that the morphometry of the shell is the best practical solution. This entails working within the conceptual frame of the taxonomic species.

2.3. Measurements.

The shell measurements utilised in this work are defined in detail in TURSCH & GERMAIN, 1985 and TURSCH & GERMAIN, 1986. They have been repeatedly tested and demonstrated to be operational (TURSCH, GERMAIN & GREIFENEDER, 1986a; TURSCH, GERMAIN & GREIFENEDER, 1986b; TURSCH & HUART, 1988; TURSCH, 1988; TURSCH & GREIFENEDER, 1989a; TURSCH & GREIFENEDER, 1989b; TURSCH & HUART, 1990).

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

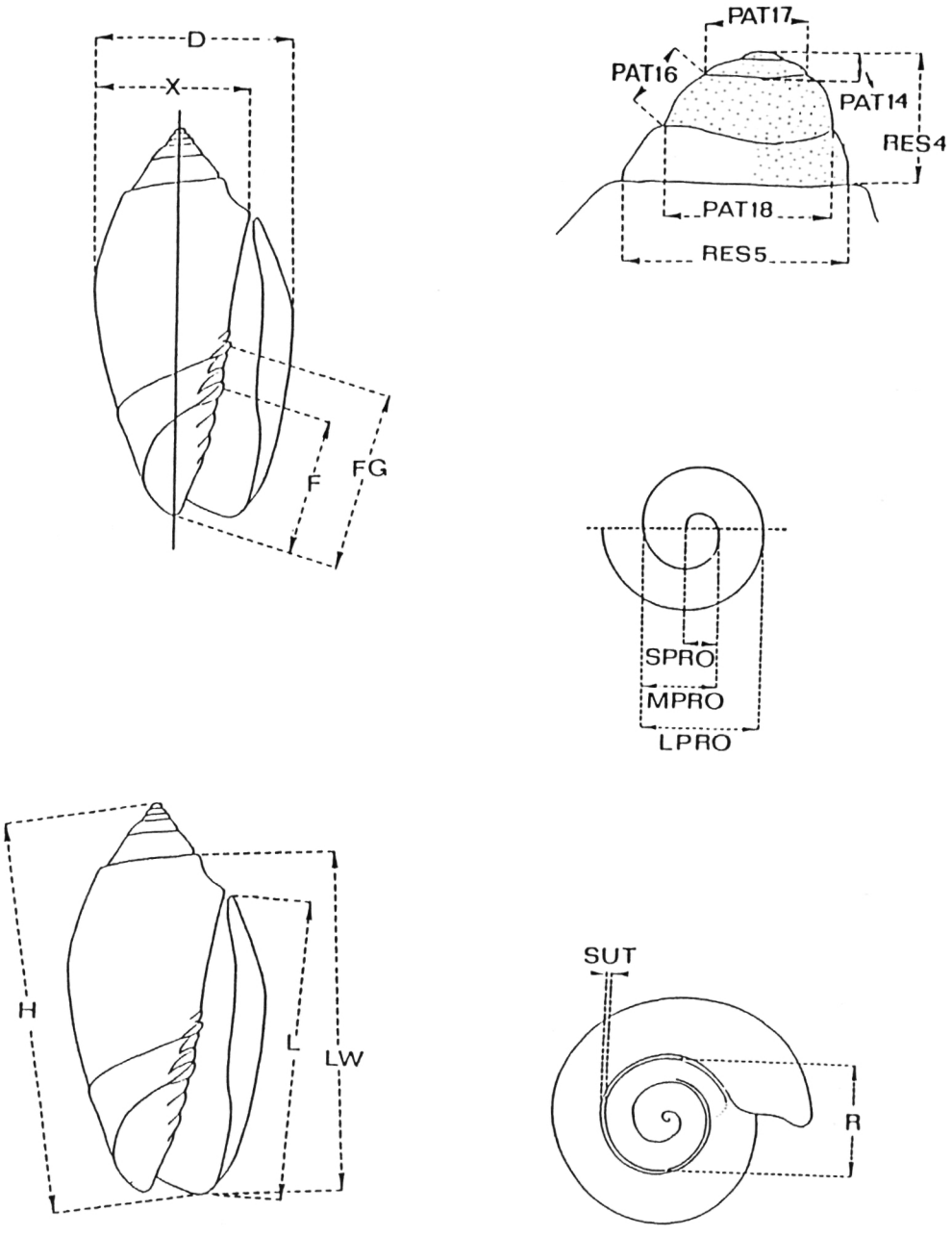


Fig. 1. Sketch of shell measurements.

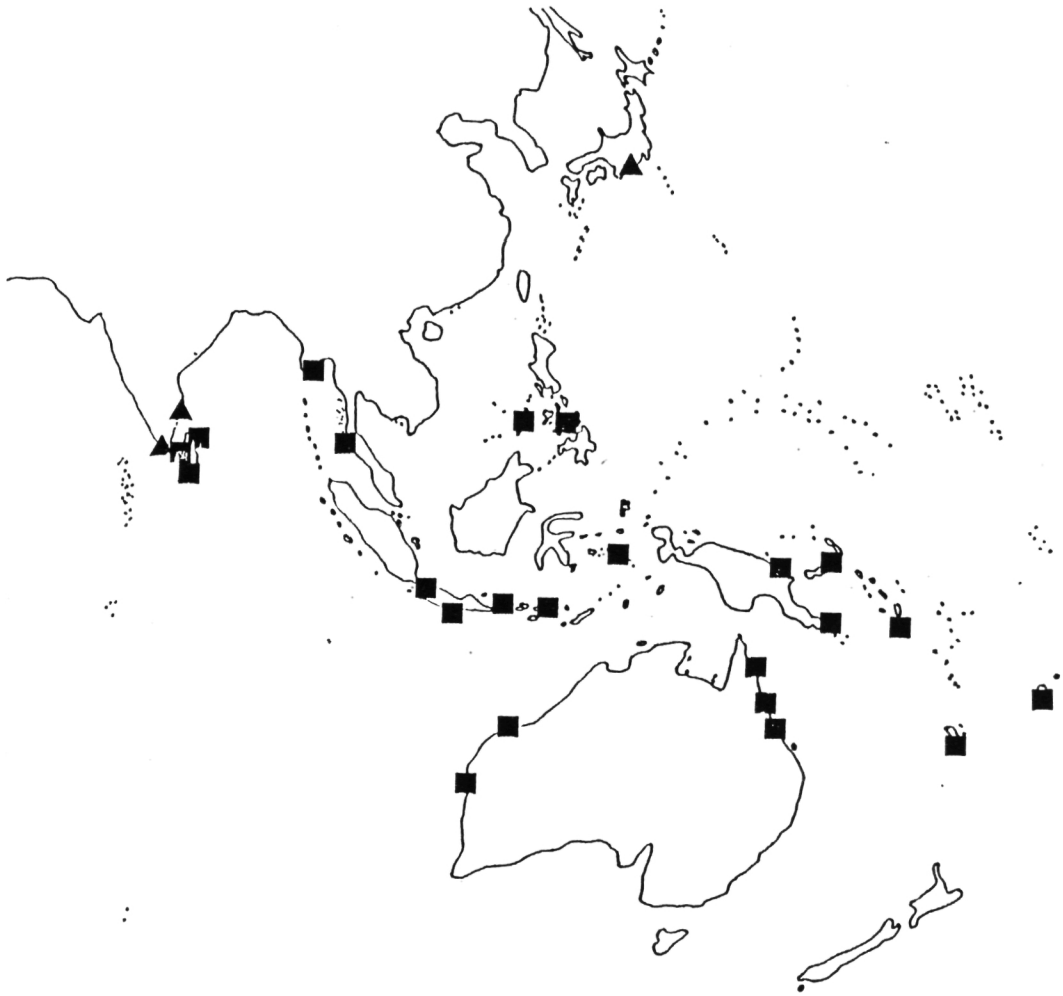


Fig. 2. Localities of material studied in this work. Black squares: measured specimens. Black triangle: observed specimens.

2.4. DATA.

Oliva shells are notoriously variable in size (TURSCH & GERMAIN, 1985) and furthermore we have no sure way of deciding if a shell is adult or not. We have thus to make sure that our data will not simply discriminate between large and small specimens. Protoconch measurements do not vary with the size of the shell and can be utilized as such.

On the contrary, teleoconch measurements are size-dependent an cannot be utilized as such. Shape factors are much more interesting and teleoconch measurements will always (with the exception of regression analysis) be used as indices (ratio of two measurements, or ratio of a given measurement to PNW).

2.5. TREATMENT OF DATA.

As for the other species concepts, the taxonomic species has no existence *per se*. It exists only in relation to other species.

Each specimen can be represented by a point in the attribute hyperspace, *i.e.* a space having as many dimensions as there are variables under consideration. A taxonomic species will be represented in the attribute hyperspace as a cloud of points, with dimensions depending on the natural variability. Two species will be distinct if their representative clouds are separated by a void region of the attribute hyperspace : a morphological gap.

Two clouds will be considered as distinct whatever the size of the gap that separates them. In theory, that gap can be very small, but must be constant (*i.e.* will persist if further specimens are added). In this work, only full separations (with no overlap) will be taken into account.

The search for such morphological gaps constitutes the main activity of the quantitative taxonomist. The attribute hyperspace has far too many dimensions to be visualized as such and the gaps will only appear in reduced spaces. Hence the intensive use of bivariate scatter diagrams (projection of the attribute hyperspace on two of its axes), principal components analysis and factorial discriminant analysis. It is important to remember that if two clouds are separated in a reduced space (let us say a plane) they are *a fortiori* separated in the attribute hyperspace.

3. MATERIAL EXAMINED

The localities of the specimens studied here are reported on the map, Fig. 2. The localities of the species utilized for comparison are not indicated.

3.1. SPECIMENS MEASURED.

For the sake of clarity the specimens in the list hereunder are already grouped into the phena delimited in this work. The provenance of specimens is indicated by their label. "AB-" refers to the collection of Mr. A. Bossuyt (Wervik), "BT-" to the collection of B. Tursch (Brussels), "DG-" to the collection of Dr. D. Greifeneder (Schwenningen), "FN-" to the collection of Mr. F. Nolf (Ostende), "ISNB-" to the collections of the Institut Royal des Sciences Naturelles de Belgiques, "JS-" to the collection of Dr. J. Senders (Brussels). Specimens followed by "P-" have no protoconch measurements, that part of the shell being damaged. Specimens indicated as *dubious* were discarded from the initial steps of the analysis and reincorporated in the final analysis. Their final attribution is indicated.

3.1.1. Species used for comparison.

Oliva australis Duclos, 1835 : BT-3600 (Brighton reef, South Australia); BT-3603 (Elliston Bay, South Australia); BT-4506 (Yorke Peninsula); BT-1475, BT-1478 (Australia, no loc.).

Oliva caldania Duclos, 1835 : BT-1607, BT-1609, BT-1611, BT-1612, BT-1614 (Queensland, Australia).

Oliva caroliniana Duclos, 1835 : BT-1567 (Mozambique); BT-2617, BT-2618 (Addington beach, South Africa); BT-3800, BT-3997 (Brighton beach, South Africa).

Oliva lignaria Marrat, 1868 :BT-3206 to BT-3208 (Broome, West Australia); BT-4831, BT-4832 (Northwest Cape, Australia).

Oliva ornata Marrat, 1867 : BT-4243, BT-4839 (Sulu, Philippines); BT-387, BT-4837 (Philippines, no loc.); FN-65a/2 (Thailand, no loc.).

3.1.2. Phena rejected from the "*Oliva oliva* complex".

group **W** (7 specimens): BT-2950 to BT-2956 (Burma, no loc.).

group Y (6 specimens): DG-P12/3 to DG-P12/7, DG-P12/9 (Awolong, Flores, Indonesia).

group Z (31 specimens): BT-5203 to BT-5208, BT-5211 to BT-5219 (Namuka I., Viti Levu, Fiji); BT-5188 to BT-5194, BT-5196 to BT-5202 (Nukoboro I., Fiji); BT-5107 (Dawa, Vanua Levu, Fiji); BT-5185 (Viti levu, Fiji).

3.1.3. The "*Oliva oliva* complex".

AUSTRALIA.

Species "***L+X***", **subsp.** "***AO***", ***phenon AO*** (West Australia, 7 specimens): BT-3348, BT-3353 (Dirk Hartog I.); BT-6352 to BT-6355 (Shark Bay); BT-6370 (Dampier).

Species "*G*", *phenon AQ* (Queensland, 21 specimens): BT-5767, BT-5807, BT-5808, BT-6121 to BT-6126 (Dingo beach); BT-4805, BT-5761, BT-5801 to BT-5803, BT-6128, BT-6130 (Port Douglas); BT-3213, BT-3214 (Yule Point); BT-4806 (Kurrimine beach); BT-3433 (Mossman); AB-001 (Cape Flatterly).

INDONESIA: Bali.

Species "*B*", *phenon BA* (22 specimens): JS-004 to JS-006, JS-008 to JS-011, JS-033, JS-034, JS-197 to JS-199, BT-178, BT-193, BT-4737, BT-4738, BT-4778 (Kuta beach); JS-030, JS-032, (Sanur); JS-205 to JS-207, BT-195 (no loc.).

Species "*L+X*", subsp. "*SJ+BB*", *phenon BB* (8 specimens): JS-001, JS-200, JS-201, JS-203, JS-204, BT-189, BT-4728, BT-4730 (Kuta beach); BT-196 (P-), BT-2035 (P-) (no loc.); JS-002 (P-), BT-4729 (P-), BT-4731 (P-), BT-4733 (P-), BT-4753 (P-) (Kuta beach).

dubious specimen: JS-075 (Sanur), final identification: species "*G*".

INDONESIA: Ceram.

Species "*G*", *phenon IC* (4 specimens): BT-167, BT-169, BT-296, BT-298 (no loc.).

INDONESIA: Flores.

Species "***G***", ***phenon IF*** (4 specimens): DG-P12/10 to DG-P12/12, DG-P12/14 (Awolong).

dubious specimen: BT-1773 (no loc.), final identification: species "***L+X***".

INDONESIA: Moluccas.

dubious specimen: BT-261 (no loc.), final identification: species "***L+X***".

INDONESIA: Sumatra.

dubious specimen: BT-6136 (no loc.), final identification: undetermined, probably intruder.

INDONESIA: Java.

Species "***L+X***", ***phenon WJA*** (West Java, 10 specimens): JS-018 to JS-021, JS-049, JS-112, JS-113, JS-122, BT-4797 (Carita beach, Sunda Straits); BT-1786 (Sukabumi).

Species "*L+X*", *phenon WJB* (West Java, 10 specimens): JS-022 to JS-025, JS-208 to JS-213 (Carita beach, Sunda Straits).

dubious specimens: JS-111 (Carita beach, Sunda Straits), final identification: species "***B***"; BT-1796 (no loc.), final identification: species "***L+X***".

Species "*L+X*", subsp. "*SJ+BB*", *phenon SJ* (South Java, 20 specimens): JS-052 to JS-062, JS-078, JS-081, JS-082, JS-085 to JS-087, JS-090 to JS-092 (Parangtritis).

NEW CALEDONIA.

2 dubious specimens: BT-2982, BT-2983 (Nouméa), final identification: both in species "***G***".

PAPUA-NEW GUINEA.

Species "***L+X***", ***phenon HB*** (Hansa Bay, 16 specimens): BT-1341 to BT-1344, BT-1347 to BT-1350, BT-4828 (no loc.); ISNB-2 to ISNB-6 (Sisimangum); BT-6378 (Laing Is.), ISNB-1 (Bogia).

Species "*L+X*", *phenon MB* (Milne Bay, 33 specimens): BT-5245 to BT-5274, BT-5276 to BT-5278 (Samarai).

dubious specimens: BT-215, BT-219 (Rabaul), final identification: both in species "***G***"; BT-224 (Rabaul); BT-4775 (no loc.), final identification: both in species "***L+X***".

PHILIPPINES.

Species "***L+X***", ***phenon PA*** (25 specimens): BT-4589 to BT-4593, BT-5700, BT-5779 to BT-5787, BT-6327 (no loc.); BT-5790, BT-6276, BT-6280, BT-6282, BT-6283, BT-6286, BT-6300, BT-6318, BT-6319 (Cebu).

Species "*G*", *phenon PB* (32 specimens): BT-4999 to BT-5003, BT-5789, BT-5791 to BT-5793, BT-5795 to BT-5800, BT-6277 to BT-6279, BT-6281, BT-6284, BT-6294 to BT-6299, BT-6302 (Cebu); BT-6210 to BT-6212 (Pamilacan Is., Bohol); BT-172 (Coron); BT-1312 (no loc.).

dubious specimen: BT-5794 (Cebu), final identification: species "***L+X***".

SOLOMONS.

5 dubious specimens: BT-2493, BT-2494 (North Malaita), final identification: species "***G***"; BT-2499 to BT-2501 (North Malaita), final identification: species "***L+X***".

SRI LANKA.

Species "***L+X***", ***phenon SR*** (47 specimens): JS-130, JS-131, JS-133, JS-134, JS-147, JS-148 (Mount Lavinia, Colombo); BT-6334 to BT-6340, BT-6342 to BT-6350 (Galle); JS-156 to JS-160, JS-161, JS-166, JS-168, BT-270 to BT-273, BT-275, BT-276, BT-278, BT-280, BT-281, BT-283, BT-284, BT-286, BT-288, BT-290, BT-291, BT-294, BT-295 (Trincomalee).

THAILAND (West).

Species "***L+X***", ***phenon THA*** (64 specimens): JS-035 to JS-041, JS-043, JS-063, JS-064, JS-066, JS-094, JS-097, JS-102, JS-103, JS-109, JS-176 to JS-184, JS-186 to JS-196 (Patong); BT-1293 to BT-1295, BT-1298, BT-4466 to BT-4468, BT-6137 to BT-6139, BT-6142 to BT-6143, BT-6147 to BT-6149, BT-6151 to BT-6158, BT-6216 (Phuket); BT-171, BT-4768 (no loc.).

Species "*B*", *phenon THB* (2 specimens): JS-104, JS-105 (Patong),.

phenon THC (later shown *dubious*: 3 specimens): JS-042, JS-044 (Patong), final identification: both in species "***L+X***"; JS-065 (Patong), final identification: species "***G***".

3.2. OBSERVED SPECIMENS.

From some localities -INDIA (from Madras to the South) and JAPAN (Tosa Bay)- we have only shells with damaged protoconchs. These shells have not been considered in our quantitative analysis but have been carefully examined and are discussed in 5.3.1.

4. RESULTS AND INTERPRETATION

This work rests upon very numerous documents (scatter diagrams, principal component analyses, discriminant analyses, see MISSA, 1991). Integral publication of these results would require a prohibitive amount of space and we shall report only on the data that are essential to follow the reasoning.

4.1. DELIMITATION OF THE "*O. OLIVA* COMPLEX".

The first question we had to answer was : Is "*Oliva oliva* (auct.)" (or part of it) a real, limited entity ? This amounts to verify if it is surrounded by morphological gaps (*i.e.* void regions of the attribute hyperspace).

The approach that was utilized consists in deliberately adding more species to the study sample (choosing species with very similar protoconch and general shape, disregarding absolute size). The test species selected are *O. australis* Duclos, 1835 (Australia), *O. caldania* Duclos, 1835 (Australia), *O. caroliniana* Duclos, 1835 (Western Indian Ocean), *O. lignaria* Marrat, 1868 (Australia) and *O. ornata* Marrat, 1867 (Western Pacific). One can then check whether these "taxonomic probes" are clearly separated from the remainder of the sample or not. It will of course be no great surprise if other, unexpected groups separate from the "*O. oliva* (auct.)".

The method (already applied by TURSCH & HUART, 1990 for the "*O. reticularis* complex") consists in successively testing scatter diagrams on selected variables. Once a group has been clearly separated in a scatter diagram (in fact, a planar projection of the attribute hyperspace) it can be considered as separated in the hyperspace and can be discarded from further separations.

The approach is examplified in Fig. 3. A scatter diagram with the protoconch variables (LPRO-SPRO) and PAT18 clearly separates five groups (*O. ornata, O. lignaria, O. australis* and two unsuspected groups: a group "*W*" containing all the specimens from Burma and a group "*Y*" containing part of the specimens from Flores, Indonesia). These groups are clearly distinct from a dense nucleus (from which *O. caroliniana* is now partly detached) and can be discarded from subsequent steps.

The next steps are quite analogous and will not be illustrated. First, *O. caldania* is separated with the variables (LPRO-SPRO)/NW versus (D-X)/D and discarded from the remainder. Then *O. caroliniana* is separated with the variables SUT/PNW versus D/H and also discarded. Finally, a scatter diagram of (H-L)/PNW versus MPRO clearly separates a third unsuspected group "Z" containing all the specimens from Fiji.

The remaining dense clouds of shells resisted all further attempts of "easy" separation ("easy" meaning univariate and bivariate methods) and will henceforth be refered to as the "*O. oliva* complex". These shells display a wide range of shapes, sizes and colour patterns (see Fig. 4) and can be suspected of being heterogeneous. It could even still contain isolated specimens (for instance juveniles) of other species.

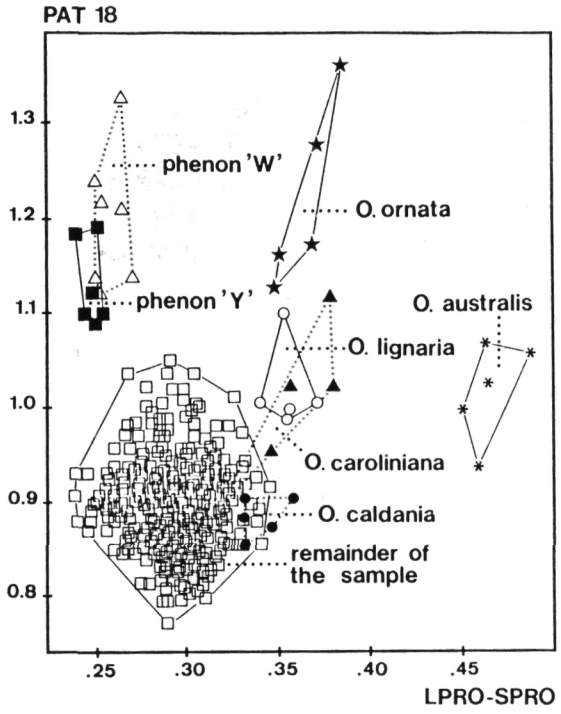


Fig. 3. Scatter diagram: variables LPRO-SPRO and PAT18. Minimum convex polygons. Separation of *Oliva ornata* (5 specimens), *O. australis* (5 specimens), *O. lignaria* (5 specimens), phenon "**W**" from Burma (7 specimens), phenon "**Y**" from Flores (6 specimens) from the remainder of the sample.

4.2. RECOGNITION OF LOCAL PHENA.

The following localities contain homogeneous local phena :

West Australia: phenon **AO** (7 specimens), Queensland: phenon **AQ** (21 specimens), Ceram, Indonesia: phenon **IC** (4 specimens), Flores, Indonesia: phenon **IF** (4 specimens), South Java, Indonesia: phenon **SJ** (20 specimens), Sri Lanka: phenon **SR** (47 specimens),

Hansa Bay, Papua-New Guinea: phenon **HB** (16 specimens), Milne Bay, Papua-New Guinea: phenon **MB** (33 specimens). For all these localities, the lots resisted all attempts of univariate and bivariate separations.

Two sympatric, distinct phena are present in Bali, Indonesia (phenon **BA**, 22 specimens, and phenon **BB**, 8 specimens), in West Java, Indonesia (phenon **WJA**, 10 specimens, and phenon **WJB**, 10 specimens) and in the Philippines (phenon **PA**, 25 specimens, and phenon **PB**, 32 specimens).

Three sympatric, distinct phena are present in Thailand (phenon **THA**, 62 specimens; phenon **THB**, 2 specimens and phenon **THC**, 3 specimens).

In each case, the separation of these sympatric phena was firmly established by bivariate and multivariate (principal components analysis) methods. As an example, Fig. 5 illustrates the situation for the Philippines sample.

In the first stage of the analysis, a few specimens from the above localities could not be attributed unambiguously to local phena. They were temporarily discarded as "dubious specimens" (see "Material") and later reincorporated in the final stages of analysis. In addition a few very small local samples were not considered in the first stages of subsequent analyses. These amount to 13 specimens (about 3% of the total sample) and will also be reincorporated in the final stages of analysis.

4.3. COMPARISON AND CLUSTERING OF LOCAL PHENA.

4.3.1. Univariate and bivariate methods.

13 of these 17 phena could not be separated by univariate methods. Only the 4 phena with very small populations could be separated, an effect we suspect to result from insufficient samples.

Bivariate methods (scatter diagrams on selected variables) are much more operational and actually segregated all possible pairs of phena, with the exception of the seven pairs **HB-WJB, THA-HB, THA-WJA, THA-HB, THA-MB, THA-PA** and **THA-SR**, that resisted all attempts at separation.

This strongly suggests the existence of a morphological continuum **THA-WJB-HB-WJA-MB-PA-SR** where **THA** overlaps all the other phena of the chain.

4.3.2. Multivariate methods.

Principal components analysis of the 17 local phena of the "*O. oliva* complex" was effected with the set of 32 variables D/H, LW/H, X/H, (X-R)/H, (H-L)/D, SUT/H, D/PNW, X/PNW, SUT/PNW, (X-R)/PNW, (H-L)/PNW, SUT/LW, SUT/L, D/LW, X/LW, (D-X)/D, (D-R)/X, H/PNW, LW/PNW, NW, LPRO, (LPRO-SPRO)/NW, RES4/NW, MPRO/NW, PAT18, PAT18/NW, PAT16/NW, MPRO/RES5, LPRO/NW, PAT18/PAT17, RES5 and LPRO-SPRO. This list includes all the variables succesfully utilized in 4.3.1.

The reduced view of the attribute hyperspace thus obtained (Fig. 6) is approximate (only 77.1 % of the total variation cumulated on the three axes) but the "V"-shaped arrangement clearly indicates a non-random distribution of the specimens. One will notice that all the sympatric phena we have separated in Section 4.2. do not overlap and the validity of that move is so far confirmed. The major portion of the left wing of the "V" is occupied by the morphological continuum formed by the phena **THA-WJB-HB-WJA-MB-PA-SR** (see section 4.3.1.) whith **THA** overlapping again all the other phena of the chain. The imbricated phena constituting the right wing of the "V" appear imbricated but can actually be separated by bivariate analysis chain (see section 4.3.1). This might be

Fig. 4 (opposite). Representative specimens of the "*Oliva oliva* complex".

1 - 4: species "B".
1: JS-104 (Phenon **THB**, Thailand, Patong, H: 36.42 mm); **2**: JS-105 (Phenon **THB**, Thailand, Patong, H: 39.19 mm); **3**: BT-193 (Phenon **BA**, Indonesia, Bali, H: 33.08 mm);
4: BT-178 (Phenon **BA**, Indonesia, Bali, H: 32.78 mm).
5 - 18: species "L+X".
5: JS-122 (Phenon **WJA**, West Java, H: 22.72 mm); **6**: JS-20 (Phenon **WJA**, West Java, H: 31.64 mm); **7**: JS-35 (Phenon **THA**, Thailand, Patong, H: 29.39 mm); **8**: JS-64 (Phenon **THA**, Thailand, Patong, H: 22.94 mm); **9**: BT-5780 (Phenon **PA**, Philippines, H: 21.86 mm); **10**: BT-6280 (Phenon **PA**, Philippines, H: 21.37 mm); **11**: JS-24 (Phenon **WJB**, West Java, H: 23.00 mm); **12**: JS-213 (Phenon **WJB**, West Java, H: 20.52 mm); **13**: BT-5258 (Phenon **MB**, Papua-New Guinea, Milne Bay, H: 23.42 mm); **14**: BT-5251 (Phenon **MB**, Papua-New Guinea, Milne Bay, H: 26.66 mm); **15**: ISNB-1 (Phenon **HB**, Papua-New Guinea, Hansa Bay, H: 24.97 mm); **16**: ISNB-6 (Phenon **HB**, Papua-New Guinea, Hansa Bay, H: 21.36 mm); **17**: BT-6340 (Phenon **SR**, Sri Lanka, Galle, H: 24.93 mm); **18**: BT-6344 (Phenon **SR**, Sri Lanka, Galle, H: 22.83 mm).
19 - 22: species "L+X", subspecies "SJ+BB".
19: JS-201 (Phenon **BB**, Indonesia, Bali, H: 18.85 mm); **20**: BT-4728 (Phenon **BB**, Indonesia, Bali, H: 21.70 mm); **21**: JS-60 (Phenon **SJ**, South Java, H: 16.82 mm); **22**: JS-81 (Phenon **SJ**, South Java, H: 18.13 mm).
23, 24: species "L+X", subspecies "AO".
23: BT-6354 (Phenon **AO**, West Australia, Shark Bay, H: 27.45 mm); **24**: BT-6353 (Phenon **AO**, West Australia, Shark Bay, H: 30.24 mm).
25 - 32: species "G".
25: BT-6126 (Phenon **AQ**, Australia, Queensland, H: 25.11 mm); **26**: BT-6125 (Phenon **AQ**, Australia, Queensland, H: 25.02 mm); **27**: BT-4999 (Phenon **PB**, Philippines, Cebu, H: 21.67 mm); **28**: BT-5789 (Phenon **PB**, Philippines, Cebu, H: 21.35 mm); **29**: DG-P12/12 (Phenon **IF**, Indonesia, Flores, H: 17.56 mm); **30**: DG-P12/10 (Phenon **IF**, Indonesia, Flores, H: 21.31 mm); **31**: BT-298 (Phenon **IC**, Indonesia, Ceram, H: 17.41 mm); **32**: BT-169 (Phenon **IC**, Indonesia, Ceram, H: 13.81 mm).

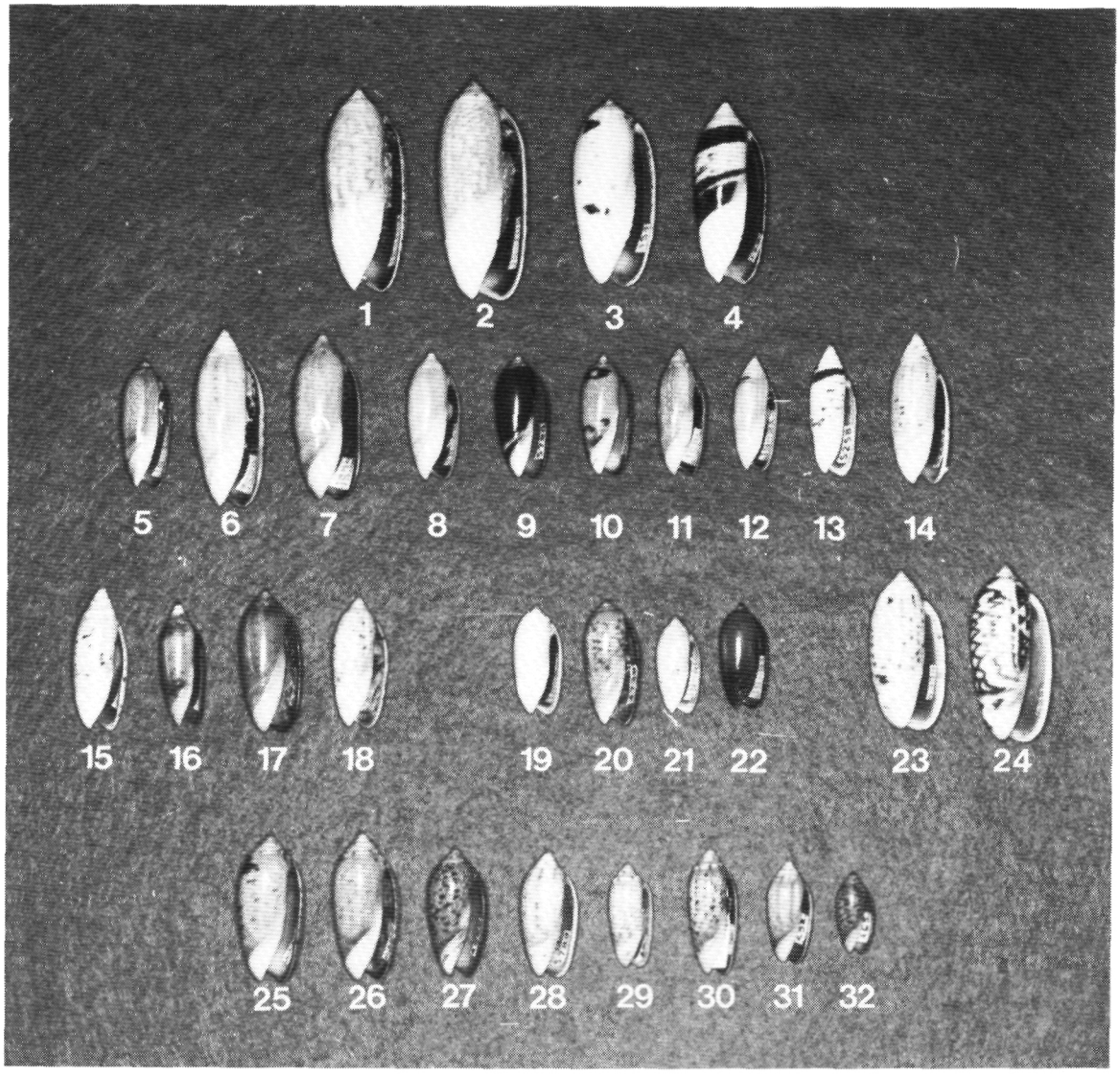
an artifact due to their relatively small populations. The rather large phenon **BA** appears separated from nearly all others. If one combines the axes 2 and 3 (not figured), it is separated from all other phena but for a very small overlap with **SR**.

The small phenon **THC** (3 specimens only) is entirely separated. It contains only 3 specimens (and might even be heterogeneous): the sensible option is to discard it temporarily and to reintroduce the specimens in the final, global analysis.

Very similar results are obtained by factorial discriminant analysis performed with the same set of variables utilized here above.

4.3.3. Hypothesis.

The above data enable us to formulate a working hypothesis, the validity of which we shall have to test. One will have noticed that phenon **THA** always overlaps the same phena **WJB, HB, WJA, MB, PA** and **SR**, in bivariate as in multivariate analyses. These phena taken together seem to constitute within the "*O. oliva* complex" a morphological continuum resisting all attempts at objective separation. We shall call it group "**L**" (203 specimens, 59% of the total sample). We do not know at this stage if this group is complete, *i.e.* if other phena are still to be incorporated in group "**L**".



4.3.3.1. It was tempting to speculate that removal of group "**L**" would considerably simplify the representation of the remainder of the specimens of the "*O. oliva* complex". This was indeed found to be the case. Factorial discriminant analysis with the set of 32 variables selected hereabove (24 variables retained in the analysis, two canonical functions accounting for 76.06% of the total variation, 97.5 % of specimens correctly attributed) now shows the remainder of the sample clearly divided into three clusters (Fig. 7). Group "**G**" (61 specimens) contains the phena **AQ**, **IC**, **IF** and **PB**. Group "**B**" (24 specimens) contains the phena **BA** and **THB**. Group "**X**" (35 specimens) contains the phena **AO**, **BB** and **SJ**.

The two canonical functions (given in order to allow the reader to verify our results) are :

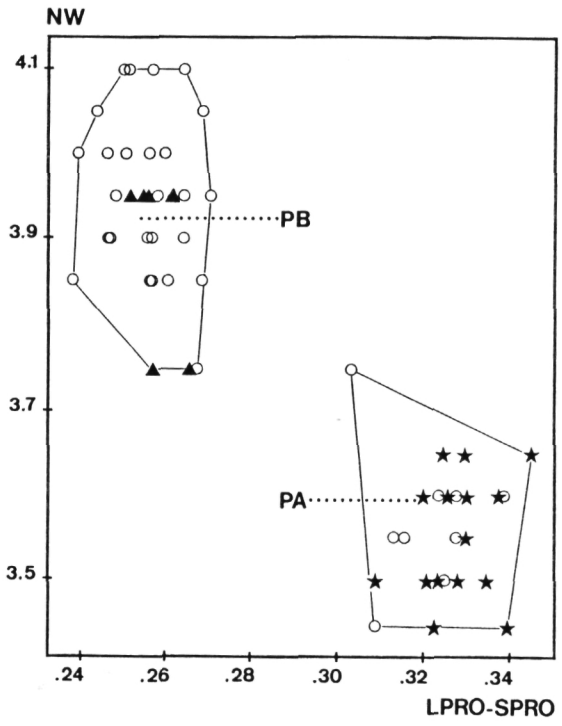


Fig. 5. Scatter diagram: variables LPRO-SPRO and NW. Minimum convex polygons. Separation of the two phena **PA** and **PB** on the entire Philippine sample. Open circles: specimens from Cebu Island; stars and triangles: other localities.

F1= 56.49*D/H +62.83*LW/H -172.74*X/H +31.67*(X-R)/H -13.89*(H-L)/D -781.37*SUT/H -13.64*D/PNW +27.23*X/PNW -207.13*SUT/PNW -6.47*(X-R)/PNW +1.27*(H-L)/PNW +1398.87*SUT/L -9.38*NW -40.9*LPRO +112.87*(LPRO-SPRO)/NW +40.26*RES4/NW -63.04*MPRO/NW +60.69*PAT18 -201.24* PAT18/NW -15.1*PAT16/NW +31.93* MPRO/RES5 +166.1*LPRO/NW +1.68*PAT18/PAT17 +5.46*RES5 -32.4 +100

F2= 25.43*D/H -25*LW/H -93.4*X/H -51.06*(X-R)/H -23.33*(H-L)/D -1066.23*SUT/H -3.12*D/PNW +9.63*X/PNW -293.45*SUT/PNW +6.93*(X-R)/PNW +4.14*(H-L)/PNW +1898.47*SUT/L +5.51*NW +49.99*LPRO +100.26*(LPRO-SPRO)/NW -26.36*RES4/NW -1126.8*MPRO/NW -103.98*PAT18 +313.02*PAT18/NW -21.34*PAT16/NW +353.37* MPRO/RES5 -109.11*LPRO/NW -2.29*PAT18/PAT17 +47.22*RES5 -18.07 +100

4.3.3.2. The discriminant analysis in 4.3.3.1 bears on 9 separated local phena. Its interpretation is confirmed by repeating the discriminant analysis, this time on the three proposed clusters "**G**", "**B**" and "**X**". The result (Fig. 8, 15 variables retained in the analysis, two canonical functions accounting for 100% of the total variation, 97.5 % of specimens correctly attributed) is fully consistent with the previous conclusion.

The two canonical functions (given in order to allow the reader to verify our results) are :

F1= 45.36*D/H -44.15*LW/H +30.58*X/H -10.01*(X-R)/H +30.64*(H-L)/D +3497.08*SUT/H -2.09*D/PNW +5.69*X/PNW +75.13*SUT/PNW -5.5*(X-R)/PNW -6.92*(H-L)/PNW -3106.25*SUT/L +1.67*NW -59.38*(LPRO-SPRO)/NW -23.1*PAT18 +20.51 +100

F2= 131.28*D/H +10.59*LW/H -132.9*X/H +88.15*(X-R)/H +72.52*(H-L)/D +3581.86*SUT/H -13.11*D/PNW +21.93*X/PNW +202.4*SUT/PNW -12.06*(X-R)/PNW -18.66*(H-L)/PNW -3734.8*SUT/L -6.48*NW -40.84*(LPRO-SPRO)/NW +27.37*PAT18 -43.8 +100

4.3.3.3. We have now the following hypothesis: the "*O. oliva* complex" can be subdivided into 4 clusters "**L**", "**G**", "**B**" and "**X**". One of the groups "**G**", "**B**" or "**X**" might be part of group "**L**".

We have reasons to suspect that cluster "**X**", formed of three local phena **AO**, **BB** and **SJ**, might not be homogeneous. These phena are all separable by scatter diagrams (see section 4.3.1.) but "**SJ**" and "**BB**" are very close and their small separation might be an artifact resulting from the small size of "**BB**" (8 specimens). It would be quite conceivable that "**X**" consists of two subunits "**AO**" and "**SJ+BB**".

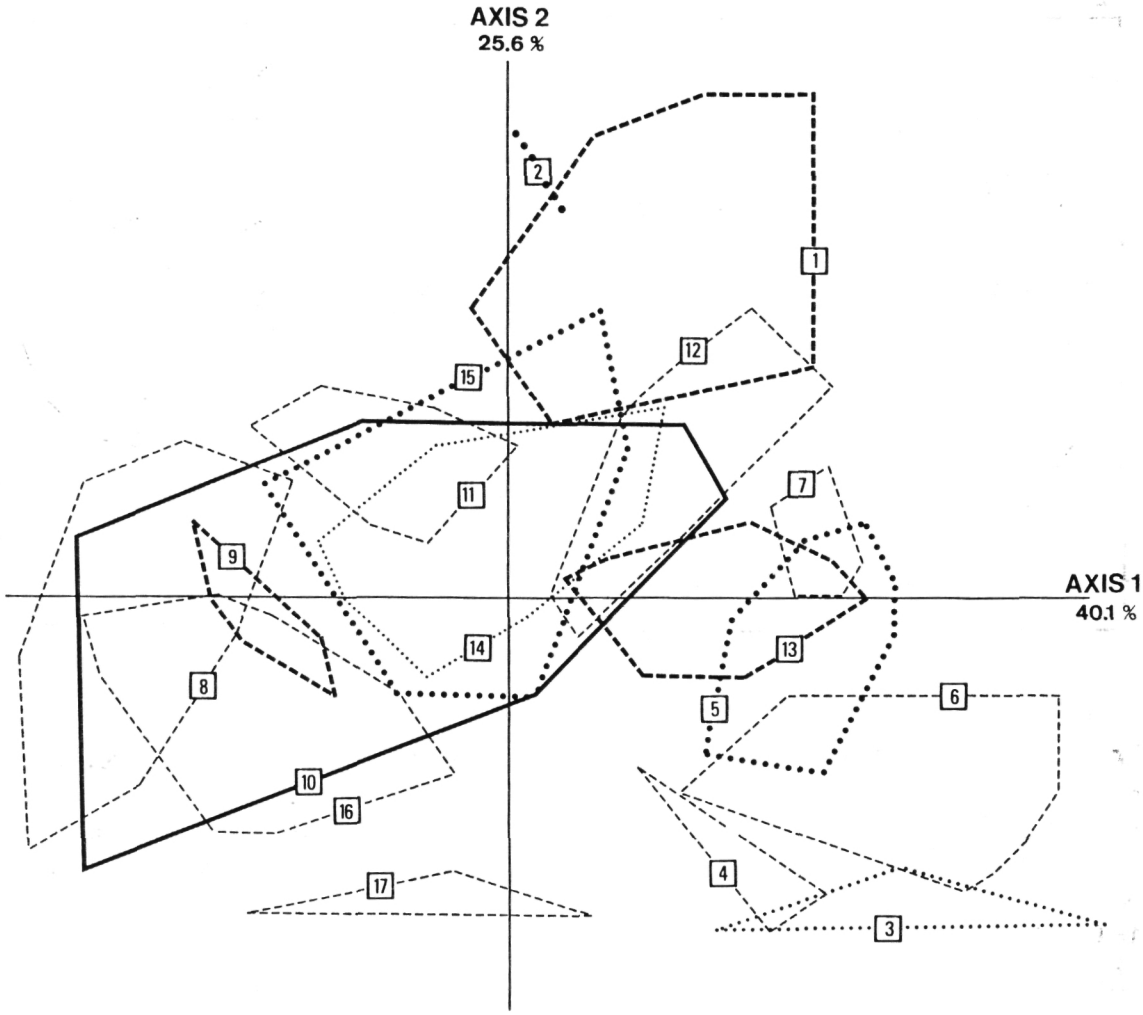


Fig. 6. Principal component analysis. 17 local phena of the "*O. oliva* complex". Correlations matrix. 32 variables (see text). Representation of the plane Axis1/Axis2. Minimum convex polygons. 1 = BA, 2 = THB, 3 = IC, 4 = IF, 5 = AQ, 6 = PB, 7 = BB, 8 = MB, 9 = WJB, 10 = THA, 11 = WJA, 12 = AO, 13 = SJ, 14 = PA, 15 = SR, 16 = HB.

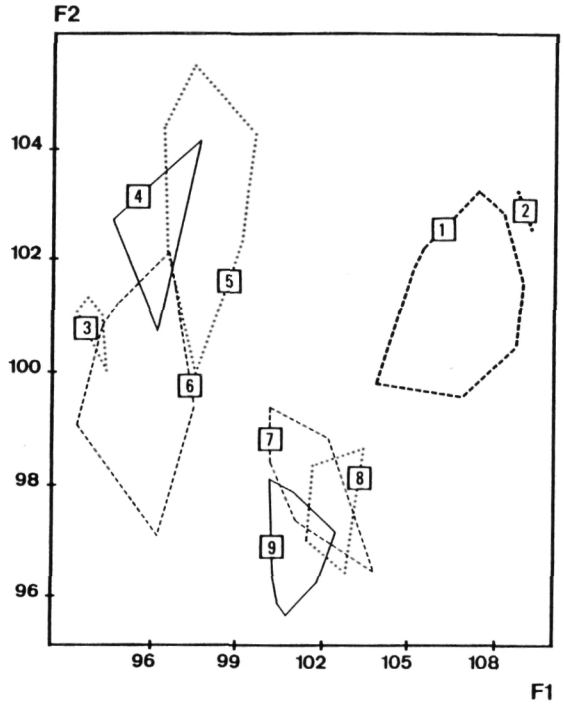


Fig. 7. Factorial discriminant analysis. Representation of local phena that do not belong to group "**L**" with two canonical functions totaling 76.6 % of the total variation (Phenon **THC** omitted, see text). Minimum convex polygons. 1= BA, 2= THB, 3= IC, 4= IF, 5= AQ, 6= PB, 7= BB, 8= AO, 9= SJ.

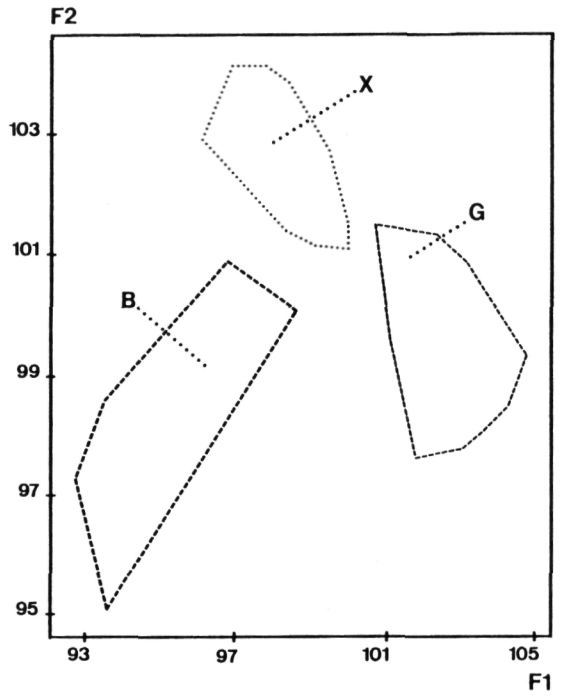


Fig. 8. Factorial discriminant analysis. Representation of the groups of local phena "**G**", "**B**" and "**X**" with two canonical functions totaling 100 % of the total variation (see text). Minimum convex polygons.

4.3.4. Test of the hypothesis.

4.3.4.1. A first verification consisted in checking which of the above clusters are objectively separated from the others. Group "**G**" is separated from group "**B**" by a scatter diagram of D/L versus D/PNW (Fig. 9). Group "**G**" is separated from group "**X**" by a scatter diagram of RES5/NW versus R/LW (Fig. 10). Group "**G**" is separated from group "**L**" by a scatter diagram of D/H versus RES4/NW (Fig. 11). Group "**B**" is separated from group "**L**" by a scatter diagram of LW/PNW versus (PAT17+PAT16) (Fig. 12). Group "**B**" is separated from group "**X**" by a scatter diagram of D/PNW versus PAT18/RES4 (Fig. 13).

Despite all efforts we could not find any scatter diagram separating group "**L**" from group "**X**" (or even from its subunits "**AO**" and "**SJ+BB**"). Factorial discriminant analysis was equally unsuccesful and indicates the existence of a morphological continuum "**L+X**".

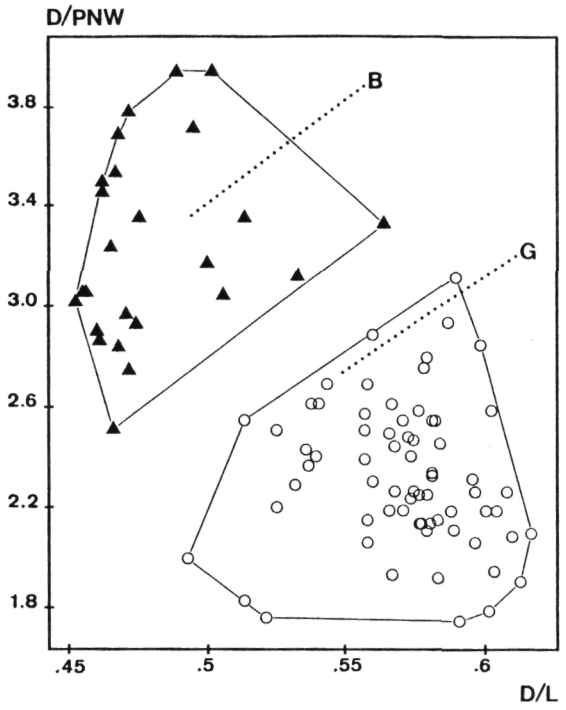


Fig. 9. Scatter diagram: variables D/L and D/PNW. Minimum convex polygons. Separation of the groups "**G**" and "**B**".

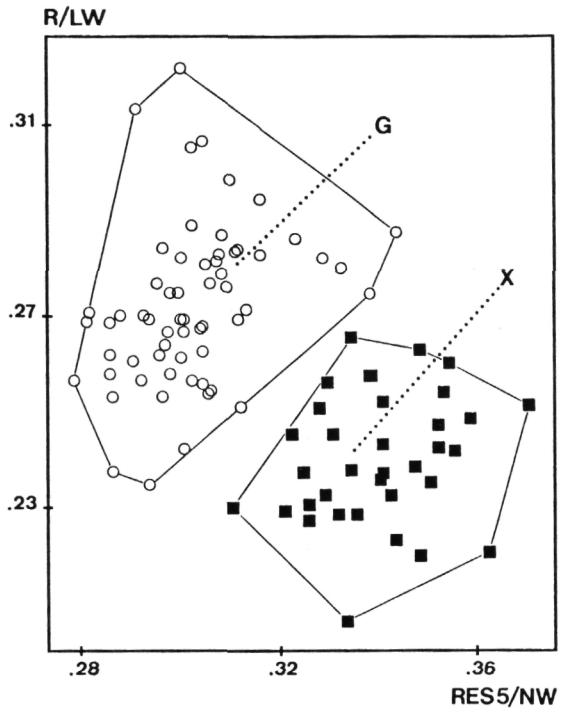


Fig. 10. Scatter diagram: variables RES5/NW and R/LW. Minimum convex polygons. Separation of the groups "**G**" and "**X**".

4.3.4.2. The three groups "**G**", "**B**" and "**L+X**" are very similar: "**G**" and "**B**" are easily separated from each other and from "**L**" and "**X**" by scatter diagrams (see above) but a total planar representation requires multivariate analysis.

Factorial discriminant analysis was performed with the 11 variables D/L, D/PNW, RES5/NW, R/LW, D/H, RES4/NW, LW/PNW, PAT17+PAT16, PAT18/RES4, X/L and MPRO/NW (these are the most performing variables for the separation of the groups "**G**", "**B**", "**L**", "**AO**" and "**SJ+BB**" in scatter diagrams). The result (Fig. 14, two canonical equations accounting for 100 % of the total variation, 98.14 % of specimens correctly attributed) confirms the hypothesis. The small overlap of groups "**B**" and "**L+X**" is certainly due to representational distorsion, as we have seen that the pairs "**B**" and "**L**" and "**B**" and "**X**" are fully separated by bivariate analysis (Figs 12 and 13).

The two canonical functions (given in order to allow the reader to verify our results) are :

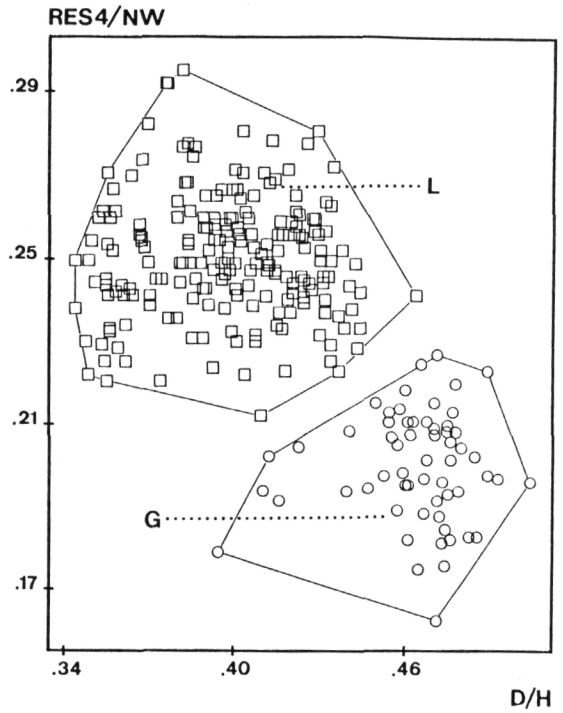


Fig. 11. Scatter diagram: variables D/H and RES4/NW. Minimum convex polygons. Separation of the groups "**G**" and "**L**".

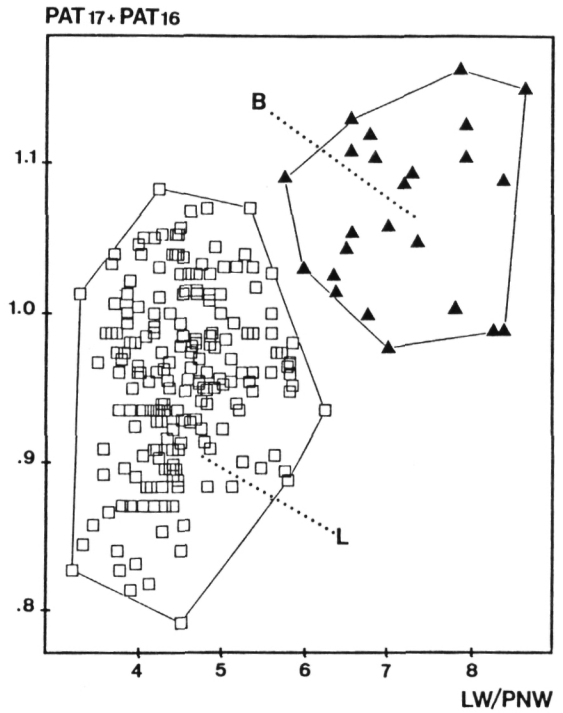


Fig. 12. Scatter diagram: variables LW/PNW and PAT17+PAT16. Minimum convex polygons. Separation of the groups "**B**" and "**L**".

F1= -1.73*LW/PNW +.46*(PAT17+PAT16) -25.98*D/H +3.79*D/PNW +50.63*RES4/NW +5.02*PAT18/RES4 -15.98*D/L -24.33*R/LW +23.96*RES5/NW +38.49*MPRO/NW +4.65*X/L -5.32 +100

F2= 10.97*LW/PNW +4.12*(PAT17+PAT16) +55.21*D/H -19.65*D/PNW -22.41*RES4/NW -2.81*PAT18/RES4 +36.6*D/L +31.67*R/LW -6.18*RES5/NW -12.48*MPRO/NW -10.46*X/L -46.17 +100

4.3.4.3. As a further check, we can now verify what happens to the 21 "dubious specimens" (5% of the total sample) that were somewhat conveniently discarded from the first steps of the analysis in sections 4.2. and 4.3.2. These would be most likely candidates to upset our classification.

All these specimens have been added to the previous analysis, using the canonical functions given in 4.3.4.2. One can see in Fig. 15 that all the "dubious specimens" now fall nicely into one of the groups "**G**", "**B**" or "**L+X**" with the exception of one unique specimen from Sumatra (probably a juvenile intruder of some other species, after careful reexamination).

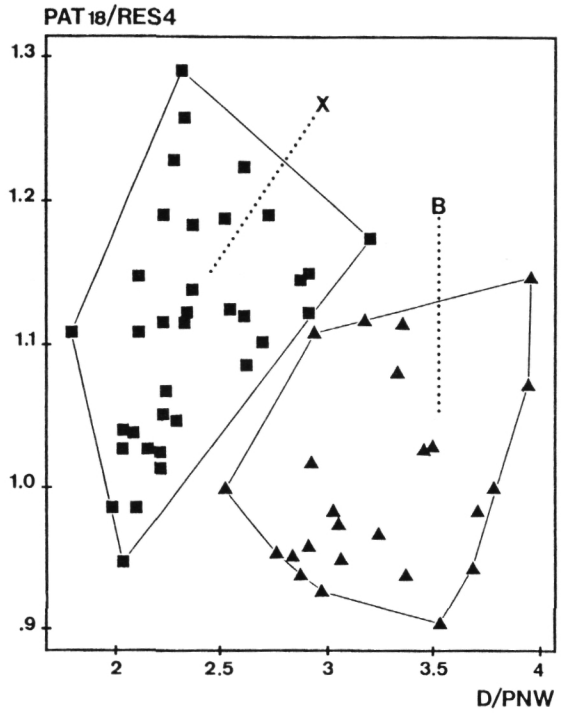


Fig. 13. Scatter diagram: variables D/PNW and PAT18/RES4. Minimum convex polygons. Separation of the groups "**B**" and "**X**".

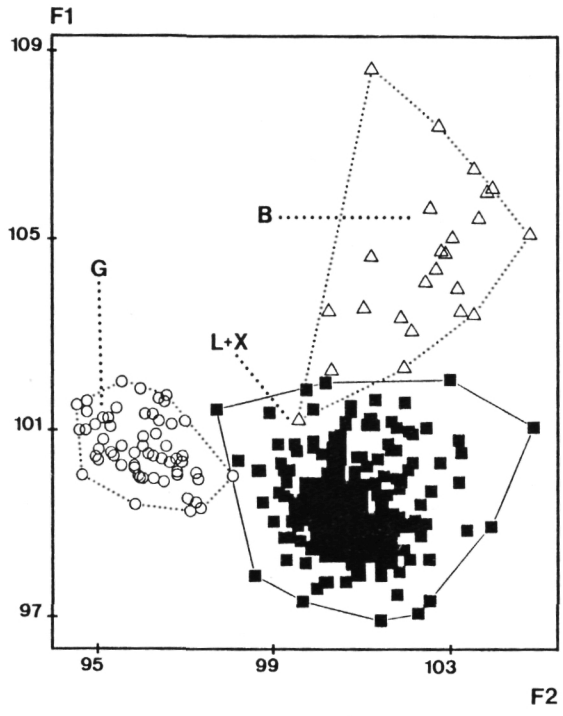


Fig. 14. Factorial discriminant analysis. Representation of the groups of local phena "**G**", "**B**" and "**L+X**" with two canonical functions totaling 100 % of the total variation (see text). Minimum convex polygons.

5. CONCLUSIONS

At this stage, it has been demonstrated that our sample of the "*O. oliva* complex" consists of three morphologically distinct groups : "**G**", "**B**" and "**L+X**". We should now decide on the taxonomical rank of these entities.

Group "**G**" is sympatric with group "**L+X**" in the Philippines and (after identification of the dubious specimens) in the Solomons and in Papua-New Guinea (Rabaul).

Group "**B**" is sympatric with group "**L+X**" in Indonesia (Bali) and in Thailand. The conclusion that "**G**", "**B**" and "**L+X**" are distinct species cannot be eluded.The distribution range is certainly wider than shown so far. Careful examination of numerous shells from Japan (not measured due to their damaged protoconchs) shows they form a very homogeneous group, with the aspect of the most characteristical specimens of species "**G**". In the same way, numerous specimens from India (not measured for the same reason) most probably consist of a mixture of the species "**B**" and "**L+X**".

Group "**X**" consists of "**AO**" restricted to Western Australia and "**SJ+BB**" restricted to South Java and Bali. "**X**" forms a morphological

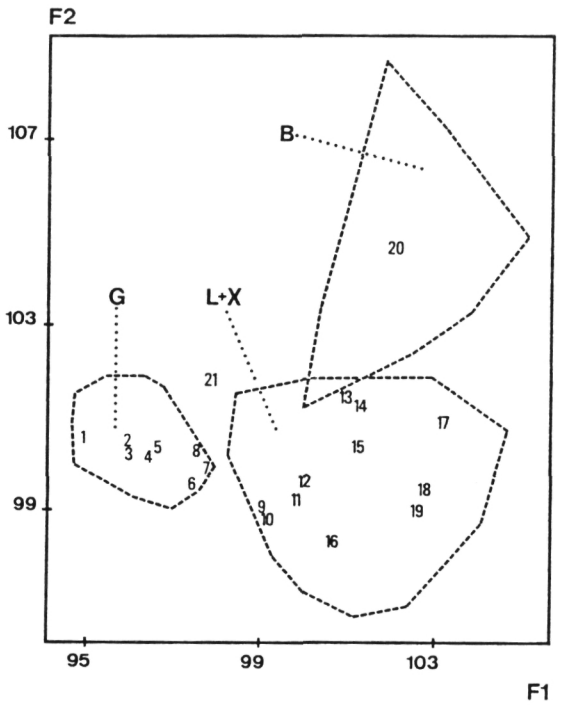


Fig. 15. Reincorporation of all discarded specimens in the global factorial analysis pictured in Fig. 14 (see text, section 4.3.4.3). **1**: BT-215 Rabaul; **2**: BT-219 Rabaul; **3**: BT-2493 Solomons; **4**: BT-2494 Solomons; **5**: JS-075 Bali; **6**: BT-2982, New Caledonia; **7**: JS-065 Thailand (THC); **8**: BT-2983 New Caledonia; **9**: BT-4775 Papua-New Guinea; **10**: JS-044 Thailand (THC); **11**: BT-2499 Solomons; **12**: BT-2051 Solomons; **13**: BT-261 Mollucas; **14**:= BT-1773 Flores; **15**: BT-2500 Solomons; **16**: JS-042 Thailand (THC); **17**: BT-224 Rabaul; **18**: BT-5794 Philippines; **19**: BT-1796 West Java; **20**: JS-111 West Java; **21**: BT-6136 Sumatra.

continuum with "**L**" but "**X**" and "**L**" are never sympatric. Furthermore, "**AO**" and "**SJ+BB**" shells (see Fig. 4) are immediately distinguished from "**L**" shells by their shape and colour pattern, while the other phena constituting "**L**" are not separable. These data support the view that "**AO**" and "**SJ+BB**" are two subspecies of "**L+X**" in the strict sense of broadly recognizable geographical varieties.

A distribution map is given in Fig. 16.

6. DISCUSSION

6.1. THE SAMPLE.

The material examined here is certainly too small (in terms of both localities and number of specimens) for a complete solution of the problem. Perfect specimens, with intact protoconch and safe locality data are difficult to find, probably because most collectors do not pay much attention to shells as common as *Oliva oliva*. The very abundance of the shells could furthermore introduce a systematic bias in our samples, as collectors will tend to collect only specimens that are extreme in size, shape or colour.

Additional, unsuspected local phena might well exist. We have unfortunately not been able to examine pertinent fossil material.

6.2. THE METHOD.

Underlying our whole approach is the assumption that there is no sexual dimorphism, a phenomenon we have never seen in any of the *Oliva* dissected so far in this laboratory (HUART, unpublished results). This appears contradiction with the results of KASINATHAN, MARUTHAMUTHU and TAGORE (1987) who reported that the two sexes of *Oliva oliva* have a different growth allometry. There fortunately is no real problem: the Indian authors state that the phenomenon occurs only in specimens over 35.9 mm, a size never approached by any of our measured specimens. Errors of interpretation due to possible sexual dimorphism would furthermore be entirely inconsistent with the observed geographical distributions (Fig. 16).

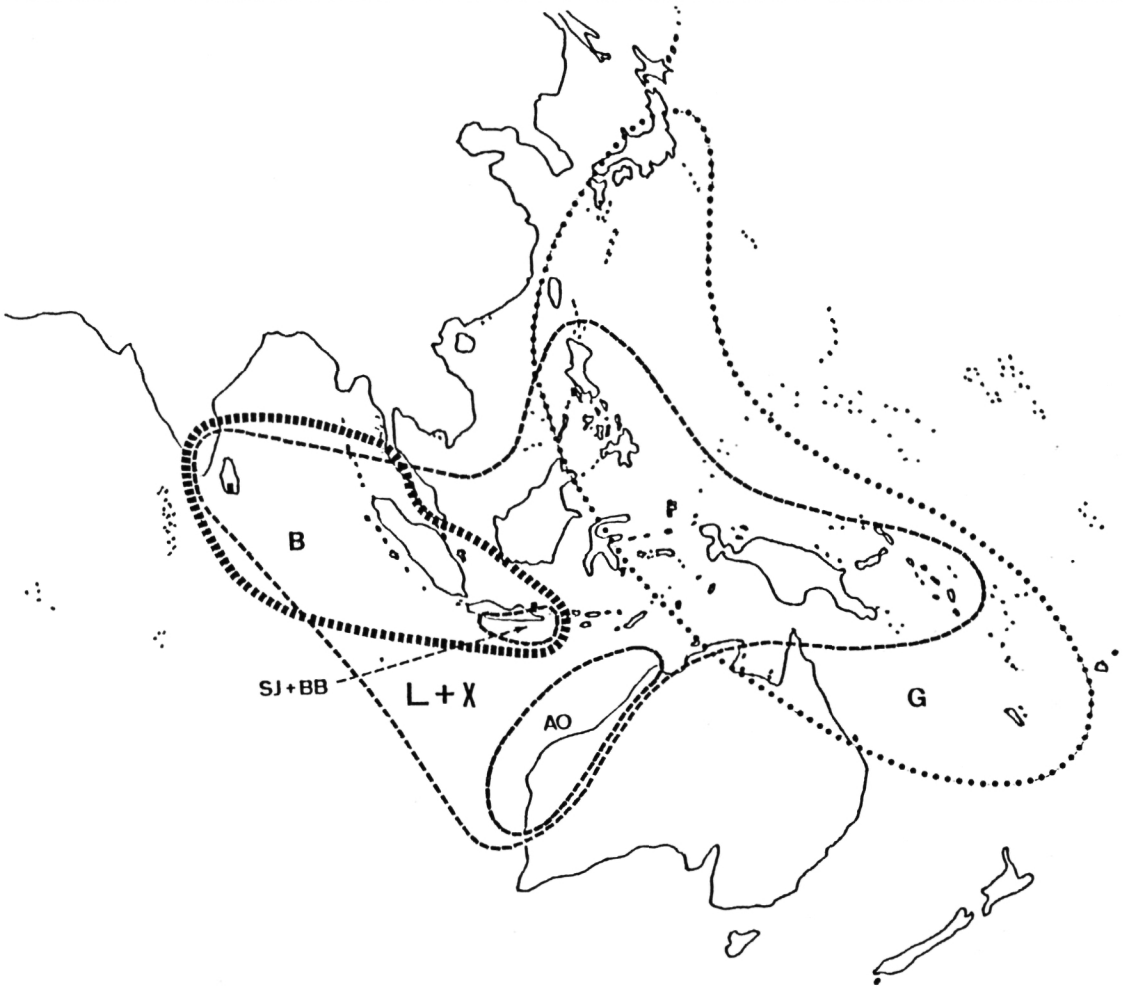


Fig. 16. Distribution areas of the three species **L+X**, **G** , **B** and the two subspecies of **L+X** (**AO** and **SJ+BB**).

6.3. THE RESULTS.

The species "**G**", "**B**" and "**L+X**" are evidently very close to each other. Local populations are generally quite homogeneous in aspect and sympatric species are rather easy to discern at the same locality. When specimens from all the localities are examined together, the species are so far undistinguishable by simple visual examination. The total range of variability far exceeds the size of the interspecies gaps as can be seen on most of the graphs hereabove. Such cases correspond to the definition of sibling species (MAYR, 1963). It is well known that sibling species are extremely frequent in the animal kingdom and indeed the surprise would have been not to find any in the genus *Oliva*.

6.4. NOMENCLATURE.

This paper aimed exclusively at the taxonomic structure of the "*O. oliva* complex". The nomenclatural puzzle presented by these shells probably matches in complexity the biological puzzle met in this first stage. We have refrained here from any nomenclatural act, pending study of more localities and detailed examination of type material. In the same manner, no attempt was made at naming phena "**W**", "**Y**" and "**Z**" that were detached from the "*O. oliva* complex".

Acknowledgements.

We are grateful to the Fonds National de la Recherche Scientifique (F.N.R.S.) for its support, to Dr. J. VAN GOETHEM (I.R.S.N.B.), Dr. D. GREIFENEDER, Dr. J. SENDERS, Mr. A. BOSSUYT and Mr. F. NOLF for the loan of specimens, to Mr. D. HUART and Mr. C. VAN OSSELAER for valuable advise and criticism.

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