Comparative morphology of Pliocene, Quaternary and Recent shells of *Ocenebra erinaceus* (Linnaeus, 1758) and *O. brevirobusta* Houart, 2000 (Mollusca, Muricidae, Ocenebrinae): reflections on the intra- and interspecific variations

Véronique BERROU
8 allée des Avocettes, Parc-Quibias,
F-56610 Arradon (France)

Didier MERLE
Département Histoire de la Terre, Muséum national d'Histoire naturelle,
UMR 5143 du CNRS, 8 rue Buffon, F-75231 Paris cedex 05 (France)
dimerle@aol.com

Jean-Louis DOMMERGUES
Université de Bourgogne, Centre des Sciences de la Terre,
6 boulevard Gabriel, F-21000 Dijon (France)
jean-louis.dommergues@u-bourgogne.fr

Catherine CRÔNIER
Université des Sciences et Technologies de Lille,
Laboratoire de Paléontologie et Paléogéographie du Paléozoïque,
UMR 8014 du CNRS, F-59655 Villeneuve d'Ascq cedex (France)
catherine.cronier@univ-lille1.fr

Didier NÉRAUDEAU
Université de Rennes 1, Campus de Beaulieu,
F-35042 Rennes cedex (France)
didier.neraudeau@univ-rennes1.fr

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ABSTRACT

The morphological variations of Pliocene, Quaternary and Recent shells of *Ocenebra erinaceus* (Linnaeus, 1758) and *O. brevirobusta* Houart, 2000 are analyzed. The study of these oyster drillers is based on various methods (cladistics, biometry, Procrustes and Fourier analyses) and concerns populations from 40 localities of the Atlantic (from Normandy to Morocco) and

Mediterranean shorelines. The results indicate a morphological distribution of North/South orientation, the more derived southern forms being closely related. In spite of a strong variability, a beginning of differentiation, probably dating from the Plio-Pleistocene, is observed between three groups: 1) Northern Atlantic Ocean (*O. erinaceus*); 2) Mediterranean Sea (*O. erinaceus*); and 3) Moroccan Atlantic (*O. brevirobusta*). *O. brevirobusta* is temporarily regarded as a geographic subspecies of *O. erinaceus*, because of its uninterrupted marginal area, and its P2 cord more atrophied than in the Italian late Pliocene *O. erinaceus*. Within these groups, the multivariate analysis of variance distinguishes local biogeographic entities. In addition, two unexpected results deserve to be stressed: 1) the population from Étang de Thau, systematically associated to those of the Northern Atlantic Ocean, is located in a zone of oyster importation from the Oléron island; and 2) the population from Algarve (Portugal), closer to those of the Mediterranean Sea, lives in an Atlantic area undergoing the influence of Mediterranean waters. Comparisons between *O. erinaceus* and *Ocinebrellus inornatus* (Récluz, 1851), an Asian species introduced on the French Atlantic coast, show more similarities with the Northern Atlantic *O. erinaceus*, than with Mediterranean or Moroccan Atlantic *O. erinaceus*.

KEY WORDS
Mollusca,
Gastropoda,
Muricidae,
Ocenebrinae,
Ocenebra,
shells,
Neogene,
Recent,
Europe,
variations,
populations,
cladistics,
morphometry,
evolution.

RÉSUMÉ

*Comparaison morphologique des coquilles pliocènes, quaternaires et actuelles d'*Ocenebra erinaceus *(Linnaeus, 1758) et d'*O. brevirobusta *Houart, 2000 (Mollusca, Muricidae, Ocenebrinae) : réflexion sur les variations intra- et interspécifiques.*

La variation morphologique de coquilles pliocènes, quaternaires et actuelles d'*Ocenebra erinaceus* (Linnaeus, 1758) et d'*O. brevirobusta* Houart, 2000 est analysée. L'étude de ces perceurs d'huîtres, fondée sur différentes méthodes (analyse cladistique, biométrie, morphométrie géométrique et transformée de Fourier), porte sur des populations de 40 localités des côtes atlantiques (de la Normandie au Maroc) et méditerranéennes. Les résultats indiquent une répartition morphologique d'orientation Nord/Sud, les formes méridionales, plus dérivées, étant étroitement apparentées. Malgré une forte variabilité, un début de différenciation, datant probablement du Plio-Pléistocène, s'observe entre trois groupes de populations : 1) Atlantique septentrional (*O. erinaceus*) ; 2) Méditerranée (*O. erinaceus*) ; et 3) Maroc atlantique (*O. brevirobusta*). *O. brevirobusta* est provisoirement considérée comme une sous-espèce géographique d'*O. erinaceus*, en raison d'une aire marginale non disjointe et d'une atrophie du cordon P2 plus marquée chez les *O. erinaceus* du Pliocène supérieur italien. Au sein des trois groupes, l'analyse multivariée de variance distingue des entités biogéographiques locales. Deux résultats inattendus méritent d'être soulignés : 1) la population de l'Étang de Thau, systématiquement associée par les analyses à celles de l'Atlantique septentrional, est située dans une zone d'échanges d'huîtres avec l'île d'Oléron ; et 2) la population de l'Algarve (Portugal), morphologiquement proche de celles de Méditerranée, est située dans une région de l'Atlantique subissant l'influence des eaux méditerranéennes. Les comparaisons entre *O. erinaceus* et *Ocinebrellus inornatus* (Récluz, 1851), espèce introduite par l'homme en Atlantique, révèlent de plus grandes similitudes avec les *O. erinaceus* de l'Atlantique septentrional qu'avec celles de Méditerranée ou du Maroc.

MOTS CLÉS
Mollusca,
Gastropoda,
Muricidae,
Ocenebrinae,
Ocenebra,
coquilles,
Néogene,
actuel,
Europe,
variations,
populations,
cladistique,
morphométrie,
évolution.

INTRODUCTION

During the last decades, numerous allochthonous species of molluscs have been introduced on the French Atlantic coast by human way (Gruet *et al.* 1976; Sauriau 1991; Montaudouin & Sauriau 2000). One of the last introductions is that of an ocenebrine, *Ocinebrellus inornatus* (Récluz, 1851). It is dated from 1997 and reported in the Marennes-Oléron basin (Charente-Maritime, France). The species is often assigned to *Ocinebrellus* Jousseaume, 1880 (type species by original designation: *Murex eurypteron* Reeve, 1845 [a junior synonym of *M. aduncus* Sowerby, 1834]), but has been recently transferred (Houart & Sirenko 2003) in the genus *Ocenebra* Gray, 1847 (type species: *O. erinaceus* Linnaeus, 1758 by monotypy). *Ocinebrellus inornatus* is an oyster driller. Although it does extend into warm temperate waters, the species is properly a low-boreal, cool water temperate form. It is native from eastern, western Japan and mainland Asia, from 33° to 51° north latitude. *O. inornatus* has already been introduced by human way on the Pacific coasts of Oregon, Washington and British Columbia (Radwin & Attilio 1976; Carlton 1992; Noda *et al.* 1993). On the French shoreline, *O. inornatus* begins dangerously to damage the oyster farming, and consequently this invasion may have economical repercussions. The molecular analysis of the French *O. inornatus* demonstrates that it has been introduced from a stock having closer relationships with the American population than the Asian (Garcia-Meunier *et al.* 2001; Martel *et al.* 2003). Moreover, its life environment corresponds to that of *O. erinaceus* (Pigeot *et al.* 2000; Koster-Sperling 2002) and a dramatic decrease of the autochthonous oyster drill is reported when *O. inornatus* shows a high density (Pigeot *et al.* 2000). Therefore, some populations of *O. erinaceus* might be locally extirpated and a study of its morphological variation also answers to the necessity to better understand the evolutionary potential of the species.

On the European and North-African coasts, three *Ocenebra* species have been recorded: *O. erinaceus*, *O. brevirobusta* Houart, 2000 (Houart 2000a) and *O. chavesi* Houart, 1996 (Houart 1996). Fossils of *O. erinaceus* have been reported from the middle Miocene of Poland (Baluk 1995), but the identification by Baluk (1995) is probably wrong, the figured specimens being more similar to members of the genus *Jaton* Push, 1837 (type species by original designation: *Murex decussatus* Gmelin, 1791), particularly *J. dufreynoi* (Grateloup, 1847) or *J. sowerbyi* (Michelotti, 1842). However, the occurrence of *O. erinaceus* is well attested in the Pliocene of Italy (Malatesta 1974), Spain (Muniz Solis & Guerra-Merchan 1994; Martinell 1979; Martinell & Marquina 1981) and in the Pleistocene of the Northern domain (Glibert 1963). The geographic range of Recent populations of *O. erinaceus* (Fig. 1A) extends from Southern England and Ireland to the Mediterranean Sea and the Gibraltar Strait. The species is also reported from Madeira (Houart 2001a), Canary Islands (Garcia-Talavera 1974) and from Azores, where it has been recently introduced (Houart & Abreu 1994; Houart 2001a). The fossils of *O. brevirobusta* are reported from the lower Pleistocene (Moghrebian-Messaoudian) of Morocco by Brébion (1978, 1979a, b) under the name *Murex torosus* Lamarck, 1816, which probably corresponds to a junior synonym of the Pliocene species *Heteropurpura polymorpha* (Brocchi, 1814) (see Houart 2000a). The geographic range of Recent populations of *O. brevirobusta* (Fig. 1A) is restricted to the Moroccan Atlantic coast (El Jadida, Rabat, Temara, Essaouira [= Mogador], Agadir and Asilah) and northward, it does not pass Tanger. Following Houart (2000a, 2001a), *O. brevirobusta* and *O. erinaceus* are sympatric at Asilah. *O. chavesi* is an endemic species from the Azores and is only known from San Miguel Island. No fossil of *Ocenebra* are reported from Miocene and Quaternary terraces of Santa Maria Island (Zbyszewski & da Veiga Ferreira 1961, 1962) belonging to this archipelago.

As seen above, the geographic range of *O. erinaceus* and *O. brevirobusta* is continuous (Fig. 1A). The absence of a clear geographic

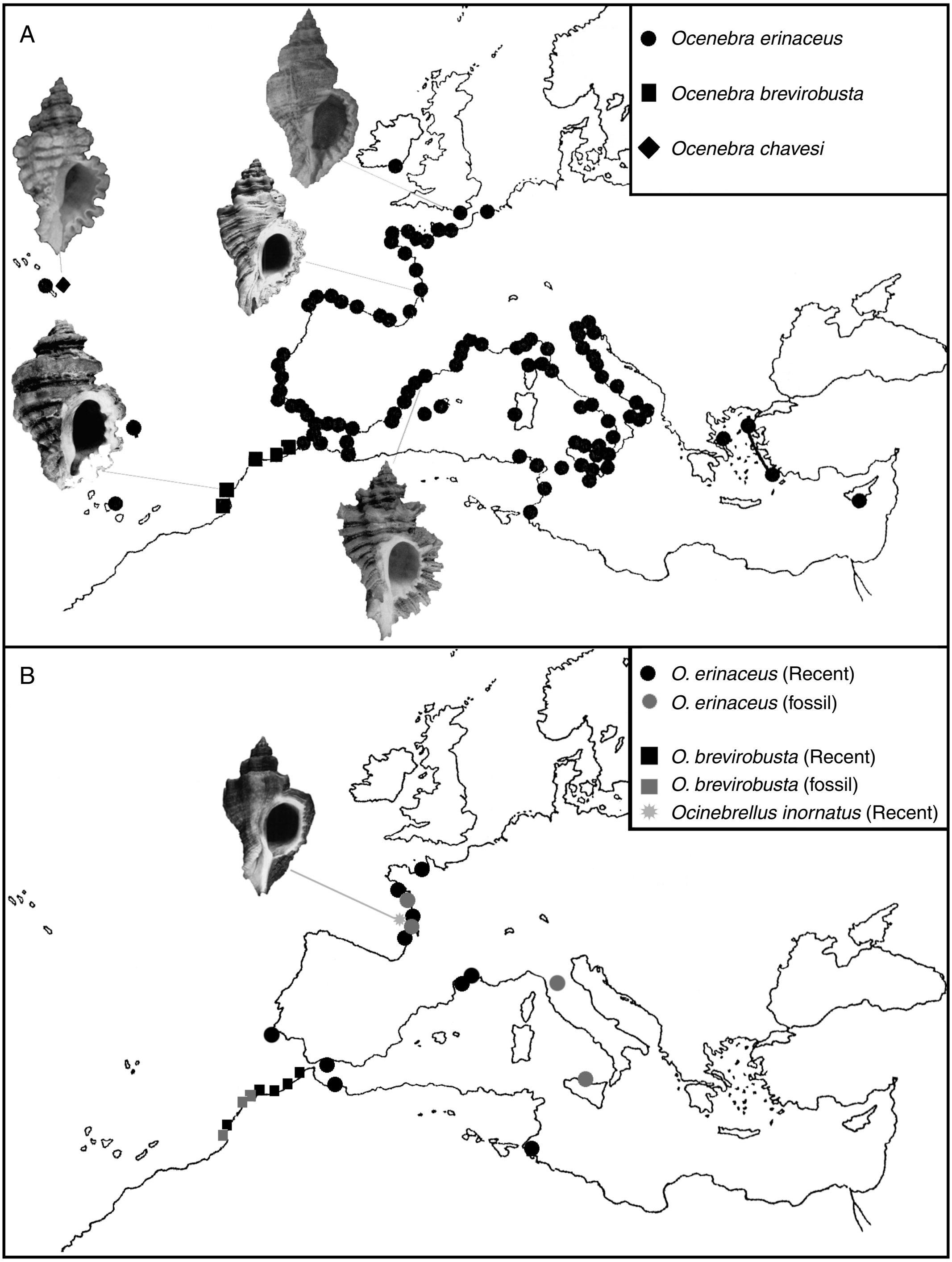

FIG. 1. — **A**, geographic range of the genus *Ocenebra* Gray, 1847 in Europe after Houart (2001a) modified; **B**, geographic location of the studied samples; photos of *Ocenebra*, courtesy of R. Houart.

discontinuity questions the biological reality of both species. In addition, the legendary intraspecific variation of *O. erinaceus* (no less than 49 superfluous names! [Houart 2001a]) and the taxonomic individualisation of *O. brevirobusta* from *O. erinaceus*, which is not based on a modern analysis of the shell variation, also justify this interrogation. These observations constitute the main source of our thought. Combining several methods of comparative morphology, the goal of this work will be to analyse the shell variation of these *Ocenebra* in order to know if the populations reflect a process of morphological differentiation. *O. erinaceus* and *O. brevirobusta* will be closely analyzed, but *Ocinebrellus inornatus* will be also included in order to compare the species with European *Ocenebra*. We used the following methods:
– cladistic analysis to search for the relationships between the populations;
– traditional biometry to describe transformations of the shell shape and the sculptural characters during the ontogeny;
– Procrustes analysis to delineate variations of sculptural characters;
– Fourier analysis to study variations of outlines.

ABBREVIATIONS

Text-conventions used to describe the spiral sculpture of the teleoconch (after Merle 1999, 2001)

abis	abapical secondary cord of the sutural ramp;
ABP	abapical primary cord of the siphonal canal;
abs	abapical secondary cord of the siphonal canal;
adis	adapical secondary cord of the sutural ramp;
ADP	adapical primary cord of the siphonal canal;
ads	adapical secondary cord of the siphonal canal;
D	denticles of the outer lip;
D1 to D6	abapical denticles;
ID	infrasutural denticle;
IP	infrasutural primary cord;
MP	median primary cords of the siphonal canal;
ms	median secondary cord of the siphonal canal;
P	primary cords (first appearance sequence);
P1	shoulder cord;
P2 to P6	primary cords of the convex part of the whorl;
s	secondary cords (second appearance sequence);
s1 to s6	secondary cords of the convex part of the whorl.

Repository

MNHN	Muséum national d'Histoire naturelle, Paris, domaine de collection Sciences de la Terre.

Other abbreviations concerning the localities: see Appendix 1.

MATERIAL

New material (V. B.) of *Ocenebra erinaceus* has been sampled on the French coast (Atlantic Ocean and Mediterranean Sea) in order to complete the available collections and to closely cover the geographic range of the species (Fig. 1B). The tidal zones have been closely prospected during the low tides for a better knowledge of its repartition. For each sample, the environmental characteristics (orientation of the sample stations, substrates, associated fauna and flora) have been also registered the soonest possible. The detailed list of the studied populations including fossil and Recent *O. erinaceus* and *O. brevirobusta* is presented in the Appendix 1. Among all populations, a random sampling of the 32, 10 or five selected specimens for the different analyses (cladistics, Fourier and Procrustes) has been processed by the computer program Microsoft Excel.

METHODS

IDENTIFICATION OF SCULPTURAL CHARACTERS AND STRUCTURAL HOMOLOGIES

The way to consider the muricid sculpture has a direct influence on the perception of their diversity and therefore on the results of morphological analyses (Merle 1999). This observation is particularly true for cladistic studies, in which structural homologies should be defined in a previous step of the analysis. For the axial sculpture, Miller

(1999) demonstrated that characters (constructional characters) are usually considered as similar, but may be built by different constructional pathways and then should not be regarded as homologous. For the spiral sculpture, the most accurate method to propose a hypothesis of homology consists in using a criterion of topological correspondence (Hylleberg & Nateewathana 1992), in associating another criterion, the ontogenetic correspondence (homologous sequences of appearance of the cords). This last criterion is fundamental because during the growth, the relative relief of cords may dramatically change and consequently represents a pitfall when the topological position of these cords is only identified by the adult morphology (Merle 1999, 2001). The propositions of structural homologies are coded by text-conventions used at familial level (Merle 1999, 2001, 2002; Houart 2000b, 2001b, 2002a, b; Houart & Dharma 2001; Merle *et al.* 2001; Merle & Pacaud 2002a, b) and are given in the Abbreviations above.

CLADISTIC ANALYSIS

The objective of the cladistic analysis is focused on the relationships between the populations of *Ocenebra erinaceus*, *O. brevirobusta* and *Ocinebrellus inornatus*. It will allow obtaining a phylogenetic hypothesis. The results will be confronted with the further analyses.

The ocenebrine phylogeny is poorly studied (Vermeij & Vokes 1997) and only the works by Kool (1993a, b), Merle (1999), Marko & Vermeij (1999), Oliverio & Mariottini (2001) and Oliverio *et al.* (2002) provide scattered data. Using anatomical characters, Kool (1993a, b) demonstrated that several genera, as *Nucella* Röding, 1798 (type species by subsequent designation [Stewart 1927]: *Buccinum filosum* Gmelin, 1791, junior synonym of *Nucella theobroma* Röding, 1798 and senior objective synonym of *Buccinum lapillus*, Linnaeus, 1758; for a complete discussion see Kool & Boss [1992]) and *Acanthina* Fischer von Waldheim, 1807 (type species: *Buccinum monodon* Pallas, 1774 by original designation), which were previously attributed to the subfamily Rapaninae Gray, 1853, are in fact more closely related to *Ocenebra* (Ocenebrinae). This result is also reached by Merle (1999) using shell characters and by Marko & Vermeij (1999) using molecular data. At subfamilial level, Oliverio & Mariottini (2001), using molecular data (12S RNA sequence) suggested that *Nucella* may be regarded as a basal taxon, which is more closely related to *Phyllonotus* Swainson, 1833 (type species by subsequent designation [Swainson 1833]: *Murex imperialis* Swainson, 1833 non *M. imperialis* Fisher von Waldheim, 1807 [new name: *M. margaritensis* Abott, 1958]; subfamily Muricinae Rafinesque, 1815) than *Stramonita* Schumacher, 1817 (type species by original designation: *Buccinum haemastoma* Linnaeus, 1767; subfamily Rapaninae). Conversely, in a further study based on the secondary structure ITS2, Oliverio *et al.* (2002) suggested, with reserve, that *Nucella* may be regarded as sister group of the Rapaninae. For the present study, all the results are useful to select two functional outgroups: *N. lapillus* and *Ocinebrina edwardsi* (Payraudeau, 1826). These taxa correspond to European ocenebrine species sharing homologous structures and bearing clear differences with *Ocenebra*.

One or several specimens of more than 30 populations of *Ocenebra* have been included in the analysis. In the matrix, each specimen has been regarded as a taxon. We have also carefully checked that all specimens correspond to a same step of growth (see Results: Growth of the outer lip). The matrix has been processed by the computer programs Winclada99 (Nixon 1999) and Hennig86 (Farris 1988).

BIOMETRIC ANALYSIS

This approach consists in using linear measurements (raw values and indices), assessing to the proportions of the organism (shell), and describing the morphogenesis of a structure. For two studied populations (*O. erinaceus* from Malaga and *O. brevirobusta* from Atlantic coast of Morocco) containing numerous young specimens, the analysis of ontogenetic series will attempt to simulate the growth of a “consensual individual”, for which the size will be assimilated to the age. In many cases, the size and the age are largely correlated and for the paleontologists, the size represents a convenient estimation, but not without pitfalls (Dommergues *et al.* 1986; Allmon 1994). The retained measurements are: H (total height), HA (height of the aperture), WA (width of the aperture), HLW (height of the last whorl), HS (height of the siphonal canal), WS (width of the shoulder), HP1 (height of the P1 cord spine), TP1 (thickness of P1), and BCS (distance between the base and the old siphonal canal) (Fig. 2). The bivariated plots provide informations on the type of growth. They are based on the law of allometric growth having as equation $Ly = \beta(Lx)^{\alpha}$ or $\log Ly = \alpha \log Lx + \log \beta$; *Lx* and *Ly* corresponding to the sizes of organs, *a* and *b* corresponding to the constants.

Procrustes and Fourier analyses

The muricid shells bear a complex morphology characterized by varices and cords varying in their size, form and number. For this reason, the methods of traditional biometry are insufficient to fully delineate intra- and interpopulation differences among the studied *Ocenebra*. Therefore, the Procrustes and the Fourier analyses are used in order to complete the biometrical study. Considering the technical necessities of these methods and time-consuming mathematical treatments, the following protocol is adopted:

– the number of localities is prioritized to the number of specimens among each population in order to cover the widest geographic range. Consequently, a limit of five to 10 specimens has been retained for the Procrustes and the Fourier analyses;

– in order to minimize effects of ontogenetic variations, only adults specimens sharing a relative equivalent size and a same degree of construction of the outer lip (see Results: Growth of the outer lip) have been considered in the analyses;

– the landmarks in ventral view (Procrustes methods) and the outlines in ventral and dorsal views (Fourier transform) have been digitalized using drawings made with a camera lucida, and then have been scanned.

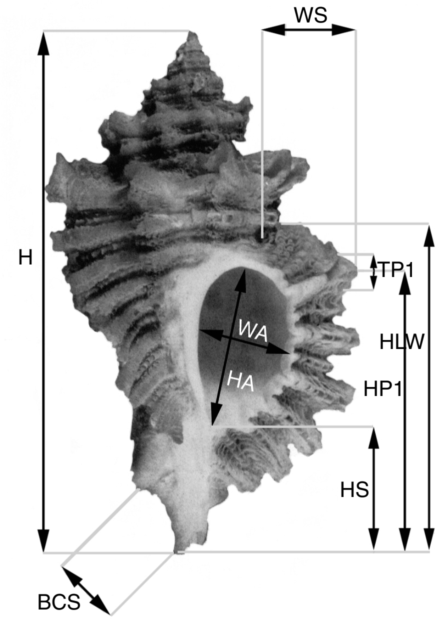

FIG. 2. — Linear measures used for the biometric study of *Ocenebra* Gray, 1847. Abbreviations: **BCS**, distance between the base and the old siphonal canal; **H**, total height; **HA**, height of the aperture excluding the siphonal canal; **HLW**, height of the last whorl; **HP1**, height of the P1 cord spine; **HS**, height of the siphonal canal; **TP1**, thickness of P1; **WA**, width of the aperture; **WS**, width of the shoulder; photo of *O. erinaceus* (Linnaeus, 1758), courtesy of R. Houart.

Procrustes analysis

These methods of morphometric geometry (Bookstein *et al.* 1985; Rohlf & Slice 1990; Bookstein 1991) are widely used to describe the morphology of various zoological groups. They are based on a set of landmarks, conspicuous homologous points, regarded as morphological descriptors. The used procedure is the lowest squares or LS (Bookstein 1991). It consists in stacking two series of landmarks. According to Laurin & David (1990), this method requires the translation, the homothety and the rotation of all configurations. The difference of shape between two objects is translated by a vectorial field, which is independent from the size and the orientation of the object. Each vector describes the origin, the direction and the amplitude of the variations. The description of 14 landmarks is given Table 1 and their place of the shell is presented in Figure 3. The coordinates

TABLE 1. — Description of 14 landmarks for the ventral view of the shells.

	Definition according to Bookstein (1991)	Location	Number of the landmarks
Type 1	Intersection points of precise and localized structures	Centre of the basal extremity of the siphonal canal	1 (Fig. 3)
Type 2	Maximum points of curvature	Maximum curvature of the cords and the spiral grooves 3: adapical base of P1 4: abapertural extremity of P1 5: abapical base of P1 6: adapical base of P2 7: abapertural extremity of P2 8: abapical base of P2 9: adapical base of P3 10: abapertural extremity of P3 11: abapical base of P3 12: adapical base of P4 13: abapertural extremity of P4 14: abapical base of P4	3 to 14 (Fig. 3)
Type 3	Points localized in the extremities	Suturation point of the outer lip	2 (Fig. 3)

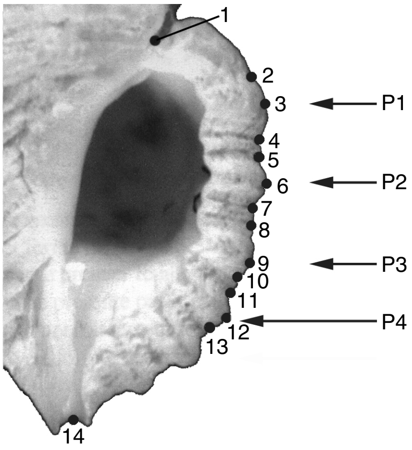

FIG. 3. — Location of 14 landmarks on the ventral view of the *Ocenebra* Gray, 1847. The correspondence between the primary cords (P1 to P4) and the landmarks is given; photo of *O. erinaceus* (Linnaeus, 1758), V. Berrou.

of each point are caught by LDMK (Dommergues 1999). All the data were computed by the PRCR software (Dommergues 1999).

Fourier analysis of outlines

The choice of ventral and apical views (Fig. 4) corresponds to a compromise between anatomical reality and representativeness of "measurements" and suggests two comments. Firstly, the outline differs following the observations. For example, the outline of the outer lip is more diversified than that of the inner lip (Fig. 4A). Secondly, there is a problem with the preservation of the material. Actually, the living fished shells may bear an important wear. Therefore, the original outline of shells may be modified and its drawing becomes too approximate to give reliable results using any outline analysis. As regards the apical view (Fig. 4B), the inclusion of a straight segment allows avoiding the representation of the extremity of the outer lip, which strongly varies during the growth (cf. Results: Growth of the outer lip).

Fourier's analysis generates a set of variables reflecting morphological changes and makes possible the statistical comparison of samples (Rohlf & Marcus 1993; Crampton 1995). The elliptic Fourier transform (Kuhl & Giardina 1982) is widely used for biological and paleontological studies of complex forms (Rohlf & Archie 1984; Crônier *et al.* 1998; Tort 2001). Within the framework of this work, another method than the elliptic Fourier transform, but using the same decomposition of the outline (into its *x* and *y*

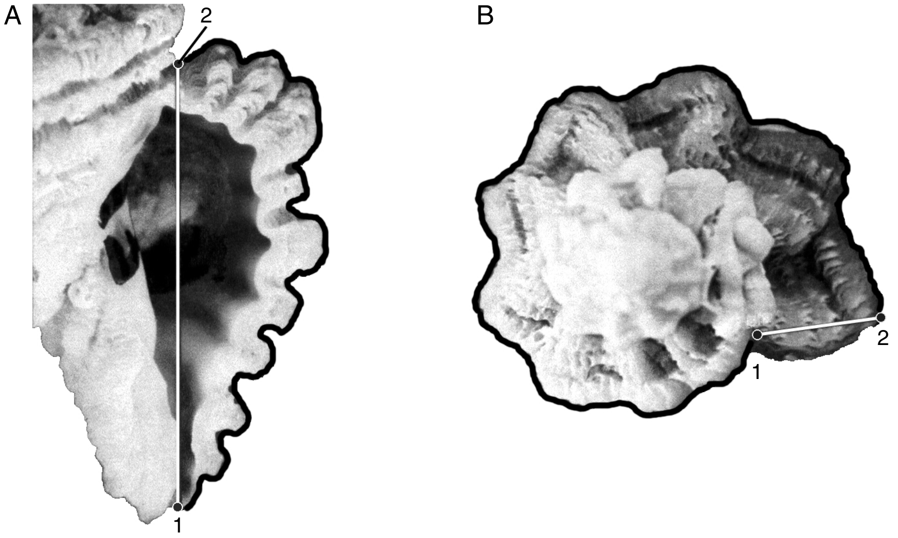

FIG. 4. — **A**, outline of the ventral view analyzed by Fourier transform (**1**, centre of the basal extremity of the siphonal canal; **2**, suturation point of the outer lip); **B**, outline of the apical view (**1**, suturation point of the outer lip; **2**, abapertural point of the outer lip); photos of *Ocenebra brevirobusta* Houart, 2000, V. Berrou.

projections) has been preferred. It simultaneously describes the *x* and *y* coordinates of every point by transcribing them in complex numbers. For a given point *k*, its coordinates can then be expressed by the following way: $S_{(k)} = x_{(k)} + iy_{(k)}$; *x* being regarded as real number, and *y* as the imaginary axis of a sequence of complex numbers (Gonzalez & Woods 1991). The use of complex numbers leads a slight asymmetry between the opposite harmonics. For 200 outline points having an equi-repartition, 200 amplitudes are calculated (A1 to A199), A0 being useless. The first and the latest harmonics (e.g., A1-A2… and A199-A198…) have high values and reflect the global characteristics of the outline. Conversely, the amplitudes of central harmonics, of weaker values, translate morphological details. The required number of harmonics to precisely describe the shape may be defined by the Fourier power spectrum (Crampton 1995). The finalized formula using the elliptic Fourier transform is adapted for this work and presented in Appendix 2. 99.95% of the shape is acquired on the 9th and the 12th harmonics, respectively for the tests in apical and ventral views (Appendix 2; Fig. 15).

In addition, a Multivariate Analysis of Variance (MANOVA) has been performed using the variations of amplitudes of the harmonics. It allows assessing morphological differences between various populations by a canonical variable analysis tending to maximize the variability. The resulting canonical space is used to visualize the shape disparity. The statistic tests of "significance" on the canonical axes are provided (Marcus 1993).

RESULTS

SCULPTURAL CHARACTERS AND HOMOLOGIES

Growth of the outer lip

As in other muricids, the shell growth of *Ocenebra* is episodic (Spigth & Lyons 1974; Linsley & Javidpour 1980) and bears intervarices and varices. The intervarical spaces correspond to periods of quick growth, whereas the successive outer lips, forming the varices, are led by a slowing down of the growth and then, by a momentary stop. The construction of the outer lip also corresponds to the implementation of microstructural layers of shelly material.

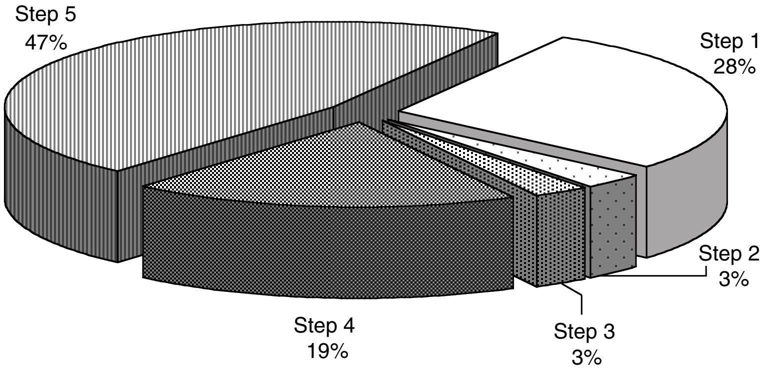

FIG. 5. — Diagram showing the relative importance of the various steps of growth of the outer lip in *Ocenebra erinaceus* (Linnaeus, 1758) (population from Quiberon, France).

According to Petitjean (1965) and Kool (1993b), the microstructure of *O. erinaceus* contains three main layers: one calcite external layer and two aragonite layers.

The close analysis of *Ocenebra* allows distinguishing several steps during the construction of the outer lip. Their identification is fundamental for the morphometric analysis, because it avoids comparisons based on outer lips bearing different steps of construction. Consequently, outer lips having a homologous degree of construction have been researched in order to retain them for the morphometric analysis. Five steps (Fig. 5) have been identified from the study of 32 adult specimens of *O. erinaceus* sampled at Quiberon (France) (following Feral [1974], a specimen of *O. erinaceus* up to 15 mm in height may be regarded as adult):

– step 1: the first layer begins its growth;
– step 2: the first layer forms a wall corresponding to an intervarical space;
– step 3: the first layer builds the outer lip corresponding to a thin varical space; an antero-posterior channel following the outer lip appears;
– step 4: growing layers thick the outer lip, without filling the channel;
– step 5: the new outer lip is entirely built, the channel being filled.

The steps 1, 4 and 5 correspond to periods of slow expansion of the outer lip and occupy an important part of the material (94% of the specimens). Conversely, the steps 2 and 3 correspond to periods of quick expansion of the outer lip and occupy only 6% of the material. In the muricids characterized by episodic growth, the steps 1, 4 and 5 correspond to durations longer than those of the steps 2 and 3, for which the animal presents a strong vulnerability and tends to hide itself (Spigth & Lyons 1974). Therefore, the duration of the steps 2 and 3 is probably underestimated. Only the steps 1 and 5 (that is 75% of the individuals) are retained for the morphometric studies, the outer lip little changing and a homologous degree of construction being easily recognizable.

Ontogeny of the spiral sculpture

The ontogeny of the spiral sculpture of *O. erinaceus* and *O. brevirobusta* has been studied in two samples containing numerous young specimens. The first one (*O. erinaceus*) comes from Malaga (Spain) and the second (*O. brevirobusta*, Lecointre coll.; MNHN) comes from Casablanca (Morocco). The observation of the limits of cord appearance is represented by schematic diagrams of an uncoiled shell (Figs 6; 7), adopted for the Muricidae by Merle (1999) and Merle & Pacaud (2002a, b). The comparison of both diagrams calls following comments:

– the onset of appearance of the primary cords is identical, with the exception of ABP and MP;
– on the siphonal canal, the most anterior cord (ABP) of *O. erinaceus* (Figs 6; 9) is present, whereas it lacks in *O. brevirobusta*. In *O. brevirobusta*, MP disappears at the end of growth (Figs 6; 7);

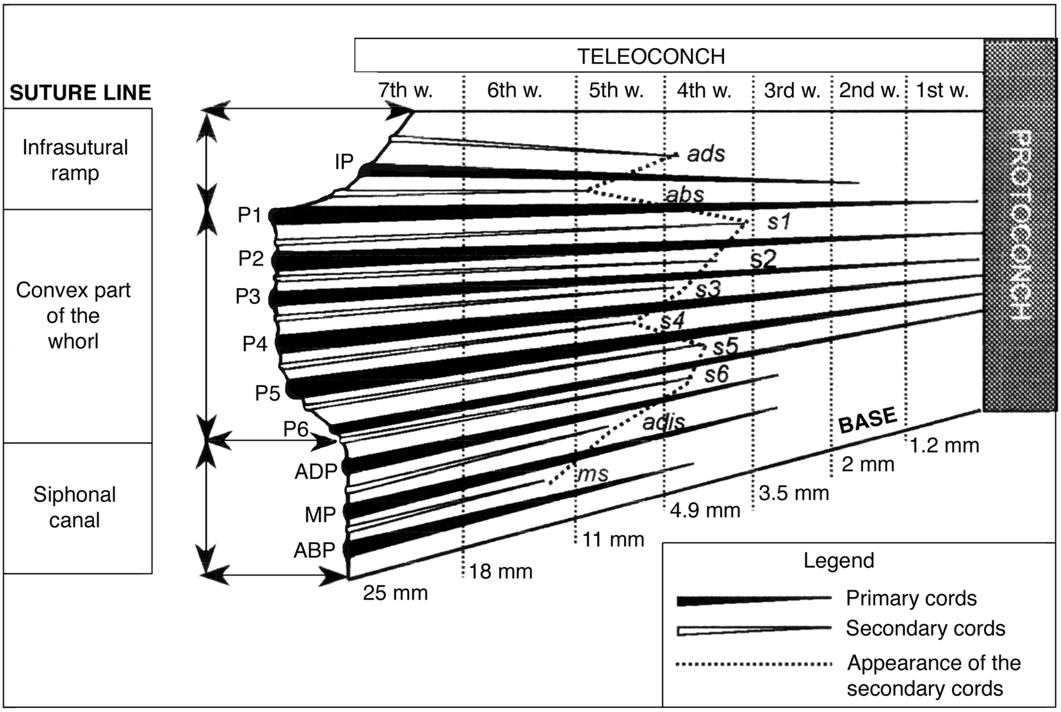

FIG. 6. — Simplistic representation of the ontogeny of the spiral cords of *Ocenebra erinaceus* (Linnaeus, 1758) (population from Malaga, Spain). Abbreviations: **ABP**, abapical primary cord of the siphonal canal; **abs**, abapical secondary cord of the sutural ramp; **adis**, adapical secondary cord of the siphonal canal; **ADP**, adapical primary cord of the siphonal canal; **ads**, adapical secondary cord of the sutural ramp; **IP**, infrasutural primary cord; **MP**, median primary cords of the siphonal canal; **ms**, median secondary cord of the siphonal canal; **P1**, shoulder cord; **P2-P6**, primary cords of the convex part of the whorl (**w.**); **s1-s6**, secondary cords of the convex part of the whorl.

– in *O. brevirobusta*, the P2 cord gradually atrophies (Fig. 7), whereas P1 and P3 take more place on the shell and may be regarded as hypermorphic. Comparing *O. brevirobusta* with *O. erinaceus*, Houart (2000a) noted a difference in the morphological organization of the primary cords. This difference mainly results from the P2 atrophy, which is poorly expressed in the adulthood of *O. brevirobusta* (Fig. 8);

– the secondary cords of *O. erinaceus* appear earlier than in *O. brevirobusta*. They are also less numerous (adis, s2, s3, s6 and ads) and poorly expressed (Figs 6; 7) in *O. brevirobusta*. The decrease of the number of its secondary cords probably results from a constraint of place, the strong development of the primary cords probably preventing the expression of several secondary cords as s1 and s4.

CLADISTIC ANALYSIS

Character list

1. Relief of the cords on the varical space (convex part of the whorl): no defined varical relief (0); slightly nodulose relief and interrupted by the intervarical space (1); subspinose relief (2); spinose relief (3); slightly nodulose relief, but not interrupted by the intervarical space (4).
2. Relief of cords between the varices: well marked (0); loss of the relief (1).
3. Cord IP: present and well distinct (0); poorly distinct (not expressed) (1).
4. Shoulder (last whorl): absent (0); present (1).
5. Shoulder spine (P1): not expressed (0); expressed (1).
6. Morphology of the P1 spine: absent (0); straight (1); dorsally curved (2).

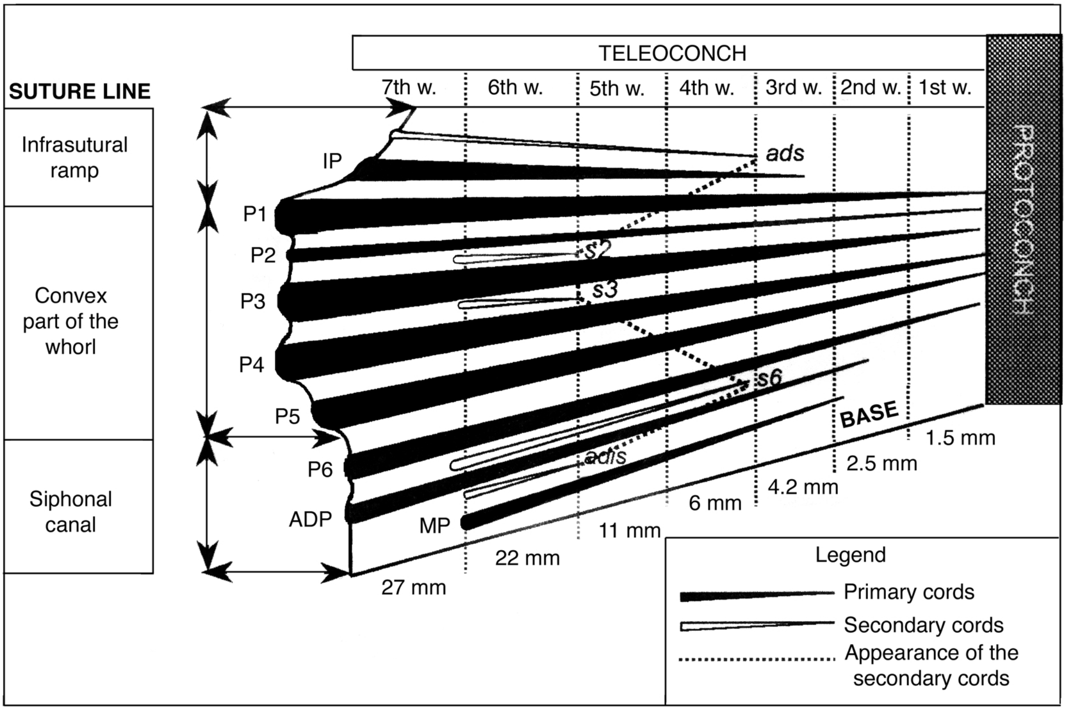

FIG. 7. — Simplistic representation of the ontogeny of the spiral cords of *Ocenebra brevirobusta* Houart, 2000 (population from Casablanca, Moroccan Atlantic). Abbreviations: **adis**, adapical secondary cord of the siphonal canal; **ADP**, adapical primary cord of the siphonal canal; **ads**, adapical secondary cord of the sutural ramp; **IP**, infrasutural primary cord; **P1**, shoulder cord; **P2-P6**, primary cords of the convex part of the whorl (**w.**); **s2**, **s3**, **s6**, secondary cords of the convex part of the whorl.

7. Development of the P1 cord: not hypermorphic (0); hypermorphic (1).
8. Development of the P2 cord: not atrophied (0); atrophied (1).
9. Development of the P3 cord: not hypermorphic (0); hypermorphic (1).
10. Development of the P4 cord: poorly distinct (0); distinct (1).
11. Development of the P5 cord: poorly distinct (0); distinct (1).
12. Varical foliation between the cords: absent (0); present (1).
13. Number of varices and intervarices: x ≥ 10 (0); x = 6 to 9 (1).
14. Intervarices: absent (0); present (1).
15. Relief of the varices: absent to poorly expressed during the whole ontogeny (0); well expressed during the whole ontogeny (1); well expressed on the young specimens but poorly expressed on the adults (2).
16. Number of intervarices/number of varices on the last whorl: x = 1 (0); 1 < x ≤ 1.5 (1); 1.5 < x ≤ 2 (2); 2 < x (3).
17. Morphology of the cords and the grooves: convex cords with shallow grooves (0); narrow cords with shallow grooves (1); wide cords with shallow grooves (2); wide cords with deep grooves (3).
18. Pinching on the base of cords: absent (0); present (1).
19. Labral thickening: absent (0); present (1).
20. Morphology of the peristome: curved (0); straight in its central part (1).
21. Length and morphology of the siphonal canal: very short (0); lengthened and prominent (1); prominent (2).

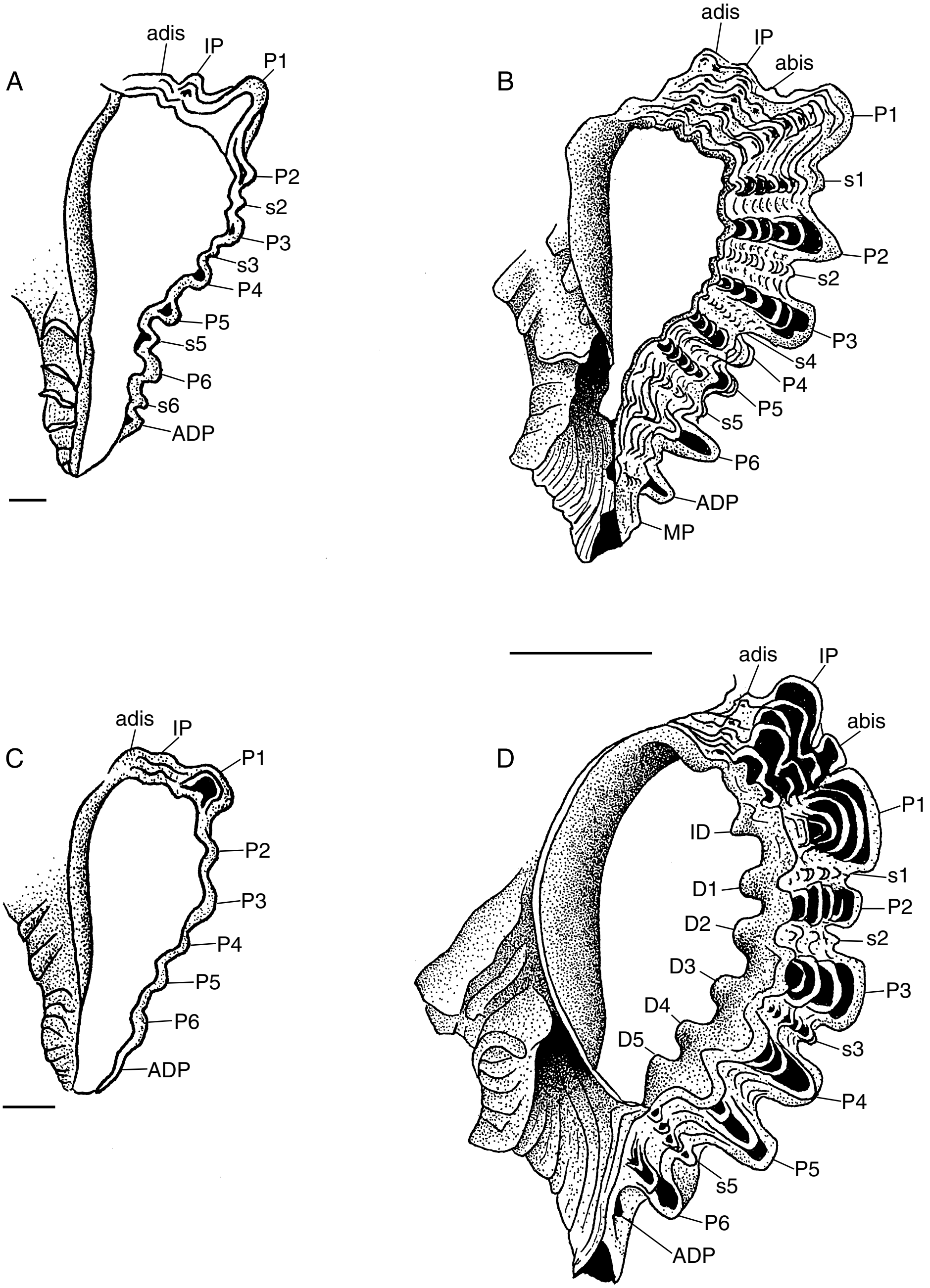

FIG. 8. — Spiral sculpture of recent *Ocenebra erinaceus* (Linnaeus, 1758) and *O. brevirobusta* Houart, 2000 (apertural view); **A**, **B**, *O. erinaceus* (Malaga, Mediterranean Sea, Spain) (MNHN, domaine de collection Botanique et Zoologie); **C**, **D**, *O. brevirobusta* (Casablanca, Atlantic, Morocco) (MNHN R11448 et R11449; Lecointre coll.). Abbreviations: see p. 267. Scale bars: A, C, 1 mm; B, D, 5 mm.

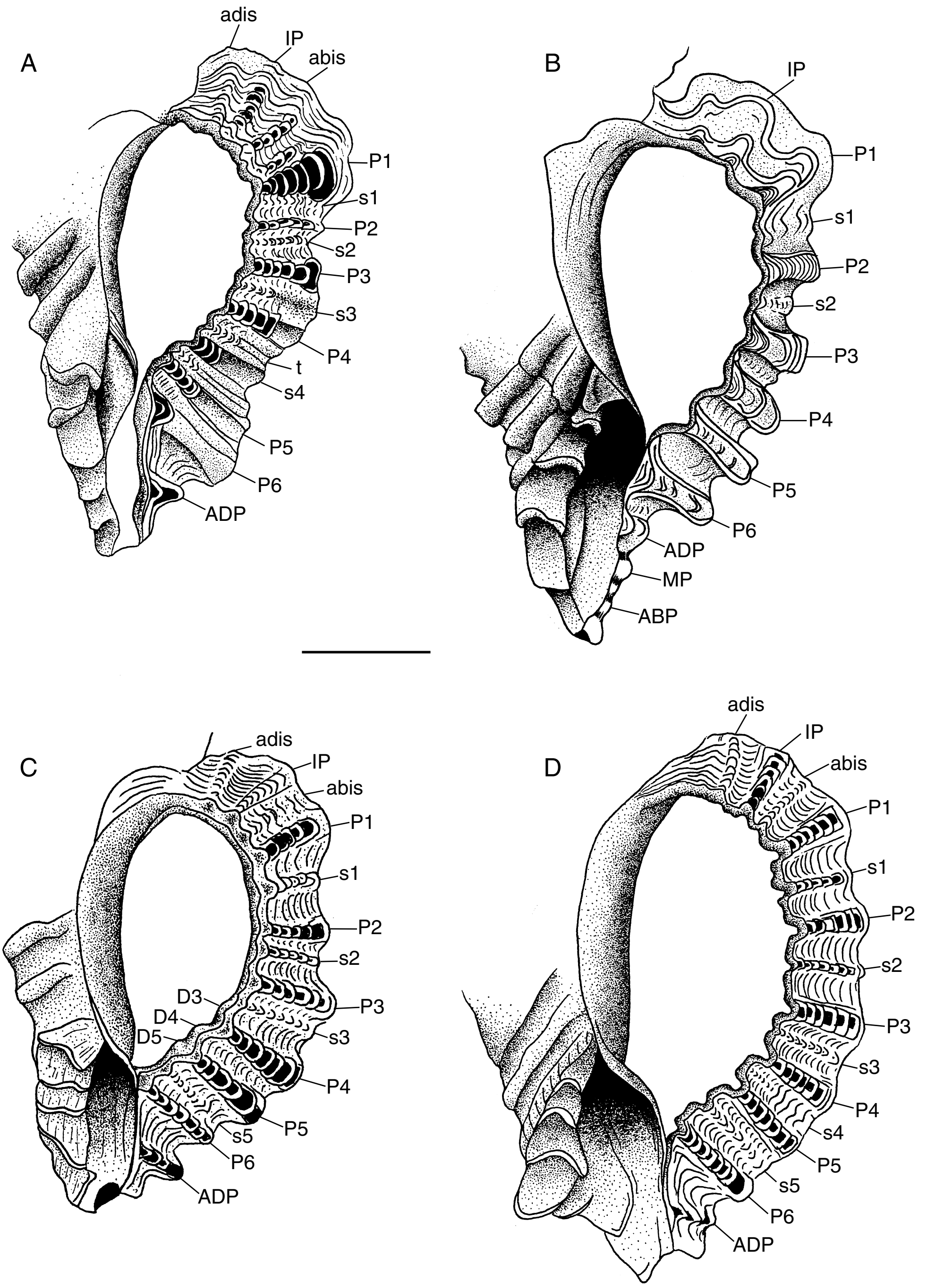

FIG. 9. — Spiral sculpture of *Ocenebra erinaceus* (Linnaeus, 1758) (apertural view); **A**, specimen from Asti (Pliocene, Italy) (MNHN R11447; Vibray coll.); **B**, specimen from Aigues-Mortes (Recent, Mediterranean Sea, France) (MNHN R63993; Merle coll.); **C**, specimen from Saint-Brieuc (English Channel, France) (MNHN R11445; Lhomme coll.); **D**, specimen from Oléron Island (Atlantic, France) (MNHN R11446; Lacour coll.). Abbreviations: see p. 267. Scale bar: 5 mm.

22. Opening of the siphonal canal: open (0); poorly close, the inner and outer sides being partially sealed (1); well close the inner and outer sides being entirely sealed (2); closed and encircled (3).
23. Total length of the shell: x ≥ 15 mm (0); x < 15 mm (1).
24. Internal morphology of the shoulder: no shoulder (0); flared curve (1); narrow curve (2).

Matrix and topologies
The matrix (Appendix 3) includes 24 characters for 41 taxa (specimens of one or several localities being regarded as taxa, see Methods above). The treatment by Hennig86 has been processed using the options (mh*.bb*; not additive) and this by Winclada99 using the options (tree max: 10,000, replications: 100, mult*max*). Hennig86 generated 2271 trees and Winclada99 10,000 trees. Both consensus trees of 96 steps of length bear the same topology (Fig. 10). The indices also are very similar (CI: Hennig86 = 0.38, Winclada99 = 0.38; RI: Hennig86 = 0.50, Winclada99 = 0.49). The strict consensus tree (Fig. 10) shows a basal polytomy (clade 1) including *Ocinebrellus inornatus*, Northern Atlantic *O. erinaceus*, several populations of Mediterranean *O. erinaceus* (Étang de Thau, Banyuls and Collioure) and one clade (clade 2) better resolved. This clade shows a polytomy. It exclusively contains Mediterranean *O. erinaceus* and an internal node (clade 3). The internal node includes the clade 4 (Mediterranean Pliocene *O. erinaceus*), having the clade 5 (*O. brevirobusta*) as sister group. A majority rule consensus tree has been generated by Winclada99 (L: 100, CI: 0.48, RI: 0.67) to minimize the low resolution found in the strict consensus tree (Fig. 11). The topology does not differ from the previous one, but is remarkable, because, with the exception of the population from Étang de Thau, all the Mediterranean *O. erinaceus* are included in the same clade.

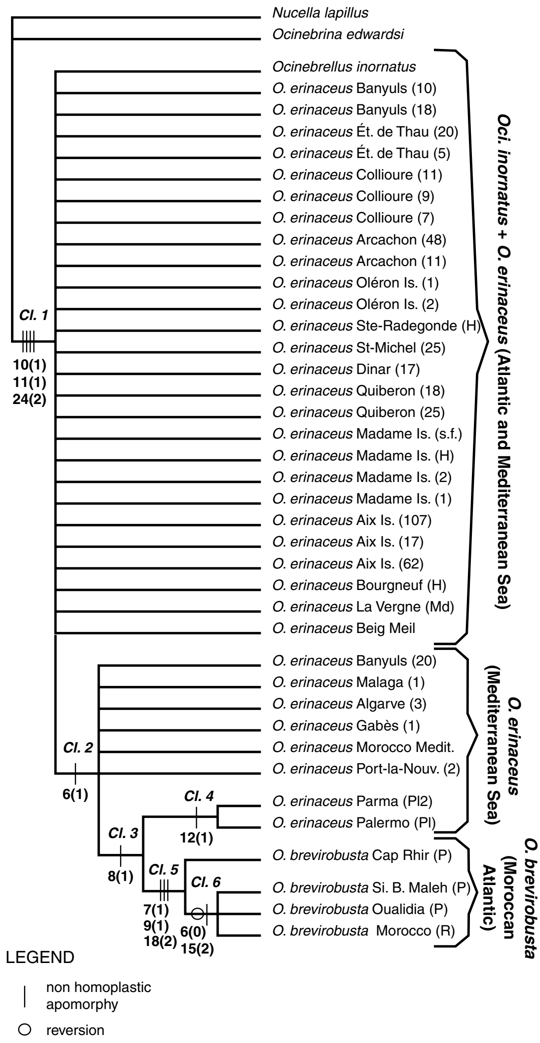

FIG. 10. — Strict consensus tree obtained by the computer programs Hennig86 (Lenght: 96, CI: 0.38, RI: 0.50) and Winclada99 (Lenght: 96, CI: 0.38, RI: 0.49). Abbreviations: ***Cl. 1*-*Cl. 6***, number of the clades; in bold, the characters and in parenthesis, the character states; **H**, Holocene; **Md**, Middle Age; **P**, Pleistocene; **Pl**, Pliocene; **R**, Recent; **s.f.**, subfossil; **O.**, *Ocenebra*.

Character transformations
The low resolution of the strict consensus tree mainly comes from a limited number of characters (Darlu & Tassy 1993). They only represent 58.54% of the number of taxa and this number cannot be easily increased, the morphological disparity at population level being more restricted, than at interspecific level. Homoplasies also contribute to generate a loss of resolution. They are probably responsible for several inconsistencies. For example, all the specimens from Banyuls

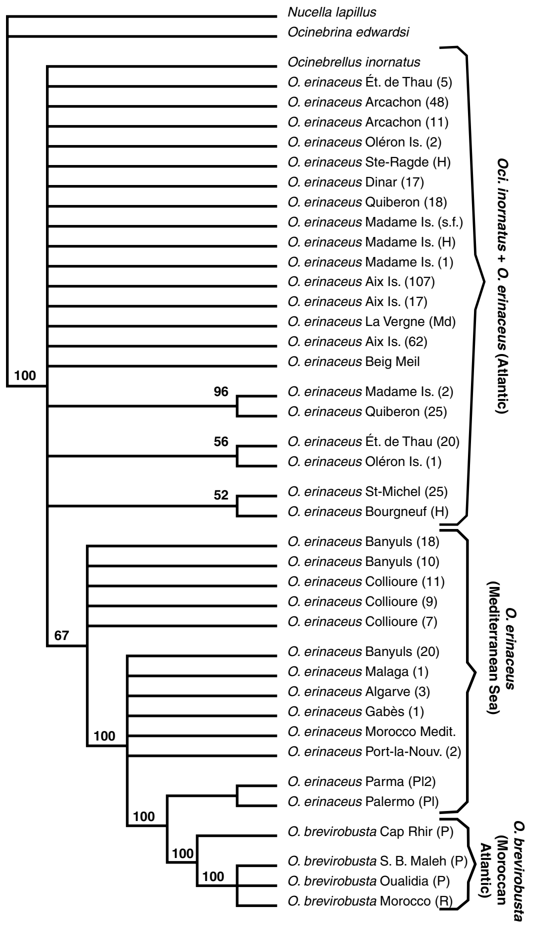

FIG. 11. — Majority rule consensus tree obtained by the computer program Winclada99 (Lenght: 100, CI: 0.48, RI: 0.67). Abbreviations: **H**, Holocene; **Md**, Middle Age; **P**, Pleistocene; **Pl**, Pliocene; **R**, Recent; **s.f.**, subfossil; ***O.***, *Ocenebra*.

(Mediterranean Sea) are not placed in the same clade (Fig. 10). These inconsistencies result to a polymorphism, because two morphs may occur in a same or several localities. Nevertheless, considering the matrix of 24 characters, 16 characters represent unambiguous apomorphies, among which 10 may be regarded as synapomorphies. This result suggests that more than the half of characters contains phylogenetic information.

The clade 1 (Fig. 10) is supported by three unambiguous synapomorphies: distinct P4 cord (10 (1)), distinct P5 cord (11 (1) and internal morphology of the shoulder narrowly curved (24 (2)) and a homoplastic apomorphy (21 (1)). The basal polytomy results of homoplasies of the characters 16, 17, 21 and 22. It mainly concerns Atlantic *O. erinaceus* and several Mediterranean specimens. The relationship between *O. erinaceus* and *O. inornatus* is not resolved, but *O. inornatus* is distinguished by six autapomorphies (characters 2, 3, 6, 16, 20 and 24).

The clade 2 is supported by one unambiguous synapomorphy: straight P1 spine (6 (1)) and five homoplastic apomorphies (1 (3), 5 (1), 16 (2), 17 (3) and 21 (2)). The character 6 firstly distinguishes *O. inornatus*, which possesses the state 2, and secondly, all Atlantic *O. erinaceus* lacking P1 spine. The basal polytomy containing Mediterranean *O. erinaceus* (Banyuls, Port-la-Nouvelle, Malaga and Mediterranean Morocco) and Algarve (Portugal) is due to homoplasies of the characters 16 and 22.

The clade 3 corresponds to an internal node including the clades 4 and 5. It is supported by one homoplastic apomorphies (21 (1)) and by one unambiguous synapomorphy: P2 atrophied (8 (1)). This synapomorphy allows grouping in a same clade Mediterranean Pliocene *Ocenebra* classified in *O. erinaceus* with *O. brevirobusta*. However, it is important to stress that the P2 atrophy is less marked in the Pliocene specimens than in *O. brevirobusta* (Figs 8C, D; 9A).

The clade 4 exclusively contains Mediterranean Pliocene *O. erinaceus* and is supported by one apomorphy: varical foliation between the cords (12 (1)). This character may be regarded as an autapomorphy, lacking in the recent *O. erinaceus* and in *O. brevirobusta*.

The clade 5 includes all the *O. brevirobusta*. It is supported by three unambiguous synapomorphies and one reversion: 1) hypermorphic P1 (7 (1)); 2) hypermorphic P3 (9 (1)); 3) primary cords basally pinched (18 (1)); and 4) number of intervarices/number of varices on the last whorl = 1 (16 (0)). The clade is divided in two parts corresponding to the terminal taxon *O. brevirobusta* from Cap Rhir (Pleistocene) and the clade 6.

The clade 6 includes Pleistocene fossils of *O. brevirobusta* (Sidi Ben Maleh and Oualidia) and the Recent forms. It is supported by one unambiguous synapomorphy and one reversion: relief of varices well expressed in the young, but poorly expressed relief (15 (2)) and poorly expressed P1 spine (5 (0)). These two transformations indicate a decline of the expression of the axial sculpture.

Congruencies

The order of appearance of the nodes largely respects the choro-clinal range of the *Ocenebra* and indicates a North/South orientation (Figs 10; 11). Thus, all the *O. erinaceus* from the French Atlantic coast take place at the base of the tree, and then comes the clade of Mediterranean *O. erinaceus*, and finally the most derived clade of *O. brevirobusta* from Atlantic Morocco. In the majority rule consensus tree, only two populations do not respect this pattern: 1) *O. erinaceus* from the Étang de Thau included in the Atlantic group; and 2) *O. erinaceus* the Algarve area (Portugal, Atlantic) always placed in the Mediterranean group. Both results do not however seem so inconsistent. Firstly, the Étang de Thau lagoon is a place of numerous maritime exchanges with the Oléron Island (oral comm., IFREMER at La Tremblade). Secondly, the Algarve area still undergoes the influence of Mediterranean waters.

The transformation series of characters also shows an increase of sculptural apomorphies in populations from warmer areas. The Mediterranean *O. erinaceus* are then characterized by the appearance of spiny processes, which are exceptional in the French Atlantic forms, and *O. brevirobusta* is distinguished by hypertrophied cords (P1 and P3), as well as by a P2 atrophy. This sculptural differentiation of a North/South orientation is consistent with observations of other muricids. So, cold water morphologies are poorly sculptured as in early Paleocene fossils (Merle & Pacaud 2002a, b), whereas warm water morphologies bear a complex sculpture, appearing in the early Eocene (Merle 1999). The P2 atrophy belongs to this group of derived characters associated to a complex ornamentation (Merle 1999, 2001; Merle *et al.* 2002). Mediterranean *O. erinaceus* from the late Pliocene and Pleistocene and Recent *O. brevirobusta* share this condition, which may be considered as a good synapomorphy appearing lately in European ocenebrines. Nevertheless, the hypothesis proposing late Pliocene Mediterranean *O. erinaceus* as sister group of *O. brevirobusta* requires a discussion, because it suggests that they possess closest relationships with Moroccan Atlantic populations. This result may be explained by the paleobiogeographic context of the Mediterranean Sea during the Pliocene. The Mediterranean waters were warmer than now and contained West African species indicating biological exchanges with the Moroccan Atlantic. Finally, the biogeographic congruence of the consensus trees (Figs 10; 11) allows proposing a scenario, which can be confronted with the following morphological analyses. It represents our favourite hypothesis (Fig. 12).

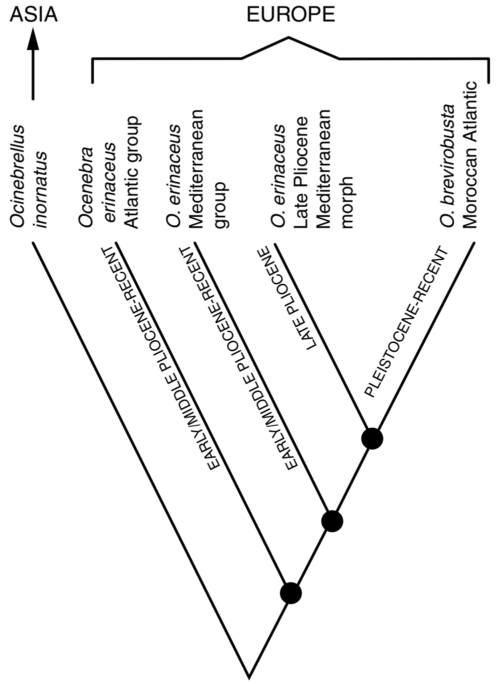

FIG. 12. — Favourite phylogenetic hypothesis.

TABLE 2. — Results of the law of allometric growth for the recent *Ocenebra erinaceus* (Linnaeus, 1758) of Malaga (Spain). Abbreviations: **BCS**, distance between the base and the old siphonal canal; **HA**, height of the aperture; **HLW**, height of the last whorl; **HP1**, height of the P1 cord spine; **HS**, height of the siphonal canal; **TP1**, thickness of P1; **WA**, width of the aperture; **WS**, width of the shoulder; ***ddl***, degree of freedom; ***r***, coefficient of correlation; ***P***, probability.

	Correlation	**N**	***ddl***	***r* threshold**	***P***	**Equation of the right-hand side**	**Coefficient of allometry**	**Type of growth**
Log H, log HA	0.956	27	25	0.4869 (to 0.01)	< 0.01	Log HA = 0.81 log H -0.27	0 < a < 1	Decreasing allometry
Log H, log WA	0.963	27	25	0.4869 (to 0.01)	< 0.01	Log WA = 0.92 log H -0.63	0 < a < 1	Slight decreasing allometry
Log H, log HLW	0.976	28	26	0.4869 (to 0.01)	< 0.01	Log HLW = 0.88 log H -0.03	0 < a < 1	Decreasing allometry
Log H, log HS	0.987	23	21	0.5368 (to 0.01)	< 0.01	Log HS = 1.21 log H -0.76	a > 1	Increasing allometry
Log H, log WS	0.926	26	24	0.5368 (to 0.01)	< 0.01	Log WS = 1.58 log H -0.55	a > 1	Increasing allometry
Log H, log HP1	0.963	28	26	0.4869 (to 0.01)	< 0.01	Log HP1 = 1.41 log H -1.29	a > 1	Increasing allometry
Log H, log TP1	0.855	26	24	0.5368 (to 0.01)	< 0.01	Log TP1 = 1.79 log H -2.20	a > 1	Increasing allometry
Log H, log BCS	0.912	23	21	0.5368 (to 0.01)	< 0.01	Log BCS = 2.62 log H -3.01	a > 1	Increasing allometry

BIOMETRICAL ANALYSIS

The biometrical analysis has been realized on *O. erinaceus* from Malaga and *O. brevirobusta* from Moroccan Atlantic. Both populations contain ontogenetic series which are sufficiently complete to follow an allometric growth. The results of each biometric variable (Fig. 2) are reported in Tables 2 and 3. From these results, ontogenetic similarities and differences are discussed.

Similarities

During the growth of an individual: 1) the apertural surface (HA × WA) decreases; 2) the last whorl also decreases in height (HLW); 3) the siphonal canal increases in height (HS); and 4) gradually moves towards the right side (BCS). Consequently, the apertural angle with regard to the coiling becomes progressively closed. A relative decrease of the apertural surface and an increase in height of the last whorl are probably related to biological functions and phylogenetical constraints. Firstly, the aperture is anatomically related to the operculum (closing the aperture and protecting the animal) and to the foot size. Secondly, many ocenebrine genera (e.g., *Jaton* Pusch, 1837, *Ceratostoma* Herrmannsen, 1846, *Chicocenebra* Bouchet & Houart, 1996 and *Africanella* Vermeij & Houart, 1999) bear similar apertural proportions, regarded by Kool (1993b) as a primitive condition. The other shared tendencies correspond to an increase in length of the siphonal canal and to a progressive spacing between its last positions. The siphonal canal protects the proboscis, lengthened trunk allowing the perforation of shells by acid secretions and the digestion by enzymes. The relative elongation of the siphonal canal during the life could be explained by attacks of greater preys (Palmer 1988). A progressive spacing between the last positions of the siphonal canal led to a flat surface becoming wider as the space is pronounced. It could answer to a mechanical constraint by establishing a balancing point, giving a greater stability for adults when they move on rocks.

TABLE 3. — Results of the law of allometric growth for the recent *Ocenebra brevirobusta* Houart, 2000 from Moroccan Atlantic. Abbreviations: **BCS**, distance between the base and the old siphonal canal; **HA**, height of the aperture; **HLW**, height of the last whorl; **HP1**, height of the P1 cord spine; **HS**, height of the siphonal canal; **TP1**, thickness of P1; **WA**, width of the aperture; **WS**, width of the shoulder; ***ddl***, degree of freedom; ***r***, coefficient of correlation; ***P***, probability.

	Correlation	**N**	***ddl***	***r* threshold**	***P***	**Equation of the right-hand side**	**Coefficient of allometry**	**Type of growth**
Log H, log HA	0.966	15	13	0.6411 (to 0.01)	< 0.01	Log HA = 0.91 log H -0.30	0 < a < 1	Slight decreasing allometry
Log H, log WA	0.873	16	14	0.6226 (to 0.01)	< 0.01	Log WA = 0.97 log H -0.68	0 < a < 1	Slight decreasing allometry
Log H, log HLW	0.978	16	14	0.6226 (to 0.01)	< 0.01	Log HLW = 0.89 log H -0.29	0 < a < 1	Decreasing allometry
Log H, log HS	0.901	12	10	0.6614 (to 0.01)	< 0.01	Log HS = 1.19 log H -0.88	a > 1	Increasing allometry
Log H, log WS	0.859	16	14	0.6226 (to 0.01)	< 0.01	Log WS = 0.86 log H -0.56	0 < a < 1	Decreasing allometry
Log H, log HP1	0.731	16	14	0.6226 (to 0.01)	< 0.01	Log HP1 = 0.79 log H -0.68	0 < a < 1	Decreasing allometry
Log H, log TP1	0.727	16	14	0.6226 (to 0.01)	< 0.01	Log TP1 = 0.82 log H -0.78	0 < a < 1	Decreasing allometry
Log H, log BCS	0.556	13	11	0.5529 (to 0.01)	< 0.05	Log BCS = 2.47 log H -3.04	a > 1	Increasing allometry

Differences

Three sculptural characters change in an opposite way. In *O. erinaceus* from Malaga, the width of the shoulder (WS), the height and the thickness of the P1 (HP1 and TP1) proportionally increase with the total height (H), whereas they decrease in *O. brevirobusta*. In their young stages, the whole shape of both populations is close. During the growth, the sculpture of the specimens from Malaga becomes exuberant, whereas the specimens from Atlantic Morocco tend to have a less ornamented shell and a rounded look (poorly expressed shoulder, wide and basally pinched cords in shape of square and with a marked relief).

PROCRUSTES ANALYSIS

The Procrustes analysis, previously realized on five specimens from Malaga (Mediterranean *O. erinaceus*), Quiberon (northern Atlantic *O. erinaceus*) and Moroccan Atlantic (*O. brevirobusta*), shows an intrapopulational variation. The variability affects the cords, particularly at Malaga (Fig. 13A), but the *Ocenebra* from each locality are correctly discriminated through three vectorial directions. These results are consistent with the biogeographic origin of the populations and allow its synthesis by the computation of "consensus specimens". The graph illustrating this second analysis is given in Figure 13B.

Ocenebra erinaceus

The Atlantic and Mediterranean groups of *O. erinaceus* are distinguished. For the Mediterranean shells, the landmarks 2, 3 and 4 indicate a well marked shoulder. Their general morphology is sharply cut, the cords having a strong relief separated by deep spiral grooves. Conversely, the Atlantic shells are shorter, their cords being poorly marked and more spread along the Y axis. The Atlantic and Mediterranean fossils are correctly placed within their biogeographic group. The population from Étang de Thau takes place in the group of Atlantic shells, as in the cladistic analysis.

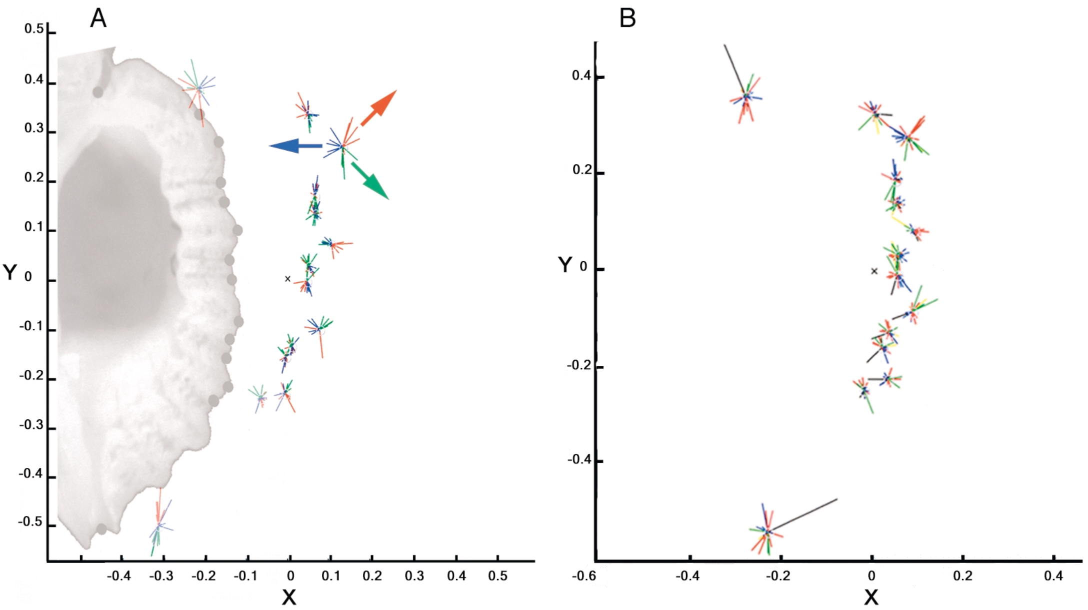

FIG. 13. — **A**, intra- and interpopulation analysis using the Procrustes analysis for five specimens of *Ocenebra erinaceus* (Linnaeus, 1758) from Malaga (red), from Quiberon (blue), and for five specimen from *O. brevirobusta* Houart, 2000 from Moroccan Atlantic (green); **B**, morphological comparisons using the Procrustes analysis for the Mediterranean populations of *O. erinaceus* (Recent: dark red; fossils: light red), the Atlantic Ocean populations of *O. erinaceus* (Recent: dark blue; fossils: light blue), *O. brevirobusta* (Recent: dark green; fossil: light green) and for *Ocinebrellus inornatus* (Récluz, 1851) (black). The populations from Cap Rhir and the Étang de Thau respectively are in yellow and brown colours.

Ocenebra brevirobusta

The shells of *O. brevirobusta* are distinguished from Atlantic and Mediterranean shells of *O. erinaceus*. They are lengthened, but bear a poorly expressed shoulder, marked and wide cords, with the exception of P2 (= character 7 of the cladistic analysis). All these characteristics give to the aperture a rounded to oval look. Becoming very fine, the P2 cord progressively allows a rebalancing of the positions occupied by P3 and P4 cords (= character 10 and 13). This rebalancing gives a good example of the mechanical organization of the spiral cords along the shell.

Ocinebrellus inornatus

The most important differences with *Ocenebra* appear on the landmarks 1 (siphonal canal) and 2 (suture of the outer lip on the penultimate whorl). *O. inornatus* bears a lengthened, narrow morphology and its siphonal canal is clearly oriented towards the right side of the aperture. Furthermore, although its most posterior primary cords (P1 and P2) are marked as well as in the other *Ocenebra*, the anterior primary cords (P3 and P4) have a less marked relief and are more spaced (Fig. 13B).

FOURIER ANALYSIS (OUTLINE ANALYSIS)

Principal Component Analysis

The Principal Component Analysis (PCA) has been realized on the amplitudes of harmonics obtained by Fourier transform, and for which the accumulated power is up to 99.95%. The first two axes explain 49.1% of the variation for the ventral view (respectively F1: 39.3%; F2: 9.8%) and 42.1% for the apical view (respectively F1: 28.3%; F2: 13.8%). The relatively average contribution of these first axes suggests a strong intraspecific variability (Fig. 14).

Ocenebra erinaceus

The morphological space, translated by the PCA (Fig. 14A, B) along F1, individualizes two

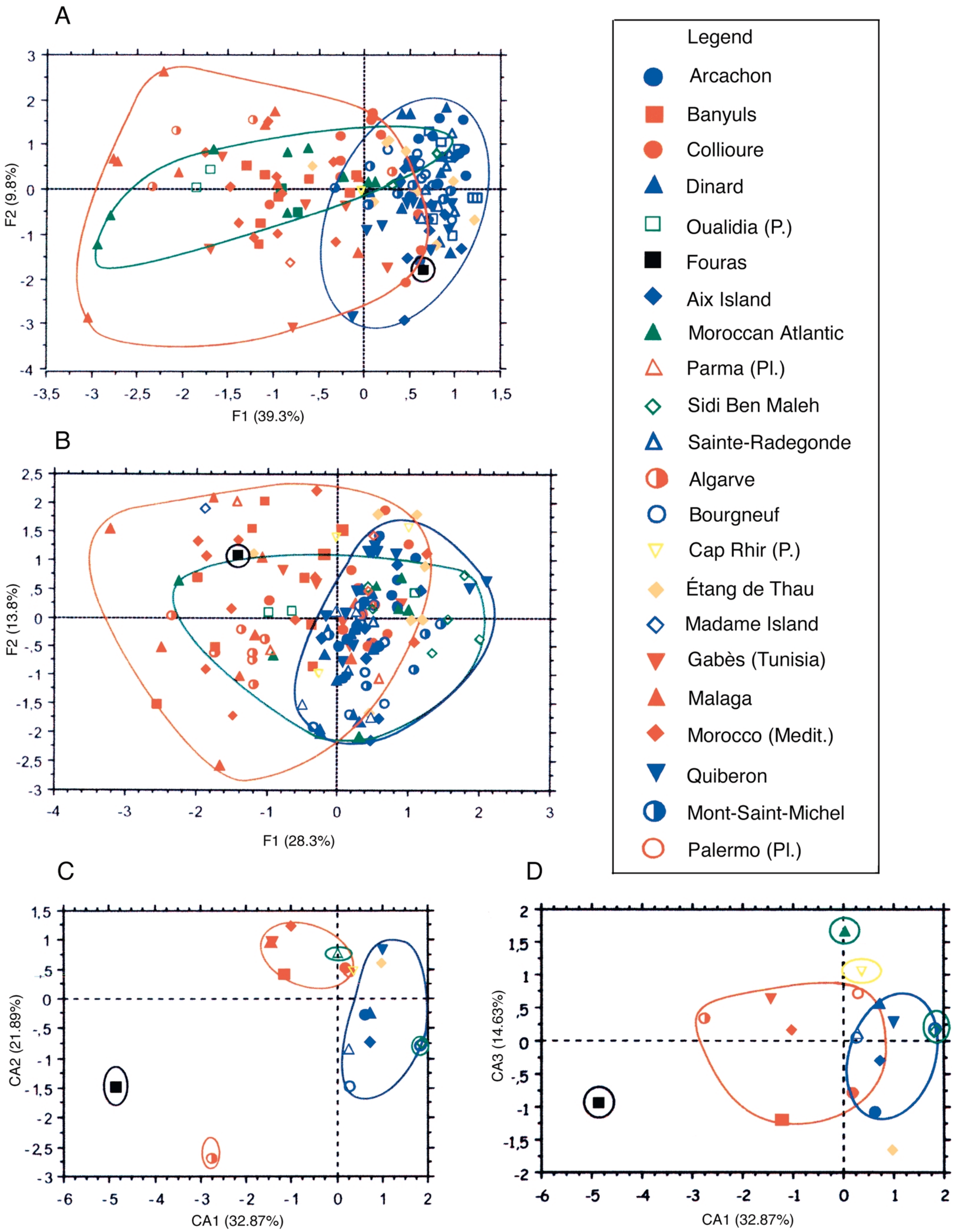

FIG. 14. — **A**, the two first axes of a PCA performed on the harmonics of Fourier for the ventral view; **B**, the same for the apical view; **C**, **D**, location of the the populations means in the canonical space corresponding to the amplitudes of the harmonics of Fourier for the apical view; **C**, the two first canonical axes CA1 versus CA2; **D**, canonical axes CA1 versus CA3; green triangle, Moroccan Atlantic; yellow triangle, Cap Rhir; green square, Oualidia (*O. brevirobusta*). Red group, Mediterranean forms (*Ocenebra erinaceus* (Linnaeus, 1758)); blue group, North Atlantic forms (*O. erinaceus*); green group, Moroccan Atlantic forms (*O. brevirobusta* Houart, 2000), black square (*Ocinebrellus inornatus* (Récluz, 1851)). Abbreviations: **P**, Pleistocene; **Pl**, Pliocene.

fields, one collecting Atlantic forms and another Mediterranean forms. The "Mediterranean group" is characterized by a wide field, suggesting a greater morphological disparity than in the "Atlantic group". The fields are partially overlapped. The shared elements come from localities, for which a strong variability of shells has been observed (e.g., Collioure, Bay of Gabès, Malaga, Dinard and Quiberon). Particular cases need to be indicated: 1) the specimens from Algarve (Portugal) are excluded from the morphological field corresponding to the "Atlantic group" and take place in the field of the "Mediterranean group" (apical view, Fig. 14B); 2) the specimens from Étang de Thau are excluded from the "Mediterranean group" and take place in the "Atlantic group" (ventral and apical views, Fig. 14A, B) as in the other analyses; and 3) the Holocene fossil from Madame Island (Atlantic Ocean) takes clearly place in the "Mediterranean group" (Fig. 14B), but this result should be considered with reserve, an important wear being detected on the specimen.

Ocenebra brevirobusta

The field of *O. brevirobusta* is included in that of *O. erinaceus* and exposes all the eventualities. For both views, the Quaternary specimens from Sidi Ben Maleh take place within the "Atlantic group", whereas the Recent specimens are spread. For ventral view (Fig. 14A), the Quaternary specimens from Oualidia take place within the "Mediterranean group", and those from Cap Rhir occupy a median place in the diagram. Therefore, this result suggests the difficulty to morphologically distinguish *O. erinaceus* from *O. brevirobusta*. However, it is important to stress that a rebalancing of the cords have been detected by the Procrustes analysis. The rebalancing of cords may explain this difficulty, because it cannot be easily discriminated by an outline analysis. Thus, further studies including spiral characters should consider this observation for which the Fourier and the Procrustes analyses appear complementary.

Ocinebrellus inornatus

According to the view, *O. inornatus* takes place either in the "Atlantic group" (ventral view), or in the "Mediterranean group" (apical view).

Multivariate Analysis of Variance

The MANOVA indicates a morphological differentiation within populations. The multivariate tests are significant (Wilk's Lambda: value = 0.024; *df1* = 270; *df2* = 1185.6; p < 0.0001***). The morphological relationships can be shown by representing the averages of the stages in a canonical space (Fig. 14C, D). This space is defined by the first three canonical axes, providing a valuable approximation of the morphological space (69.39% of the total variance). Only the graphic of the apical view (Fig. 14C, D) will be commented, the graphic of the ventral view being very similar.

Ocenebra erinaceus

On the CA1/CA2 axes (Fig. 14C), the fields of the Atlantic and Mediterranean groups break up, whereas they slightly overlap on the CA1/CA3 axes (Fig. 14D). Several populations are grouped by biogeographic entities and respect a north/south polarity. On the CA3 axis, the Atlantic populations are ordered as follows: Dinard/Quiberon (North of France), Bourgneuf/Sainte-Radegonde (both Holocene fossils) and Aix Island/Arcachon (West and South-West of France). The place of the population from Mont-Saint-Michel is astonishing, because it is always associated to that of Pleistocene *O. brevirobusta* (Sidi Ben Maleh) and is slightly remote towards other Atlantic forms. On the CA1/CA2 axes, the population from Collioure occupies a rather central position (close to that of the Atlantic group) in the Mediterranean field, whereas other populations (Banyuls [France], Malaga [Spain], Gabès [Tunisia] and Mediterranean Morocco) constitute a subgroup placed in the opposite periphery of the field. On the CA3 axis, a South/North polarity is observed in these populations and is ordered as follows: Gabès/Mediterranean Morocco in the South and Banyuls/Collioure in the North. The population from Étang de Thau takes place once in the "Atlantic group". The population from Algarve (Portugal) presents a surprising distance with the Atlanto-Mediterranean field on the CA1/CA2 axes, whereas it gets closer to the Mediterranean field on the CA1/CA3 axes.

Ocenebra brevirobusta

On the first two CA1/CA2 axes, the field of *O. brevirobusta* overlaps that of the Mediterranean (*O. brevirobusta* from Moroccan Atlantic and from Cap Rhir) and the Atlantic groups *O. erinaceus* (*O. brevirobusta* from Sidi Ben Maleh). On the CA1/CA3 axes, the Recent specimens from the Moroccan Atlantic and the Pleistocene specimens from Cap Rhir are excluded from the Atlantic and Mediterranean fields of *O. erinaceus*. However, it is important to indicate that the specimens from Cap Rhir occupy a central place, closer to that of the Italian Pliocene *O. erinaceus*.

Ocinebrellus inornatus

Ocinebrellus inornatus is clearly excluded from the fields of *Ocenebra*.

SYNTHESIS OF THE RESULTS

SYNTHESIS OF THE MORPHOLOGICAL ANALYSES

The different analyses (cladistics, traditional biometry, morphometric geometry, Fourier analysis and MANOVA) suggest two reports of general order on the shell variations of European *Ocenebra*. Firstly, they confirm a strong variability, previously suggested by numerous superfluous names of species, subspecies and varieties (Houart 2001a). Secondly, in spite of this variability, a repartition of the populations by biogeographic groups is identified. Within these groups, the specificity of each population may be often discriminated by the canonical analysis (MANOVA) and local entities may be recognized.

Atlantic and Mediterranean O. erinaceus

The results indicate a morphological distribution delineating two biogeographic origins, the Northern Atlantic (French Atlantic coast) and the Mediterranean Sea. Although a restricted number of characters and homoplasies do not authorize a full resolution of the consensus trees (Figs 10; 11), the cladistic analysis allows identifying a clade grouping the Mediterranean populations (Fig. 11). Independently, the PCA and the MANOVA also distinguish an Atlantic and a Mediterranean group, with an overlap zone. Therefore, a slight differentiation between Atlantic and Mediterranean populations is suggested here.

The Atlantic *Ocenebra*. The Atlantic *Ocenebra* bear a sturdy morphology (short shoulder, spaced primary cords having weak relief and short aperture) and the local populations are very comparable. Consequently, their relationships are difficult to identify by the cladistic analysis. Nevertheless, the canonical analysis (Fig. 14C, D) allows grouping them by consistent biogeographic entities (Quiberon/Dinard, Aix Island and Bourgneuf/Sainte-Radegonde in Vendée), except for the specimens from Mont-Saint-Michel (Fig. 14C, D). In spite of powerful tides, the bay of Mont-Saint-Michel corresponds to a sheltered environment. It probably favours the appearance of a singular morphology, characterized by the construction of ADP and MP cord spines before those of P5 and P6. All the northern populations from Atlantic Ocean are also well distinct from the population from Algarve (Portugal). The cladistic and the PCA analyses exclude this population from the Northern Atlantic group and place it within the Mediterranean group (Fig. 14A, B). However, according to the canonical analysis, it reaches a particular morphology (Fig. 14C, CA1/CA2 axes), which may be excluded from the Mediterranean group. Finally, the population from Algarve may be interpreted as a "satellite" of the Mediterranean group. The interpretation of the result is still difficult, but two points need to be considered: 1) if the morphology of *O. erinaceus* was exclusively controlled by environmental factors, the population from Algarve would be more closely related to *O. brevirobusta*, which also live in warm temperate Atlantic waters. However, no analysis confirms this hypothesis; and 2) the Algarve undergoes the influence of the Mediterranean waters and an exchange with Mediterranean populations cannot be excluded. Genetic analyses would be necessary for closer investigations on this problem.

The Mediterranean *Ocenebra*. The Mediterranean *Ocenebra* tend to have a more projecting morphology (well marked shoulder, high relief of primary cords, spiny processes and prominent siphonal canal) than those of the Atlantic Ocean (Fourier and Procrustes). Within the Mediterranean group, the canonical analysis clearly distinguishes biogeographic entities (North: Banyuls-Collioure and South: Malaga-Gabès-Morocco). Only the population from Étang de Thau (France) arouses an interrogation. Indeed, all the analyses (cladistics, outline and Procrustes) exclude this population from the Mediterranean group and place it in the Atlantic group. One such convergence in the results was unexpected. An inquiry on Étang de Thau and oral communication from IFREMER (La Tremblade) revealed numerous importations of oysters from Oléron, credibly causing the introduction of specimens from Oléron, which still have an Atlantic morphology. This introduction has been confirmed by oyster farmers, who precised that the *Ocenebra* are regularly collected. Therefore, the results are not so surprising and are even encouraging, because they clearly suggest reliability in the different methods.

Ocenebra erinaceus and O. brevirobusta

The cladistic analysis suggests very close relationships between *O. brevirobusta* and the Mediterranean *O. erinaceus*, particularly with those of Italian Pliocene, with which they share a sculptural synapomorphy, the P2 atrophy (Figs 10; 11). This hypothesis is consistent with the biogeographic dispersal of *Ocenebra*, because it indicates that the most southern populations are closer. In addition, the canonical analysis allows distinguishing two consistent biogeographic entities, among which the Pleistocene *O. brevirobusta* from Cap Rhir is closer to the Recent *O. brevirobusta* from Moroccan Atlantic (Fig. 14D). In the canonical space, they are close to the Italian Pliocene *O. erinaceus*, as suggested by the cladistic analysis.

The close relationship between *O. erinaceus* and *O. brevirobusta* being well attested, the degree of differentiation between both groups needs to be discussed. Except for two populations (Cap Rhir and Recent Moroccan Atlantic), the PCA analysis indicates weak differences, the morphological field of *O. brevirobusta* being included in that of *O. erinaceus* (Fig. 14). Moreover, the study of shell growth indicates other similarities (see Biometrical analysis). Nevertheless, indices of differentiation are suggested by two methods (study of growth and Procrustes methods). Thus, the ontogeny of the spiral sculpture of *O. brevirobusta* differs from that of *O. erinaceus*: late appearance of the secondary cords, late appearance and loss of MP, loss of ABP and strong atrophy of P2 (Figs 6-9). Other sculptural differences are also revealed by the biometric analysis (progressive decreases in width of the shoulder, in height and in thickness of P1 spine) and by the Procrustes analysis distinguishing three groups: 1) *O. brevirobusta*; 2) North Atlantic *O. erinaceus*; and 3) Mediterranean *O. erinaceus* (Fig. 13). In conclusion, a morphological differentiation between *O. erinaceus* and *O. brevirobusta* is mainly suggested by the ontogeny of sculptural characters, but other analyses (Procrustes and Fourier) emphasised that it is not higher than those observed between Atlantic and Mediterranean *O. erinaceus*.

EVOLUTIONARY STORY OF THE *OCENEBRA ERINACEUS*-*O. BREVIROBUSTA* COMPLEX

The Atlanto-Mediterranean Miocene corresponds to a phase of diversification for the Ocenebrinae, in which the evolutionary history of the *O. erinaceus*-*O. brevirobusta* complex probably takes root. However, this hypothesis cannot be easily demonstrated. Firstly, old reports of Miocene *O. erinaceus* seem erroneous and secondly, no Miocene species appear clearly related to *O. erinaceus*. *O. vindobonensis* (Hörnes, 1853), originally described from the middle Miocene of

Paratethys and recorded from the middle/upper Miocene of Atlantic Ocean (Glibert 1952; Brébion 1964), shares several similarities (whole shape and late appearance of a trivaricated morphology) but lacks derived characters of the *O. erinaceus-O. brevirobusta* complex, as the calcitic layer.

The occurrence of *O. erinaceus* is only given evidence during the Pliocene. From the Atlantic Ocean, it is recorded in Portugal (Lisbon area, Brébion [1970]) and in France (Normandy, at Blainville-sur-Mer, Glibert [1963]). From the Mediterranean Sea, which recovers waters with normal salinity after the Messinian event, *O. erinaceus* is recorded in Spain (Muniz Solis & Guerra-Merchan 1994) and in Italy (Sacco 1904; Malatesta 1974). The Spanish specimens figured by Muniz Solis & Guerra-Merchan (1994) look like more the Recent forms from the Northern Atlantic Ocean, whereas the Italian specimen figured by Malatesta (1974) looks like more the Mediterranean forms. During the late Pliocene, a new morph characterized by a slight atrophy of P2 cord also appears in the Mediterranean Sea.

In the Early Pleistocene, *O. erinaceus* is well attested in the Northern Atlantic domain, in England and in Ireland (Glibert 1963), and it has been recently found in the Rennes basin by one of us (D. N.). In the Southern domain, *O. brevirobusta* appears on the Moroccan Atlantic coast and seems derived from the late Pliocene Italian morph of *O. erinaceus* which disappears. *O. brevirobusta* is unknown in the Mediterranean Pleistocene. Thus, the Pleistocene clearly prefigures the recent biogeographic range of the *O. erinaceus-O. brevirobusta* complex.

In the Recent, the Northern Atlantic shoreline is more exposed to the amplitudes of tides, than the Mediterranean coast. The temperature of the surface waters is also lower than in the Mediterranean Sea. These environmental parameters have an influence on the shell variations. Indeed, thick and little sculptured morphologies, as the Atlantic *O. erinaceus* or *O. brevirobusta* essentially occur in environments of high hydrodynamism (e.g., *Nucella lapillus* [Dupont & Gruet 2000]), poorly sculptured morphologies are common in cold waters (e.g., *Boreotrophon clathratus* (Linnaeus, 1767) [Houart 2001a]), whereas the sculptured morphologies, as the Mediterranean *O. erinaceus*, mainly occur in warmer and sheltered environments. Thus, the Mediterranean muricid fauna still contains species with spiny processes (e.g., *Bolinus brandaris* (Linnaeus, 1758) and *Truncularіopsis trunculus* (Linnaeus, 1758)), which disappear in the cold waters of the Atlantic Ocean. The construction of spines has an anti-predatory function allowing shell reinforcements, as thickenings of the outer lip, varices, nodules, etc. An evidence of this function is also given by the increase of shell reinforcements in warm tropical and temperate provinces, when the predatory selective pressure became more intense (Vermeij 1976, 1977a, b, 1993). Therefore, it is likely that the beginning of the differentiation detected between Atlantic and Mediterranean *O. erinaceus* answers to a balance between abiotic constraints (hydrodynamism, climate, etc.) and the predatory selective pressure. From the early Pleistocene to the Recent, *O. brevirobusta* has a marginal range restricted to the Moroccan Atlantic coast. Brébion (1979a, b: fig. 2) recorded *O. erinaceus* from the Moroccan Pleistocene suggesting a sympatric area with *O. brevirobusta*. However, the specimens studied by this author (Oualidia, Cap Rhir and Sidi Ben Maleh) bear a strong atrophy of P2, characteristic of *O. brevirobusta*. Therefore, a sympatric area shared between *O. brevirobusta* and *O. erinaceus* is erroneous for the indicated localities. In the Recent, a sympatric area has been reported near the Gibraltar Strait, at Asilah (Houart 2000a). Unfortunately, Houart (2000a) did not illustrate *O. erinaceus*, which is known by a single specimen (Houart *in litt.*). In any cases, two factors may play in favour of a differentiation of the Moroccan populations. Firstly, their lecithotrophic protoconchs implies a small larval dispersal, favourable to the preservation of a local morph in a marginal range. Secondly, the appearance of this sturdy morphology (with thick primary cords) is encountered in other species of the sector (e.g., *Cymatium doliarum* (Linnaeus, 1767) and *Spinucella plessisi* (Lecointre, 1952)) and could be related to a strong hydrodynamism of the Moroccan Atlantic shoreline. Thus, the degree of differentiation of *O. brevirobusta* and its geographic range could correspond to a model of speciation from peripheral populations. Nevertheless, the final individualization of both species remains difficult to demonstrate because: 1) in many analyses, differences between *O. brevirobusta* and *O. erinaceus* are not higher than between North-Atlantic and Mediterranean *O. erinaceus*; sculptural differences, particularly the P2 cord atrophy, could represent indices of speciation, but the occurrence of this condition in Italian Pliocene *O. erinaceus* and its polymorphism in the Oligo-Miocene species *Murexsul rostralis* (Grateloup, 1847) (Merle 1999) justify a great care in the interpretations; and 2) the biogeographic areas are more contiguous than separated by a gap. Waiting for genetic and molecular investigations, the hypothesis of a species in process of individualization seems the most likely. Therefore, it would be preferable to temporarily consider *O. brevirobusta* as a subspecies of *O. erinaceus* (= *O. erinaceus brevirobusta*).

Finally, this study of shells shows that the evolutionary history of the *O. erinaceus-brevirobusta* complex may be reconstructed in using additional techniques of morphological analysis. Nevertheless, these promising results should not mask several dark points. Actually, the Pliocene and Pleistocene *O. erinaceus* are still known by few specimens and the results need to be improved by a new material. New samples near the Gibraltar Strait would be necessary for a closer analysis of the relationships between Western Mediterranean and Moroccan Atlantic populations. In order to enlarge the study to the whole biogeographic range of the Recent European *Ocenebra*, *O. chavesi* from Azores should be included.

THE CASE OF *OCINEBRELLUS INORNATUS*

The canonical analysis based on shell outlines and the Procrustes methods illustrate differences with the *O. erinaceus-O. brevirobusta* complex and the cladistic analysis regards several characters as autapomorphies of *O. inornatus*. However, the PCA analysis (outline) does not clearly distinguish it from this complex. Therefore, the attribution of *Ocinebrellus inornatus* to another genus than *Ocenebra* was questioned (Berrou 2001). This opinion joins that of Houart & Sirenko (2003), who prefer to assign *Ocinebrellus inornatus* to *Ocenebra*. The scope of this paper is not focused on a taxonomic revision at generic level, but comments using the present results and the relevant literature may be given. Firstly, the PCA analysis includes a single specimen of *O. inornatus* from Fouras and the result concerning this species must be considered as preliminary. Secondly, following Amano & Vermeij (1998) and Vermeij (2001), *O. inornatus* is closely related to *Ocinebrellus*, which comprises two stocks: 1) the *O. inornatus* stock including *O. inornatus* and *O. lumarius* (Yokohama, 1926); and 2) the *O. aduncus* (type species of *Ocinebrellus*) stock including *O. aduncus* (Sowerby, 1834), *O. protoaduncus* (Hatai & Kotaka, 1959) and *O. ogasawarai* (Amano & Vermeij, 1998). *O. nagaokai* Matsubara & Amano, 2000 is morphologically intermediate between *O. inornatus* and *O. aduncus* (Matsubara & Amano 2000). These species often have a short labral tooth (Vermeij 2001), lacking in *Ocenebra*. Since its appearance in the early Miocene, *Ocinebrellus* is limited to shallow seas of Northeastern Asia, whereas late Neogene *Ocenebra* evolved in Europe and West Africa. Third, no *Ocinebrellus* has been recorded from Europe. For these reasons, we prefer to keep assigning *O. inornatus* to *Ocinebrellus*. Nevertheless, a common origin for both genera cannot be excluded, as suggested by Vermeij (2001) and by the results of Houart & Sirenko (2003) and they may explain the detected similarities.

Considering that the shell shape reflects the functional answer of an organism to a given environment, the morphological comparisons may be discussed in term of adaptation. The PCA analysis reveals that the apical face of *O. inornatus* looks like more Mediterranean *O. erinaceus* whereas the ventral face is closer to Atlantic specimens (Fig. 14A, B). A weak development of abapical cords is also shared with the Atlantic Ocean morph. These morphological resemblances suggest that *O. inornatus* is probably well adapted to the life environment of Northern Atlantic *O. erinaceus*.

CONCLUDING REMARKS

With 49 synonyms given for *O. erinaceus*, the shell variation of European *Ocenebra* may be considered as legendary, but no general study has been made on the subject. The study of shells is here given considering a wide geographic scale covering the area of the *O. erinaceus*-*O. brevirobusta* complex (Northern Atlantic Ocean, Mediterranean Sea and Moroccan Atlantic). The temporal dimension is also considered, Pliocene and Quaternary forms being analyzed. Various methods (cladistic analysis, traditional biometry, ontogeny of sculptural characters, morphometric geometry and Fourier analysis) have been confronted in order to obtain a close representation of shell variations.

In spite of a strong variability, these methods mostly indicate a morphological differentiation respecting a North/South orientation, with three main groups: 1) the Northern Atlantic Ocean; 2) the Mediterranean Sea for *O. erinaceus*; and 3) Moroccan Atlantic for *O. brevirobusta*. Furthermore, they stress that this differentiation probably appears during the Pleistocene, but remains weak. Thus, *O. brevirobusta*, which occupies a marginal area, is regarded as a geographic subspecies of *O. erinaceus*. In addition, two results deserve to be reminded, because they illustrate the interest to combine different methods. They concern: 1) the population from Étang de Thau (France, Mediterranean Sea), closely related to Northern Atlantic populations and probably introduced with oysters imported from the Oléron Island; and 2) the Atlantic population from Algarve (Portugal), closely related to Mediterranean populations and living in an area undergoing the influence of Mediterranean waters. Finally, *Ocinebrellus inornatus*, a species introduced on the French Atlantic coast, shares morphological similarities with the *O. erinaceus* from the Northern Atlantic Ocean, suggesting its ability to successfully colonizing this domain. Variations and homoplasies were an excuse to exclude shells and therefore fossils from phylogenetic and evolutionary models (Kool 1993a). However, this opinion was biased, because the traditional shell descriptions remained too superficial (Hylleberg & Nateewathana 1992; Merle 1999; Miller 1999). Since 1993, recent methodological progresses were done in order to perform descriptions of sculptural characters (Miller 1999; Merle 1999, 2001) and the morphometric methods can accurately describe variations of the whole shell shape. The confrontation of both approaches and the results demonstrate their complementarities. Obviously, the scope of such a confrontation is not restricted to the muricid family and should be extended to other molluscs.

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APPENDIX 1

List, origin of the studied material and abbreviations. **MNHN-DSE**, Muséum national d'Histoire naturelle, Paris, département Systématique et Évolution; **UPMC**, Université Pierre et Marie Curie, Paris.

Taxa	Age	Sea/ Ocean	Localities	Abbre- viations	Samples	Date of sample
Nucella lapillus	Recent	N Atlantic	Oléron Island, La Brée (France)	NI	Néraudeau	1998
Ocinebrellus inornatus	Recent	N Atlantic	Fouras (France)	O. i	Néraudeau	IV.2001
Ocinebrina edwardsi	Recent	Medit. Sea	Collioure (France)	O. e	Berrou	III.2001
Ocenebra erinaceus	**Recent**	**Medit. Sea**	Banyuls, Racou (France)	B	Noël	1972-1977
					(MNHN-DSE)	V.1997
			Banyuls, Port (France)	B	Gofas (MNHN-DSE)	
			Collioure (France)	C	Berrou	III.2001
			Thau (France)	ET	Berrou	II.2001
			Port-la-Nouvelle (France)	PLN	Néraudeau	1983
			Gabès (Tunisia)	GG	Bouchet & Warén	1982
			Malaga, Marbella (Spain)	M	Gofas (MNHN-DSE)	1976-1981
			Malaga, Calahonda (Spain)	M	Gofas (MNHN-DSE)	1976-1981
			Malaga, Rincon de la Victoria (Spain)	M	Gofas (MNHN-DSE)	VII.1990
			Malaga, Paseo maritimo (Spain)	M	Gofas (MNHN-DSE)	V.1991
			M'dig (Morocco)	MM	Gofas (MNHN-DSE)	1971
	Fossil		Asti, Pliocene (Italy)	Aast	UPMC	-
			Castelarquato, Pliocene (Italy)	Caplio	UPMC	-
			Parma, Pliocene (Italy)	Plais	UPMC	-
			Palermo, Pliocene (Italy)	Psic	UPMC	-
	Recent	**Atlantic Ocean**	Arcachon, Muscla (France)	A	Berrou	II.2001
			Beig Meil (France)	BM	Rousseau	IV.2001
			Dinard, St-Enogat (France)	D	Berrou	III.2001
			Dinard, St-Enogat (France)	D	Rousseau	IV.2001
			Aix Island (France)	IA	Berrou	III.2001
			Madame Island (France)	IM	Berrou	III.2001
			Oléron Island (France)	O	Berrou	IV.2001
			Quiberon (France)	Q	Bouget	2001
			Mont-St-Michel, Cherueix (France)	SM	Berrou	III.2001
			Algarve, Punta de Baleeira (Portugal)	Al	MNHN-DSE	1998
			Algarve (Portugal)	Al	Dommergues	1999
	Fossil		Bourgneuf, Subrecent (France)	BN	Gruet	1977
			Madame Island, Holocene (France)	IMholo	Néraudeau	IV.2001
			Madame Island, Middle Age (France)	IMmeso	Duday & Courtaud	-
			St-Jacques-de-la-Lande, Pleistocene (France)	SJL	Néraudeau	VII.2002
Ocenebra brevirobusta	**Recent**		Essaouira (Morocco)	MA	-	-
			Safi (Morocco)	MA	Gofas (MNHN-DSE)	IX.1991
			Rabat, shell accumulation (Morocco)	MA	Gofas (MNHN-DSE)	1970-1972
			Asilah (Morocco)	MA	Gofas (MNHN-DSE)	IX.1991
			El Jadida (Moroco)	MA	Gofas (MNHN-DSE)	IX.1991
			Temara (Morocco)	MA	Gofas (MNHN-DSE)	IX.1991
			Casablanca (Morocco)	CAS	Lecointre	-
	Fossil		Cap Rhir, Pleistocene (Morocco)	CR	Plaziat	-
			Oualidia, Pleistocene (Morocco)	Oual	Brébion	-
			Sidi Ben Maleh, Pleistocene (Morocco)	SBM	Brébion	-

APPENDIX 2

Adaptation of the equation of the Fourier power spectrum (Crampton 1995) to the study of *Ocenebra*.

"The number of harmonics required can be estimated from the average Fourier power (or variance) spectrum. The Fourier power of a harmonic is proportional to its amplitude and provides a measure of the amount of 'shape information' described by that harmonic. For the nth harmonic, Fourier power is given by the expression: Power = $(a\mathrm{n}^2 + b\mathrm{n}^2 + c\mathrm{n}^2 + d\mathrm{n}^2) / 2$, where *a-d* are the Fourier coefficients of the nth harmonic. The Fourier series can be truncated at the value of n at which the average cumulative power is, for example, 99% of the average total power." Crampton (1995).

In this analysis, *A*n corresponds to the amplitude of the harmonic n divided by the number of sampled points, *Nbs*. In order to calculate Fourier power of a harmonic and knowing that the amplitude of a harmonic corresponds to: $\sqrt{(a\mathrm{n}^2 + b\mathrm{n}^2 + c\mathrm{n}^2 + d\mathrm{n}^2)}$, we have : amplitude = $A\mathrm{n} \times Nbs = \sqrt{(a\mathrm{n}^2 + b\mathrm{n}^2 + c\mathrm{n}^2 + d\mathrm{n}^2)} \Leftrightarrow (A\mathrm{n} \times Nbs)^2 = a\mathrm{n}^2 + b\mathrm{n}^2 + c\mathrm{n}^2 + d\mathrm{n}^2$ and $(A\mathrm{n} \times Nbs)^2 / 2 = (a\mathrm{n}^2 + b\mathrm{n}^2 + c\mathrm{n}^2 + d\mathrm{n}^2) / 2$. Therefore, $(A\mathrm{n} \times Nbs)^2 / 2$ is equivalent to the Fourier's power of a harmonic. The sum of these individual powers gives the total power (for the harmonics 1 to n). Then, the spectrum of the Fourier's power corresponds to a graph having the numbers of used harmonics as abscissas and the accumulated individual powers as ordered.

Remarks: 1) *A*n is connected to the size of objects, contrary to Fourier coefficients used by Crampton. Then, it is preferable to use strictly similar conditions, by disregarding the size (in other words in dividing, beforehand, every *A*n by the surface of the studied specimen); 2) in the case of Fourier analysis of outline represented by complexes with sampling curvilinear (method used during this study), a slight asymmetry is generated in the harmonics. However, the spectrum of the Fourier power is built by only one of the series of "pseudo-symmetric" harmonics, by selecting the series translating in its extremity the highest value of *A*n and then in keeping its parallel. Fig. 15.

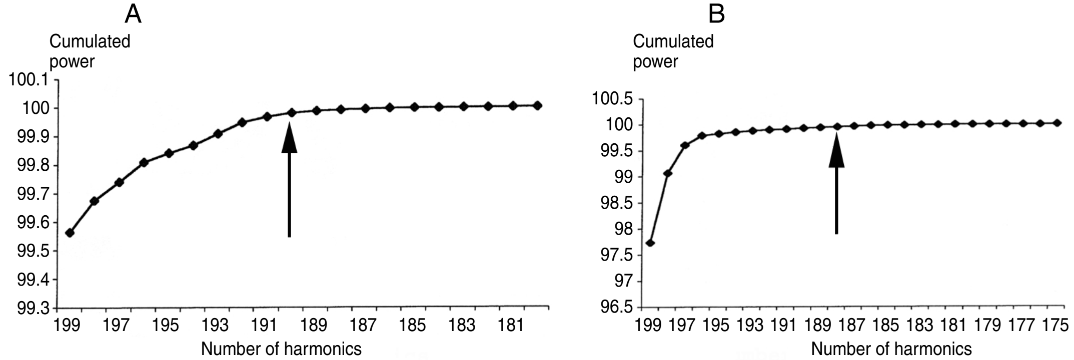

FIG. 15. — **A**, average Fourier power spectrum for the apical view, 99.95% of the power is described by the first nine harmonics, represented by the arrow; **B**, same for the ventral view, 99.95% of the power is described by the first 12 harmonics, represented by the arrow.

APPENDIX 3

Matrix of the characters used in the cladistic analysis. Abbreviations: **H**, Holocene; **Md**, Middle Age; **P**, Pleistocene; **Pl**, Pliocene; **R**, Recent.

	5	**10**	**15**	**20**	**24**
Nucella lapillus (R)	00000	00000	00–00	–0000	0000
Ocinebrina edwardsi (R)	40010	00000	00011	01010	0310
Ocinebrellus inornatus (R)	11111	20001	00111	3–011	1101
Ocenebra erinaceus Banyuls (R20)	30011	10001	10111	13010	2302
O. erinaceus Banyuls (R10)	30010	00001	10111	03010	2?02
O. erinaceus Banyuls (R18)	30010	00001	10111	23010	2202
O. erinaceus Malaga (R1)	30011	10001	10111	23010	2202
O. erinaceus Étang de Thau (R20)	10010	00001	10111	12010	1102
O. erinaceus Étang de Thau (R5)	10010	00001	10111	22010	1102
O. erinaceus Algarve (R3)	30011	10001	10111	23010	2302
O. erinaceus Gabès (R1)	30011	10001	10111	13010	2202
O. erinaceus Collioure (R11)	30010	00001	10111	13010	2202
O. erinaceus Collioure (R9)	30010	00001	10111	13010	2302
O. erinaceus Collioure (R7)	30010	00001	10111	23010	2302
O. erinaceus Mor. M'dig (R)	30011	10001	10111	23010	2202
O. erinaceus Port-la-Nouvelle (R2)	30011	10001	10111	23010	?202
O. erinaceus Parma (Pl2)	30011	10101	11111	23010	?202
O. erinaceus Palermo (Pl)	30011	10101	11111	23010	1202
O. erinaceus Arcachon (R48)	10010	00001	10111	11010	1202
O. erinaceus Arcachon (R11)	10010	00001	10111	11010	1202
O. erinaceus Oléron (R2)	10010	00001	10111	22010	1202
O. erinaceus Oléron (R1)	10010	00001	10111	12010	1102
O. erinaceus Ste-Radegonde (H)	10010	00001	10111	11010	1002
O. erinaceus Mont-St-Michel (R25)	10010	00001	10111	12010	2202
O. erinaceus Dinard (R17)	10010	00001	10111	22010	1302
O. erinaceus Quiberon (R18)	10010	00001	10111	22010	1202
O. erinaceus Quiberon (R25)	10010	00001	10111	02010	2002
O. erinaceus Madame Is. (H)	10010	00001	10111	21010	1202
O. erinaceus Madame Is. (H)	10010	00001	10111	?1010	1202
O. erinaceus Madame Is. (R2)	10010	00001	10111	02010	1002
O. erinaceus Madame Is. (R1)	10010	00001	10111	12010	1202
O. erinaceus Aix Is. (R107)	10010	00001	10111	22010	1202
O. erinaceus Aix Is. (R17)	10010	00001	10111	22010	1302
O. erinaceus Aix Is. (R62)	10010	00001	10111	12010	1002
O. erinaceus Bourgneuf (H)	10010	00001	10111	12010	2202
O. erinaceus La Vergne (Md)	10010	00001	10111	11010	1?02
O. erinaceus Beig Meil (R)	10010	00001	10111	12010	1202
O. brevirobusta Sidi Ben Maleh (P)	10010	01111	10112	03110	1002
O. brevirobusta Oualidia (P)	10010	01111	10112	03110	1202
O. brevirobusta Cap Rhir (P)	20011	11111	10111	03110	1202
O. brevirobusta Morocco (R)	10010	01111	10112	03110	1?02