C. R. Palevol 10 (2011) 171–179

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General palaeontology

Contribution of residual colour patterns to the species characterization of Caenozoic molluscs (Gastropoda, Bivalvia)

Apport des motifs colorés résiduels dans la caractérisation des espèces de mollusques cénozoïques (Gastropoda, Bivalvia)

Bruno Caze*, Didier Merle, Jean-Paul Saint Martin, Jean-Michel Pacaud

UMR 7207 du CNRS, département histoire de la Terre, centre de recherches sur la paléobiodiversité et les paléoenvironnements (CR2P), Muséum national d'histoire naturelle, 8, rue Buffon, CP 38, 75005 Paris, France

ARTICLE INFO

Article history:
Received 16 August 2010
Accepted after revision 13 October 2010
Available online 22 December 2010

Written on invitation of the Editorial Board

Keywords:
Residual colour patterns
Molluscs
Caenozoic
Palaeontological species

Mots clés :
Motifs colorés résiduels
Mollusques
Cénozoïque
Espèce paléontologique

ABSTRACT

In order to characterize fossil species of molluscs, palaeontologists can only rely on shell morphology. The lack of many data used by biologists to describe the extant species of molluscs (e.g., anatomy, molecular sequences, colours, ecology, behaviour) represents an obstacle to understanding the structure of palaeobiodiversity structure and its evolution. Observation under ultraviolet light of residual colour patterns on the shells of numerous Caenozoic gastropods and bivalves provides a new set of characters that can enrich and refine the description of palaeontological species. The results using this new approach and various value perspectives (several thousands of species may show patterns, phylogenetic analyses, etc.) reveal the considerable potential of residual patterns for future work on the Caenozoic molluscs.

RÉSUMÉ

Pour caractériser les espèces fossiles de mollusques, les paléontologues ne peuvent s'appuyer que sur la morphologie de la coquille. L'absence de nombreuses données utilisées par les biologistes pour décrire les espèces de mollusques actuels (par exemple, anatomie, séquences moléculaires, couleurs, écologie, comportement) représente ainsi un obstacle pour la compréhension de la structure de la paléobiodiversité et son évolution. L'observation, sous lumière ultraviolet, de motifs colorés résiduels sur les coquilles de très nombreux gastéropodes et bivalves cénozoïques fournit un nouveau corpus de caractères permettant d'enrichir et d'affiner la description des espèces paléontologiques. Les résultats obtenus avec cette nouvelle approche, ainsi que les nombreuses perspectives qu'elle laisse entrevoir (plusieurs milliers d'espèces susceptibles de porter des motifs, analyses phylogénétiques, etc.) révèlent le potentiel considérable et le caractère incontournable des motifs colorés résiduels pour les travaux à venir sur les mollusques cénozoïques.

---

* Corresponding author.
E-mail addresses: bruno.caze@mnhn.fr (B. Caze), dmerle@mnhn.fr (D. Merle), jpsmart@mnhn.fr (J.-P. Saint Martin), pacaud@mnhn.fr (J.-M. Pacaud).

1631-0683/$ – see front matter © 2010 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2010.10.005

1. Introduction

Biologists have, with anatomical (digestive, respiratory, reproductive systems), molecular, ecological and behavioural data, and colours, an important and varied set of characters to define living molluscan species. By contrast, the fossils of molluscs are generally only known by their calcareous shells and the distinction of species is exclusively based on conchological characters (chiefly shell morphology). This species concept, also known as morphological or palaeontological concept, reaches its limits when shells are devoid of ornamentation or when several different species display very similar shell shapes. In a study on two living European species of *Trivia* Gray, 1837 (*T. arctica* Pulteney, 1799 and *T. monacha* da Costa, 1778), Dommergues et al. (2006) demonstrated that both species cannot be distinguished from the shell shape, but are only recognizable by many anatomical characters and by different colour patterns. This result obviously demonstrates the interest of colour patterns for the species definition.

In this article, we propose to extend and refine the concept of palaeontological species by incorporating all new characters provided by the residual colour patterns of fossil shells.

2. The colour patterns of molluscs in the Caenozoic

Molluscs are currently the most diversified group in terms of biodiversity and mode of life in marine ecosystems. Their colour patterns, which are visual structures (drawings, geometric elements, often repeated and organizing the different colours), are common on the shell of extant gastropods and bivalves. These highly varied patterns are often used as a distinction criterion, especially for an easy identification of species displaying few or no discriminating shape characters.

The record of fossil colour patterns is an outstanding phenomenon because of the fast pigment degradation after the animal's death and during fossilization. Only a few remarkably well-preserved specimens from different periods of the Phanerozoic (from Ordovician to Pleistocene), display remnants of colour pattern. The scarcity of such 'evidence' is logically a methodological obstacle to the use of this criterion for the definition of palaeontological species (Joly and Baudouin, 2006). A new approach consisting of exposing fossil shells under ultraviolet light (Cate, 1972; Dockery, 1980; Hoerle, 1976; Hoerle and Vokes, 1978; Merle et al., 2008a; Olsson, 1967; Vokes and Vokes, 1968) allows, however, to reveal faithfully and frequently residual colour patterns that are invisible in natural light (Fig. 1). It should be noted that the fluorescent regions revealed under UV light on the surface of fossil shells correspond to pigmented regions on relative extant shells. For the first time, this method has been successfully applied on Lutetian shells from the Paris Basin, France (Merle et al., 2008a).

In order to estimate the potential of this method at a large scale, the residual colour patterns of various gastropods and bivalves from the European Caenozoic have been examined. The material was selected taking into account the presence of colour patterns among the closest extant relatives and according to the preservation of the specimens. We have observed under UV light several thousand specimens of 444 gastropod and bivalve species (Caze, 2010). This material comes from 159 Caenozoic sites (from the Danian to the Piacenzian) of eight European countries (Austria, Belgium, England, France, Greece, Italy, Romania, Turkey). The observations provided positive results for all tested stages (Fig. 2), which represents around 60 million years. Moreover the tested species are associated to numerous sedimentary environments (from the lagoonal zone to the circalittoral stage). These results demonstrate that the residual colour patterns are potentially detectable continuously throughout the Caenozoic, when shells are sufficiently preserved (non-decalcified and non-recrystallized). On the other hand, among gastropod families tested, most of these whose living relatives display colour patterns gave positive results. We can therefore affirm that residual colour patterns are not scarce, but they rather represent a common phenomenon in Caenozoic molluscs, especially in gastropods. In addition, the large sample of examined shells demonstrates clearly the high diversity of the colour patterns during the Caenozoic.

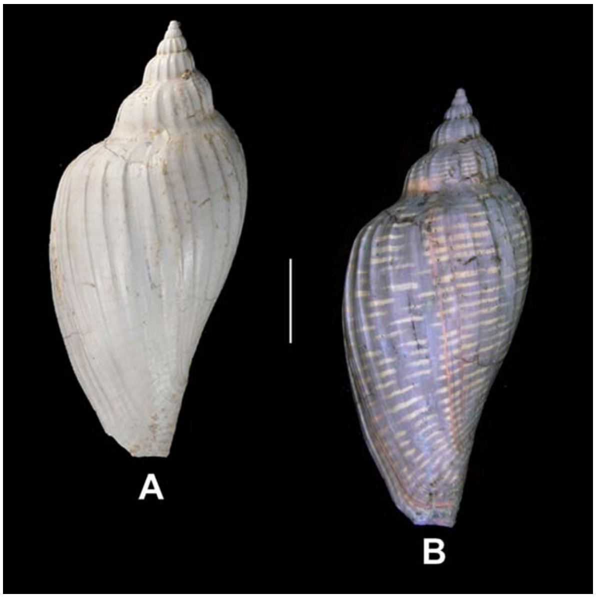

Fig. 1. Specimens of *Athleta (Neoathleta) lyra* (Lamarck, 1802) in natural light (**A**) and under UV light (**B**) with the residual colour pattern. Dorsal view, MNHN A25031, Monts, France, Lutetian (scale bar represents 10 mm). Photographs by C. Lemzaouda and P. Loubry (MNHN).

Fig. 1. Spécimen de *Athleta (Neoathleta) lyra* (Lamarck, 1802) vu en lumière naturelle (**A**) et sous lumière UV (**B**), avec le motif coloré résiduel. Vue dorsale, MNHN A25031, Monts, France, Lutétien (la barre d'échelle représente 10 mm). Prises de vue par C. Lemzaouda et P. Loubry (MNHN).

The examination of numerous specimens from many gastropod families allows a first estimation of the number of species that can potentially reveal residual colour patterns through the French Atlantic Caenozoic (Table 1). We used available data from Merle et al. (2008b) for the Lutetian and from Lozouet (1997) for the Oligocene and Miocene and considered each family whose extant species display colour patterns or families without extant

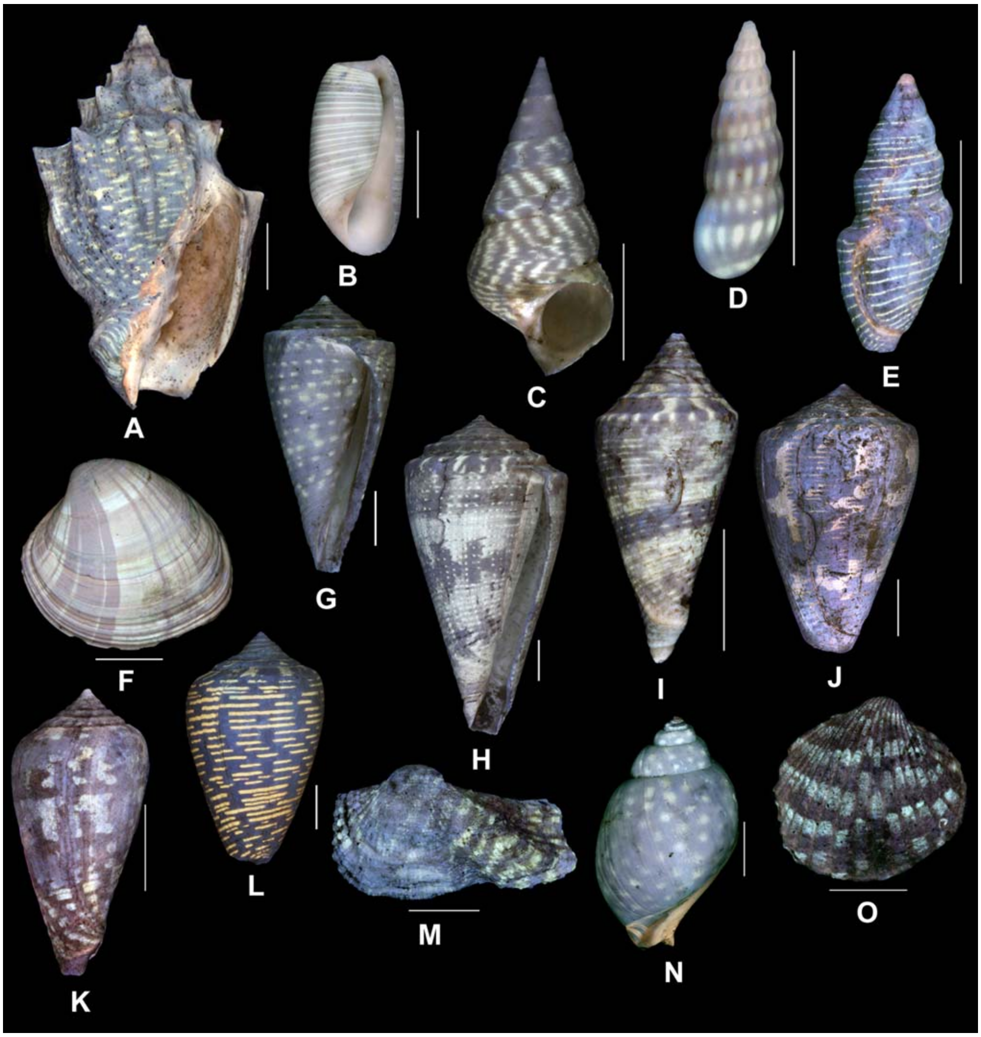

Fig. 2. Residual colour patterns revealed under UV light in various molluscs from European Caenozoic. **A**. Volutidae Rafinesque, 1815 from the French Ypresian (Cuisian), *Plejona wateleti* (Deshayes, 1865), ventral view, MNHN A25035, Mercin-et-Vaux. **B–D**. Gastropoda from the French Lutetian. **B**. Haminoeidae Pilsbry, 1895, *Roxania lamarckii* (Deshayes, 1863), ventral view, MNHN A31512, Fercourt. **C**. Turritellidae Lovén, 1847, *Sigmesalia multisulcata* (Lamarck, 1804), ventral view, MNHN A31256, Grignon. **D**. Rissoidae Gray, 1847, *Rissoina (Rissoina) clavula* (Deshayes, 1825), dorsal view, MNHN A31577, Fontenay-en-Vexin. **E**. Conidae Fleming, 1822 from the French Bartonian, *Cryptoconus* sp., dorsal view, MNHN A32191, Barisseuse. **F–H**. Mollusca from the French Rupelian. **F**. Veneridae Rafinesque, 1815, *Pelecyora incrassata* (Sowerby, 1817), Ormoy-la-rivière. **G–H**. Conidae. **G**. *Conus grateloupi* d'Orbigny, 1852, ventral view, MNHN A32210, Gaas (Espibos). **H**. *C. grateloupi* d'Orbigny, 1852, ventral view, MNHN A32211, Gaas (Espibos). **I–J**. Conidae from the French Burdigalian. **I**. *C. aquitanicus* Mayer, 1858, abapertural view, MNHN A30831, Saucats (Le Peloua). **J**. *C. (Chelyconus) gallicus* Mayer-Eymar, 1890, dorsal view, MNHN A30827, Saucats. **K**. Conidae from the Austrian « Badenian », *Conus* sp., abapertural view, MNHN A31705, unknown locality. **L**. Conidae from the Greek Tortonian (Crete), *Conus bitorosus* Fontannes, 1880, dorsal view, MNHN A30841, Makrilla. **M**. Arcidae Lamarck, 1809 from the Romanian « Badenian », *Arca noae* Linnaeus, 1758, MNHN A31072, Lapugiu. **N–O**. Mollusca from the French Piacenzian. **N**. Babyloniidae Kuroda, Habe & Oyama, 1971, *Babylonia* sp., dorsal view, MNHN A31068, Le Boulou (Nidolère). **O**. Carditidae Fleming, 1828, *Cardita* sp., MNHN A31922, Le Boulou (Nidolère) (scale bar represents 10 mm for **A** and **C–O** and 5 mm for **B**). Photographs by C. Lemzaouda and P. Loubry (MNHN).

Fig. 2. Motifs colorés résiduels révélés sous lumière UV, chez divers mollusques du Cénozoïque d'Europe. **A**. Volutidae Rafinesque, 1815 de l'Yprésien (Cuisien) de France, *Plejona wateleti* (Deshayes, 1865), vue ventrale, MNHN A25035, Mercin-et-Vaux. **B–D**. Gastropoda du Lutétien de France. **B**. Haminoeidae Pilsbry, 1895, *Roxania lamarckii* (Deshayes, 1863), vue ventrale, MNHN A31512, Fercourt. **C**. Turritellidae Lovén, 1847, *Sigmesalia multisulcata* (Lamarck, 1804), vue ventrale, MNHN A31256, Grignon. **D**. Rissoidae Gray, 1847, *Rissoina (Rissoina) clavula* (Deshayes, 1825), vue dorsale, MNHN A31577, Fontenay-en-Vexin. **E**. Conidae Flemimg, 1822 du Bartonien de France, *Cryptoconus* sp., vue dorsale, MNHN A32191, Barisseuse. **F–H**. Mollusca du Rupélien (Stampien) de France. **F**. Veneridae Rafinesque, 1815, *Pelecyora incrassata* (Sowerby, 1817), Ormoy-la-rivière. **G–H**. Conidae. **G**. *Conus grateloupi* d'Orbigny, 1852, vue ventrale, MNHN A32210, Gaas (Espibos). **H**. *C. grateloupi* d'Orbigny, 1852, vue ventrale, MNHN A32211, Gaas (Espibos). **I–J**. Conidae du Burdigalien de France. **I**. *C. aquitanicus* Mayer, 1858, vue abaperturale, MNHN A30831, Saucats (Le Peloua). **J**. *C. (Chelyconus) gallicus* Mayer-Eymar, 1890, vue dorsale, MNHN A30827, Saucats. **K**. Conidae du « Badénien » d'Autriche, *Conus* sp., vue abaperturale, MNHN A31705, localité inconnue. **L**. Conidae du Tortonien de Grèce (Crète), *Conus bitorosus* Fontannes, 1880, vue dorsale, MNHN A30841, Makrilla. **M**. Arcidae Lamarck, 1809 du « Badénien » de Roumanie, *Arca noae* Linnaeus, 1758, MNHN A31072, Lapugiu. **N–O**. Mollusca du Piacenzien de France. **N**. Babyloniidae Kuroda, Habe & Oyama, 1971, *Babylonia* sp., vue dorsale, MNHN A31068, Le Boulou (Nidolère). **O**. Carditidae Fleming, 1828, *Cardita* sp., MNHN A31922, Le Boulou (Nidolère) (la barre d'échelle représente 10 mm pour **A** et **C–O** et 5 mm pour **B**). Prises de vue par C. Lemzaouda et P. Loubry (MNHN).

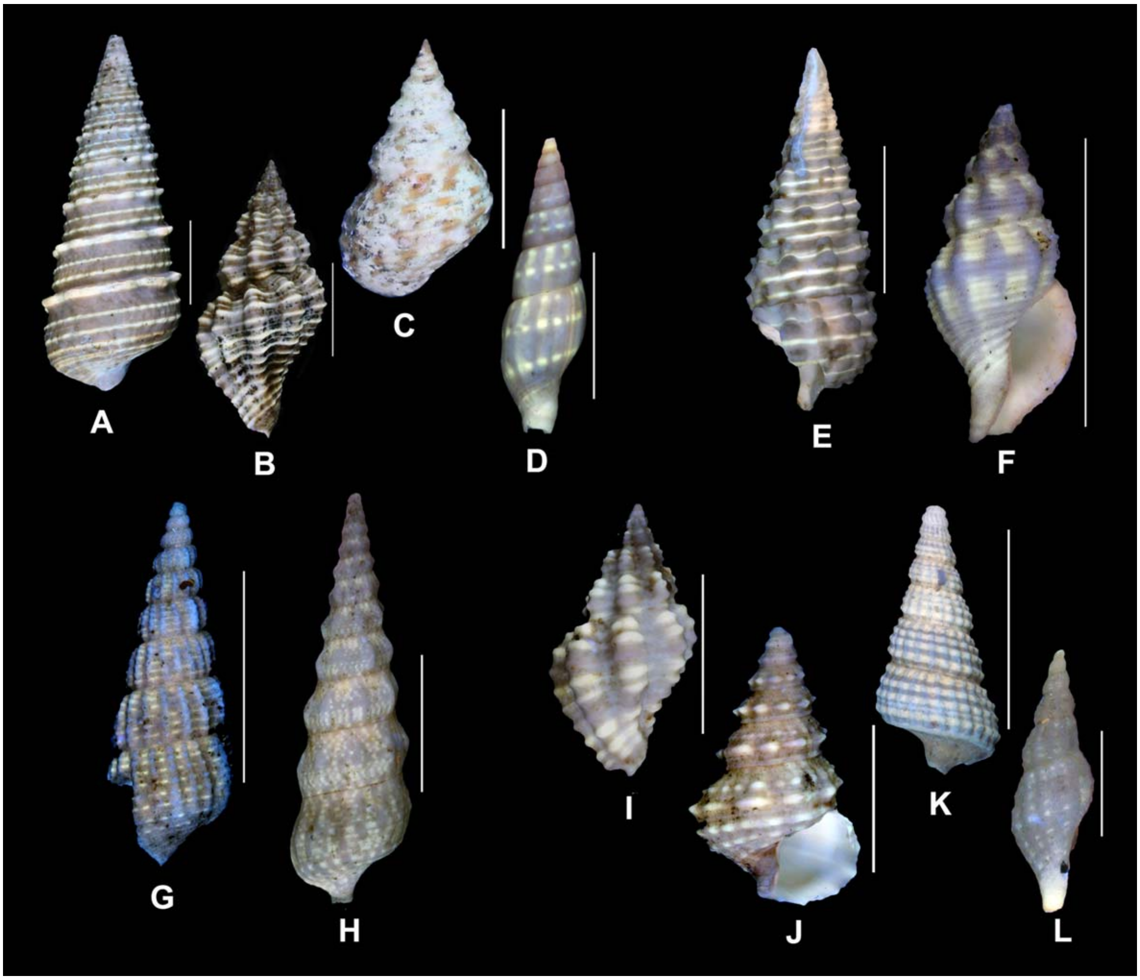

Fig. 3. Diverse relationships between the pattern elements revealed under UV light and the sculpture elements. **A–D**. Residual patterns with elements displaying a positive relationship with the sculpture parallel or perpendicular to the growing edge. **A**. *Tympanotonos (Eotympanotonos) conulus* (Bruguière, 1792), dorsal view, MNHN A31757, Montchauvet, France, Lutetian. **B**. *Janiopsis calvimontensis* (Cossmann, 1889), dorsal view, MNHN A31719, Thionville-sur-Obton, France, Lutetian. **C**. *Littoraria (Littorinopsis) elongata* (Defrance, 1827), dorsal view, MNHN A31327, Villiers-Saint-Frédéric, France, Lutetian. **D**. *Vexillum (Uromitra) terebellum* (Lamarck, 1803), dorsal view, MNHN A31509, Villiers-Saint-Frédéric. **E–F**. Residual patterns with elements displaying a negative relationship with the sculpture parallel or perpendicular to the growing edge. **E**. *Granulolabium (Granulolabium) multinodosum* (Deshayes, 1833), labral view, MNHN A31733, Villiers-Saint-Frédéric. **F**. *Endopachychilus excisus* (Lamarck, 1803), ventral view, MNHN A31316, Villiers-Saint-Frédéric. **G–H**. Residual patterns with elements displaying a positive relationship with some sculpture elements and a negative one with the perpendicular sculpture elements. **G**. *Diastoma costellata* (Lamarck, 1804), labral view, MNHN A31187, Grignon, France, Lutetian. **H**. *Tenuicerithium subulatum* (Lamarck, 1804), dorsal view, MNHN A31731, Grignon. **I–L**. Residual patterns with elements displaying a positive or negative relationship with the sculpture parallel and perpendicular to the growing edge. **I**. *Janiopsis parisiensis* (Deshayes, 1835), dorsal view, MNHN A31745, Venteuil-Arty, France, Lutetian. **J**. *Benoistia muricoides* (Lamarck, 1804), ventral view, MNHN A31585, Beynes (Ferme de l'Orme), France, Lutetian. **K**. *Laiocochlis chevallieri* (Cossmann, 1889), dorsal view, MNHN A31326, Fontenay-en-Vexin, France, Lutetian. **L**. *Pseudoandonia gougeroti* Le Renard, 1989, abapertural view, MNHN A31811, Fontenay-en-Vexin (scale bar represents 10 mm for **A–B**, **E–F**, **G** and **I**, 5 mm for **C–D**, **H** and **J–K** and 2 mm for **L**). Photographs by C. Lemzaouda and P. Loubry (MNHN).

Fig. 3. Différentes relations entre les éléments de motif révélés sous lumière UV et les éléments d'ornementation. **A–D**. Motifs résiduels dont les éléments présentent une relation positive avec l'ornementation parallèle ou perpendiculaire au bord de croissance. **A**. *Tympanotonos (Eotympanotonos) conulus* (Bruguière, 1792), vue dorsale, MNHN A31757, Montchauvet, France, Lutétien. **B**. *Janiopsis calvimontensis* (Cossmann, 1889), vue dorsale, MNHN A31719, Thionville-sur-Obton, France, Lutétien. **C**. *Littoraria (Littorinopsis) elongata* (Defrance, 1827), vue dorsale, MNHN A31327, Villiers-Saint-Frédéric, France, Lutétien. **D**. *Vexillum (Uromitra) terebellum* (Lamarck, 1803), vue dorsale, MNHN A31509, Villiers-Saint-Frédéric. **E–F**. Motifs résiduels dont les éléments présentent une relation négative avec l'ornementation parallèle ou perpendiculaire au bord de croissance. **E**. *Granulolabium (Granulolabium) multinodosum* (Deshayes, 1833), vue labrale, MNHN A31733, Villiers-Saint-Frédéric. **F**. *Endopachychilus excisus* (Lamarck, 1803), vue ventrale, MNHN A31316, Villiers-Saint-Frédéric. **G–H**. Motifs résiduels dont les éléments présentent une relation positive avec certains éléments d'ornementation et une relation négative avec leurs perpendiculaires. **G**. *Diastoma costellata* (Lamarck, 1804), vue labrale, MNHN A31187, Grignon, France, Lutétien. **H**. *Tenuicerithium subulatum* (Lamarck, 1804), vue dorsale, MNHN A31731, Grignon. **I–L**. Motifs résiduels dont les éléments présentent une relation positive ou négative avec l'ornementation parallèle et perpendiculaire au bord de croissance. **I**. *Janiopsis parisiensis* (Deshayes, 1835), vue dorsale, MNHN A31745, Venteuil-Arty, France, Lutétien. **J**. *Benoistia muricoides* (Lamarck, 1804), vue ventrale, MNHN A31585, Beynes (Ferme de l'Orme), France, Lutétien. **K**. *Laiocochlis chevallieri* (Cossmann, 1889), vue dorsale, MNHN A31326, Fontenay-en-Vexin, France, Lutétien. **L**. *Pseudoandonia gougeroti* Le Renard, 1989, vue abaperturale, MNHN A31811, Fontenay-en-Vexin (la barre d'échelle représente 10 mm pour **A–B**, **E–F**, **G** et **I**, 5 mm pour **C–D**, **H** et **J–K** et 2 mm pour **L**). Prises de vue par C. Lemzaouda et P. Loubry (MNHN).

Table 1
Evaluation of the number of families and species bearing residual colour patterns for three epochs of the French Atlantic Caenozoic.
Tableau 1
Estimation du nombre de familles et d'espèces pouvant présenter des motifs colorés pour trois époques du Cénozoïque atlantique français.

Stratigraphic epochs	Number of gastropod families	Number of gastropod species
Miocene	68	1525
Oligocene	71	1511
Eocene (Lutetian)	71	1073

species that has shown colour patterns. We have found that more than 4000 species can display residual colour patterns (Table 1). This number is underestimated, the Ypresian and Bartonian faunas being not included in our estimation.

This number of 4000 gastropod species, based only on a part of the French Caenozoic, gives an indication of the enormous prospects of this new approach in terms of specific richness. At the European scale, we should add Oligocene and Neogene species from the northern Domain (Germany, Denmark, Belgium, England), those from the Neogene of the Mediterranean and those from the Miocene of the Paratethys. Moreover, according to previous works (Bouniol, 1982; Cate, 1972; Dockery, 1980; Hoerle, 1976; Hoerle and Vokes, 1978; Kase et al., 2008; Kelley and Swann, 1988; Pitt and Pitt, 1993; Swann and Kelley, 1985; Vokes and Vokes, 1968), we can assert that the fossil gastropods from North America, Central America and Indo-West Pacific present also a huge potential. Finally, the bivalves, little studied up to now, should be taken into consideration too.

3. The classification of the residual colour patterns

In order to accurately describe species bearing residual colour patterns, it is necessary to classify them. Here, we attempt to present a short classification of these patterns taking account of their elements.

The elements constituting the residual patterns are highly diversified (Fig. 2) and include stripes, segments, patches and rows. They have a more or less regular distribution on the shell. The stripes, segments, or rows, can show different curvatures or tilt following the growing edge of the shell.

The observed residual colour patterns can be discriminated into two classes: (1) the elementary colour patterns; and (2) the composite colour patterns, resulting from the juxtaposition or superposition of two or three components observed alone in species showing elementary colour patterns. The elementary patterns can be divided into two subgroups: (a) the colour patterns present on non-sculptured shells or showing no relationship with the sculpture; and (b) the colour patterns whose elements are related to the sculpture (the location, shape and/or size of pattern elements depend on the sculpture). Within this last subgroup, we distinguish several cases depending on the type of sculpture and on the relationship, positive or negative, between the pattern elements and the sculpture elements (Fig. 3). The pattern elements can show: (1) a positive relationship with the sculpture elements, parallel or perpendicular to the growing edge (Fig. 3A–D); (2) a negative relationship with the sculpture elements, parallel or perpendicular to the growing edge (Fig. 3E–F); (3) a positive relationship with some sculpture elements and a negative one with the perpendicular sculpture elements (Fig. 3G–H); (4) a positive or negative relationship with the sculpture elements, parallel and perpendicular to the growing edge (Fig. 3I–L).

The exposure of Caenozoic shells under UV light revealed two different types of fluorescence: the wavelength is variable depending on species. The residual colour patterns are most frequently revealed by a pale fluorescence, yellow-beige to white and sometimes very bright (Fig. 4A). This type of fluorescence is often found among the Caenogastropoda. More rarely, the fluorescence is darker and red (Fig. 4B). This occurs mainly in the Vetigastropoda.

This presentation of some of the many characters available through the residual colour patterns found in Caenozoic molluscs gives an overview of their contribution to the characterization of fossil species.

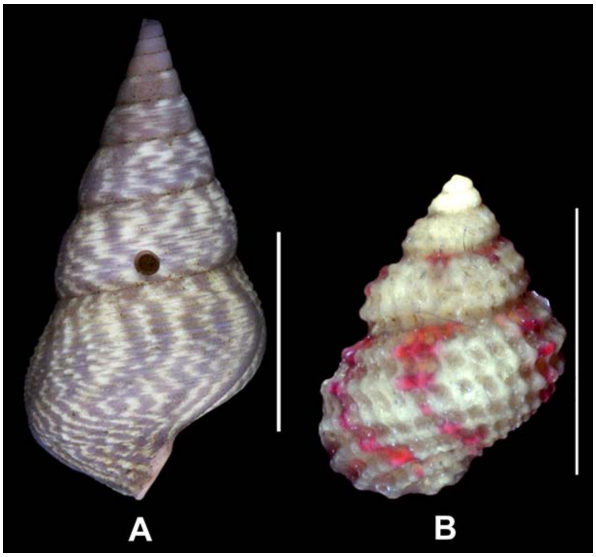

Fig. 4. Two types of fluorescence observed under UV light. **A**. Pale fluorescence of *Sigmesalia multisulcata* (Lamarck, 1804), MNHN A31257, Grignon, France, Lutetian. **B**. Dark fluorescence of *Danilia perelegans* (Deshayes, 1863), MNHN A31541, Les Groux, Lutetian (scale bar represents 10 mm for **A** and 5 mm for **B**). Photographs by C. Lemzaouda and P. Loubry (MNHN).
Fig. 4. Deux types de fluorescence observés sous lumière UV. **A**. Fluorescence claire chez *Sigmesalia multisulcata* (Lamarck, 1804), MNHN A31257, Grignon, France, Lutétien. **B**. Fluorescence sombre chez *Danilia perelegans* (Deshayes, 1863), MNHN A31541, Les Groux, France, Lutétien (la barre d'échelle représente 10 mm pour **A** et 5 mm pour **B**). Prises de vue par C. Lemzaouda et P. Loubry (MNHN).

4. Systematic interest

The use of the residual colour patterns is particularly helpful and relevant in the case of species with very similar shell morphology and lacking sculpture. The example of two species of Volutidae from the Lutetian of the Paris Basin, *Harpula mitreola* Lamarck, 1802 and *Leptoscapha variculosa* Lamarck, 1802, is notably illustrative. Although these species, coexisting especially in Fontenay-en-Vexin and Villiers-Saint-Frédéric, have been attributed to two different genera, they exhibit almost identical shell morphology and are very difficult to distinguish (Fig. 5). The examination of these species under UV light (53 spm of *H. mitreola* and 26 of *L. variculosa*) greatly facilitates their identification and highly supports, also, legitimacy of their distinction at specific level. Two distinct pattern morphologies are indeed revealed (Fig. 6). The pattern of *H. mitreola* consists of spiral rows of pale patches on a dark background, while that of *L. variculosa* is composed of triangular dark patches irregularly distributed on a pale background. These two pattern morphologies could be compared to those of other Volutidae. A current study on Caenozoic *Mitreola* allowed us defining two distinct groups of residual patterns without any intermediate or transitional form. *H. mitreola* residual pattern is alike those of *Mitreola labratula* group and the pattern of *L. variculosa* is very similar to those of *M. maxwelli* group. Although each figured species displays an intraspecific variability (Fig. 6), the lack of any intermediate between both patterns easily supports their distinction (Fig. 6).

In order to demonstrate that this method could provide access also to the intraspecific variability of the residual colour pattern a large number of specimens belonging to the family Seraphsidae have been studied. A strong variability of the residual colour pattern has been revealed in several species, as for the example the Ypresian *Paraser-*

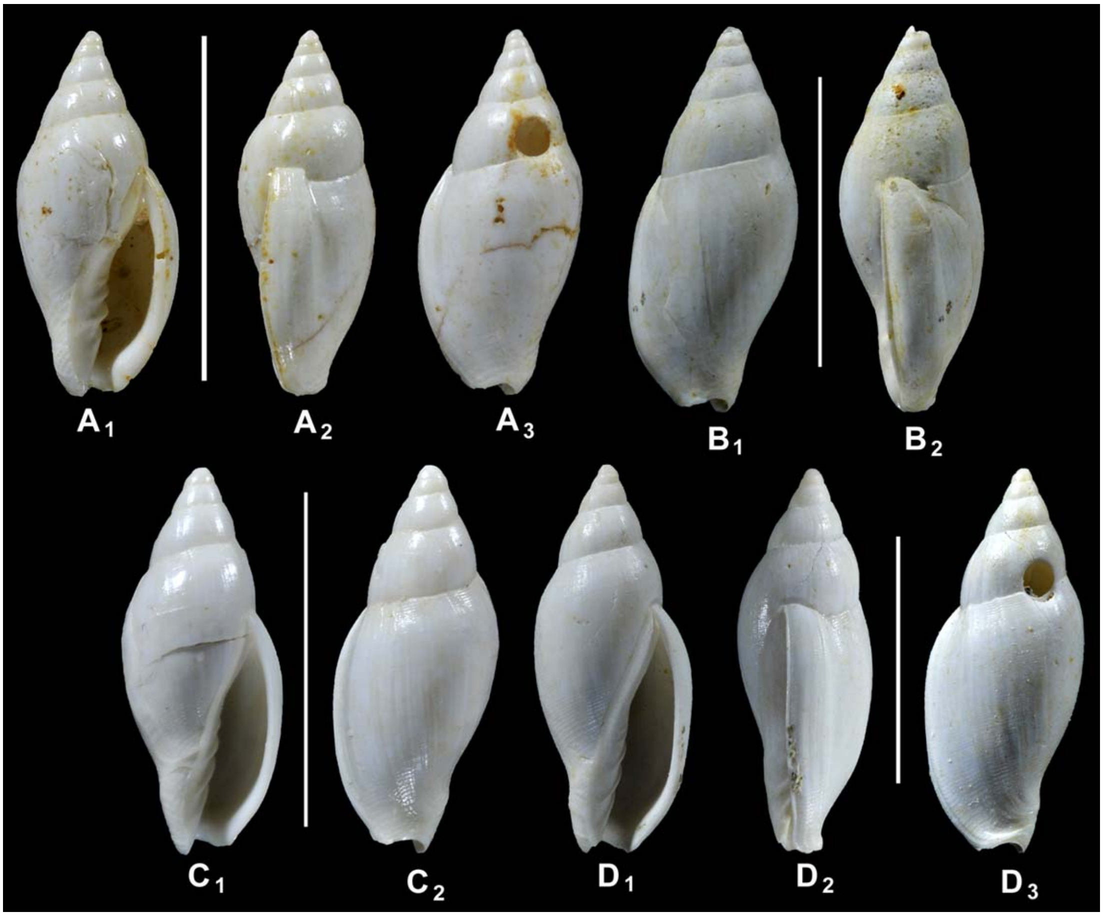

Fig. 5. Shell morphology of *Harpula mitreola* (Lamarck, 1802) and *Leptoscapha variculosa* (Lamarck, 1802) from the Lutetian of the Paris Basin in natural light. **A**. *H. mitreola* (A$_1$, ventral view, A$_2$, labral view, A$_3$, dorsal view), MNHN A31370, Fontenay-en-Vexin. **B**. *H. mitreola* (B$_1$, dorsal view, B$_2$, labral view), MNHN A31371, Fontenay-en-Vexin. **C**. *L. variculosa* (C$_1$, ventral view, C$_2$, dorsal view), MNHN A31374, Fontenay-en-Vexin. **D**. *L. variculosa* (D$_1$, ventral view, D$_2$, labral view, D$_3$, dorsal view), MNHN A31375, Villiers-Saint-Frédéric (scale bar represents 10 mm). Photographs by C. Lemzaouda and P. Loubry (MNHN).
Fig. 5. Morphologie des coquilles de *Harpula mitreola* (Lamarck, 1802) et *Leptoscapha variculosa* (Lamarck, 1802) du Lutétien du bassin de Paris en lumière naturelle. **A**. *H. mitreola* (Lamarck, 1802) (A$_1$, vue ventrale, A$_2$, vue labrale, A$_3$, vue dorsale), MNHN A31370, Fontenay-en-Vexin. **B**. *H. mitreola* (Lamarck, 1802) (B$_1$, vue dorsale, B$_2$, vue labrale), MNHN A31371, Fontenay-en-Vexin. **C**. *L. variculosa* (Lamarck, 1802) (C$_1$, vue ventrale, C$_2$, vue dorsale), MNHN A31374, Fontenay-en-Vexin. **D**. *L. variculosa* (Lamarck, 1802) (D$_1$, vue ventrale, D$_2$, vue labrale, D$_3$, vue dorsale), MNHN A31375, Villiers-Saint-Frédéric (la barre d'échelle représente 10 mm). Prises de vue par C. Lemzaouda et P. Loubry (MNHN).

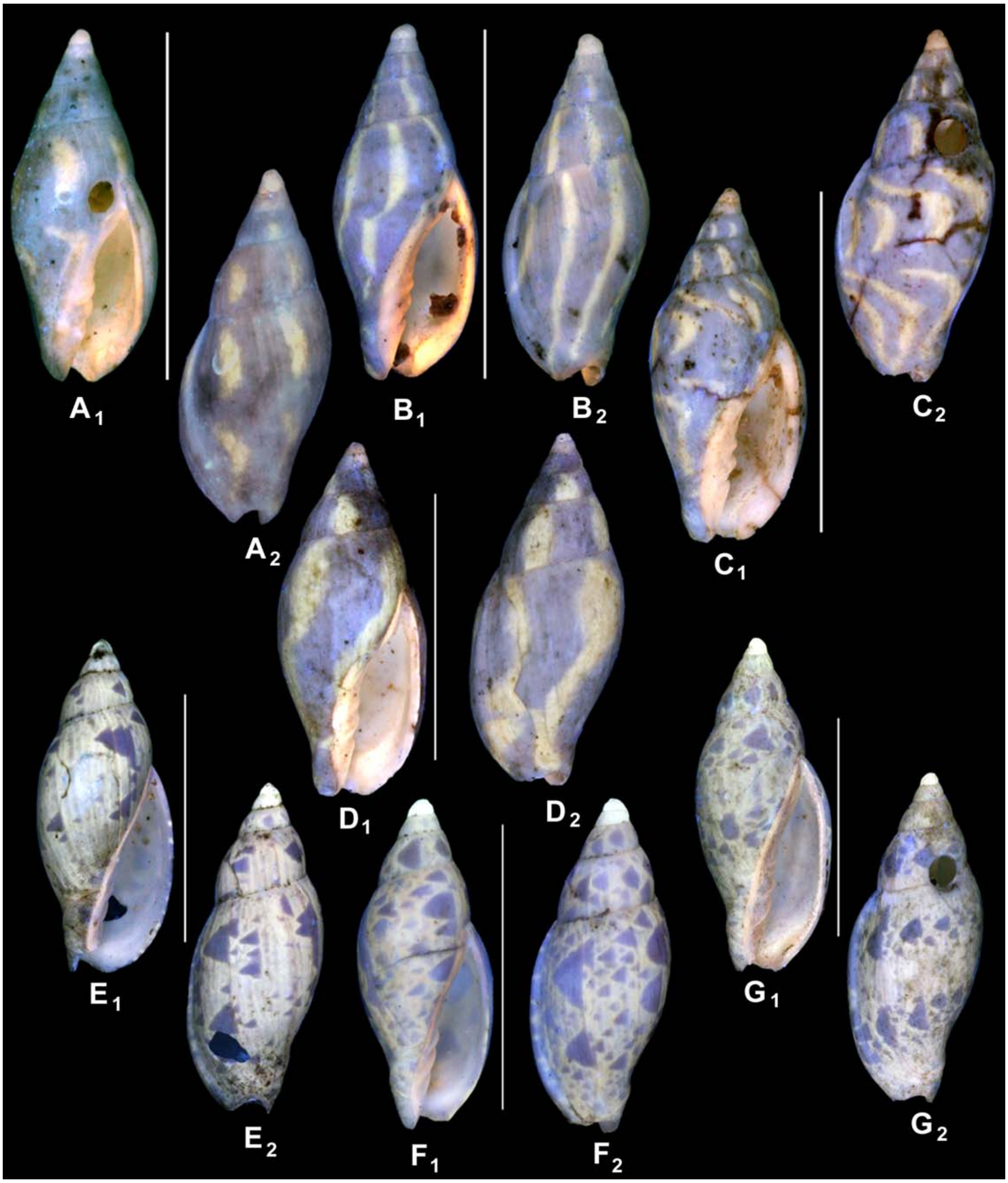

Fig. 6. Residual colour patterns in *Harpula mitreola* (Lamarck, 1802) and *Leptoscapha variculosa* (Lamarck, 1802) from the Lutetian of the Paris Basin under UV light. **A**. *H. mitreola* (A_1, ventral view, A_2, dorsal view), MNHN A31347, Chaussy. **B**. *H. mitreola* (B_1, ventral view, B_2, dorsal view), MNHN A31346, Chaussy. **C**. *H. mitreola* (C_1, ventral view, C_2, dorsal view), MNHN A31370, Fontenay-en-Vexin. **D**. *H. mitreola* (D_1, ventral view, D_2, dorsal view), MNHN A31371, Fontenay-en-Vexin. **E**. *L. variculosa* (E_1, ventral view, E_2, dorsal view), MNHN A31373, Fontenay-en-Vexin. **F**. *L. variculosa* (F_1, ventral view, F_2, dorsal view), MNHN A31374, Fontenay-en-Vexin. **G**. *L. variculosa* (G_1, ventral view, G_2, dorsal view), MNHN A31375, Villiers-Saint-Frederic (scale bar represents 10 mm). Photographs by C. Lemzaouda and P. Loubry (MNHN).

Fig. 6. Motifs colorés résiduels de *Harpula mitreola* (Lamarck, 1802) et *Leptoscapha variculosa* (Lamarck, 1802) du Lutétien du bassin de Paris sous lumière UV. **A**. *H. mitreola* (Lamarck, 1802) (A_1, vue ventrale, A_2, vue dorsale), MNHN A31347, Chaussy. **B**. *H. mitreola* (Lamarck, 1802) (B_1, vue ventrale, B_2, vue dorsale), MNHN A31346, Chaussy. **C**. *H. mitreola* (Lamarck, 1802) (C_1, vue ventrale, C_2, vue dorsale), MNHN A31370, Fontenay-en-Vexin. **D**. *H. mitreola* (Lamarck, 1802) (D_1, vue ventrale, D_2, vue dorsale), MNHN A31371, Fontenay-en-Vexin. **E**. *L. variculosa* (Lamarck, 1802) (E_1, vue ventrale, E_2, vue dorsale), MNHN A31373, Fontenay-en-Vexin. **F**. *L. variculosa* (Lamarck, 1802) (F_1, vue ventrale, F_2, vue dorsale), MNHN A31374, Fontenay-en-Vexin. **G**. *L. variculosa* (Lamarck, 1802) (G_1, vue ventrale, G_2, vue dorsale), MNHN A31375, Villiers-Saint-Frédéric (la barre d'échelle représente 10 mm). Prises de vue par C. Lemzaouda et P. Loubry (MNHN).

aphs tetanus Jung, 1974 (Caze et al., 2010). It often results from the coalescence of pattern elements; some elements can, by dilatation, merged partially or totally forming a larger element or a connection in case of stripes or rows. So, the access to intraspecific variability allows enriching the definition of the palaeontological species as it was noted in Seraphsidae. Considering this kind of results and the simplicity of the technical means needed for implementation, the integration of the data provided by residual colour patterns now appears inevitable for the descriptions of palaeontological species. The geometric aspect of the pattern elements, their organization, their distribution on the shell surface, the type of fluorescence and the easy access to the intraspecific and interspecific variability are all new characters concretely contributing to the characterization of a fossil taxon. Thus, the residual colour patterns can provide a valuable assistance for distinguishing, or even identifying, fossil species whose shells are similar and almost devoid of sculpture and diagnostic characters. This case is observed in many gastropod families as for example the Conidae Fleming, 1822, the Costellariidae MacDonald, 1860, the Naticidae Guilding, 1834, the Buccinidae Rafinesque, 1815, the Marginellidae Fleming, 1828 or the Seraphsidae Gray 1853.

Another fruitful perspective is the possibility to test data provided by the residual colour patterns in a phylogenetic framework including fossils. A clear and rigorous definition of the various colour pattern types, including the intraspecific variability, is a necessary step for the statement of hypotheses of homology. The hypotheses of homology must then be carefully defined on the basis of three criteria used in combination: (1) the topographical criterion (relationship between the pattern elements and the growing edge or the growth direction, location of pattern elements on the whorl); (2) the formation criterion, reflecting the modalities of formation of the pattern; and (3) the ontogenetical criterion, allowing determining the appearance stage of the pattern elements and their frequent variations during the shell growth.

5. Conclusion

The potential contribution of the residual colour patterns for the characterization of Caenozoic molluscan species is considerable. These patterns revealed thanks to the exposure of fossils under UV light appear rich in additional data (e.g., geometry of the pattern elements, organization and distribution on the shell, wavelength of the fluorescence, intraspecific variability) complementing those provided by the shell morphology. This new approach also brings to light many innovative research opportunities (e.g., systematics, palaeobiogeography, biostratigraphy), which can lead to a better understanding and reconstruction of the Caenozoic biodiversity. Moreover, the impact of the results presented herein exceeds widely the framework of research on Caenozoic. This period is a crucial testimony of the radiation of many groups, mainly within the Neogastropoda, which has a decisive influence on the aspect of the extant biodiversity. This statement therefore demonstrates that the study of residual patterns is a central issue in the general problem of mollusc evolution. In addition, this new approach can enhance the communication between Palaeontology and Neontology and foster closer links between the respective approaches of these two sciences: morphological descriptions frequently devoid of evolutionary interpretation in Palaeontology and anatomical and molecular studies with or without consideration of the shell appearance in Neontology. It appears indisputable that residual colour patterns constitute an underexploited source of data we can not ignore in future works on mollusc palaeobiodiversity and evolution.

Acknowledgements

We are anxious to thank Didier Néraudeau (université de Rennes 1) for encouragement to write this contribution. The photographs have been taken by Christian Lemzaouda and Philippe Loubry (MNHN). Our thanks go also to Philippe Courville (université de Rennes 1) and Jean-Louis Dommergues (université de Bourgogne, Dijon) for their careful review of the manuscript.

References

Bouniol, P., 1982. L'ornementation pigmentaire des coquilles de Cerithidés actuels et fossiles (s.l): apport de la technique de l'Ultra-Violet. Malacologia 22 (1–2), 313–317.

Cate, J.M., 1972. On the occurrence of the volutid subgenus *Eneata*. Tulane Studies in Geology and Paleontology 10 (1), 47–50.

Caze, B., 2010. Intérêt systématique de l'étude des motifs colorés résiduels chez les mollusques du Cénozoïque d'Europe. Thèse de doctorat du MNHN, 558 p.

Caze, B., Merle, D., Pacaud, J.M., Saint Martin, J.P., 2010. First systematic study using the variability of the residual colour pattern: the case of the Palaeogene Seraphsidae (Gastropoda, Stromboidea). Geodiversitas 32 (3), 417–477.

Dockery, D.T., 1980. Color patterns of some Eocene molluscs. Mississippi Geology 1 (1), 3–7.

Dommergues, E., Dommergues, J.-L., Dommergues, C.H., 2006. Deux espèces sous un même masque. Le point de vue paléontologique piégé par les coquilles de deux espèces européennes de *Trivia* (Mollusca, Gastropoda). Revue de Paléobiologie 25 (2), 775–790.

Hoerle, S.E., 1976. The genus *Conus* (Mollusca: Gastropoda) from the Alum Bluff group of Northwestern Florida. Tulane Studies in Geology and Paleontology 14 (1–2), 1–31.

Hoerle, S.E., Vokes, E.H., 1978. A review of the volutid genera *Lyria* and *Falsilyria* (Mollusca: Gastropoda) in the Tertiary of the Western Atlantic. Tulane Studies in Geology and Paleontology 14 (3), 105–130.

Joly, B., Baudouin, C., 2006. Découverte récente de deux Phylloceratidae colorés appartenant au genre *Adabofoloceras* Joly, 1977. Hypothèses sur le lien entre style de coloration de la coquille et mode de vie. Bull. Soc. geol. France 177 (1), 51–59.

Kase, T., Fumimasa, K., Maac Aguilar, Y., Kurihara, Y., Pandita, H., 2008. Reconstruction of color markings in *Vicarya*, a Miocene potamidid gastropod (Mollusca) from SE Asia and Japan. Paleontogical Research 12 (4), 345–353.

Kelley, P.H., Swann, C.T., 1988. Functional significance of preserved color patterns of molluscs from the Gosport sand (Eocene) of Alabama. Paleontogy 62 (1), 83–87.

Lozouet, P., 1997. Le domaine atlantique européen au Cénozoïque moyen: diversité et évolution des gastéropodes. Thèse de doctorat du Muséum National d'Histoire Naturelle, Paris, 309 p.

Merle, D., Pacaud, J.M., Kriloff, A., Loubry, P., 2008a. Les motifs colorés résiduels des coquilles lutétiennes du bassin de Paris. In: Merle, D. (Ed.), Stratotype Lutétien. Biotope Mèze, MNHN, Paris, BRGM, Orléans, Collection Patrimoine géologique. pp. 182–227.

Merle, D., de Franceschi, D., Masure, E., Chaix, C., Roman, J., Dutheil, D., Lapierre, H., Gaudant, J., de Lapparent, F., Jouve, S., Rage, J.C., Gheerbrant, E., Carriol, R.P., Guernet, C., Pacaud, J.M., Moissette, P., 2008b. Le contenu paléontologique du Lutétien. In: Merle, D. (Ed.), Stratotype Lutétien. Biotope Mèze, MNHN, Paris, BRGM, Orléans, Collection Patrimoine géologique, CD Rom, 105 p.

Olsson, A.A., 1967. Some Tertiary Mollusks from South Florida and the Caribbean. Paleontological Research Institution. Ithaca, New York, p. 161.

Pitt, W.D., Pitt, L.J., 1993. Ultra-violet light as a useful tool for identifying fossil molluscs, with examples from the Gatun formation, Panama. Tulane Studies in Geology and Paleontology 26 (1), 1–13.

Swann, C.T., Kelley, P.H., 1985. Residual colour patterns in Molluscs from the Gosport sand (Eocene), Alabama. Mississippi Geology 5 (3), 1–8.

Vokes, H.E., Vokes, E.H., 1968. Variation in the genus *Orthaulax* (Mollusca: Gastropoda). Tulane Studies in Geology and Paleontology 6 (2), 71–79.