Taxonomic Implications of the Residual Colour Patterns of Ampullinid Gastropods and Their Contribution to the Discrimination from Naticids

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Taxonomic implications of the residual colour patterns of ampullinid gastropods and their contribution to the discrimination from naticids

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The diversity of residual colour patterns is revealed for the first time in the European fossil Ampullinidae. The colour patterns were studied under Ultraviolet (UV) light in approximately 3100 specimens belonging to 83 species, 12 genera (*Ampullina*, *Globularia*, *Crommium*, *Amaurellina*, *Pachycrommium*, *Amauropsina*, *Ampullonatica*, *Eocernina*, *Ampullinopsis*, *Vanikoropsis*, *Pictavia*, and *Ampullospira*) and three subgenera (*Globularia*, *Deshayesia*, and *Cernina* within the genus *Globularia*). Forty-six Cainozoic species revealed residual colour patterns and 29 of them, belonging to six genera (*Ampullina*, *Globularia*, *Crommium*, *Amaurellina*, *Pachycrommium*, *Amauropsina*), are described herein as examples representing the entire diversity of the encountered colour patterns. These patterns are most diverse during the Middle Eocene coincident with the period of highest taxonomic diversity of the Ampullinidae. Four basic classes, regarded as containing possible homologous colour patterns in terms of pigments incorporation modalities, are proposed. Class I, a fluorescent wide diffuse area or spiral stripes, occurs in most of the species, while the three others are more peculiar. Class II, fluorescent axial zigzagging stripes, Class III, fluorescent axial to slightly opisthocline stripes or segments, and Class IV, fluorescent patches forming axial segments by coalescence, allow an easy distinction between the genera *Globularia*, *Pachycrommium*, and three peculiar species of *Ampullina*. The bauplan of the colour patterns revealed in *Globularia* is very similar to that of the single extant species, *Globularia* (*Cernina*) *fluctuata*. This supports the view of previous authors who classified them in the same genus. Furthermore, at the family level, the peculiar residual patterns belonging to classes II, III, and IV have not been observed in naticid gastropods. Thus our results for the Cainozoic fossil record are consistent with the conclusions based on anatomy and feeding habits, namely that ampullinid gastropods, regarded for a long time as belonging to the family Naticidae, constitute a family apart.

Key words: Ampullinidae, Naticidae, residual colour patterns, taxonomy, shell character, evolution, Cainozoic, Europe.

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Introduction

The ampullinids are represented by numerous Mesozoic and Cainozoic shells. In the European Cainozoic, their shells are particularly common (81 of 93 species listed in worldwide Cainozoic; see Supplementary Online Material (SOM 1, for all SOMs see http://app.pan.pl/SOM/app56-Caze_etal_SOM.pdf) and well preserved, constituting an appropriate material for studies of residual colour patterns. While Ampullinidae were quite diverse in the past, now they are represented by single species, *Globularia* (*Cernina*) *fluctuata* (Sowerby, 1825), living in marine waters of the Philippines. The ampullinids first appeared in the Late Triassic (genus *Falorina* from Carnian of San Cassiano formation; Bandel 2006). In Europe, this group reached its biodiversity optimum during the Middle Eocene (at least 40 European species, particularly in the Paris Basin). Later, the number of species decreased dramatically after the Eocene/Oligocene crisis (only 6 species in the Early Neogene of Europe) and disappeared in the Late Neogene of Europe.

Ampullinid shells display a very similar morphology (Lamarck 1804) to those of the naticids (globose shape, semilunar aperture, generally low spire and flattened suture, absence of ornamentation) and historically most authors (e.g., Deshayes 1864; Cossmann 1888; Wenz 1941; Wrigley 1946; Glibert 1963) have considered ampullinids as belonging to the Naticidae. Later, some authors (e.g., Wenz 1941; Wrigley 1946; Glibert 1963), however, proposed for them a

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separate subfamily Globulariinae (a junior synonym of Ampullininae) within the family Naticidae, including there also the single living ampullinid species. Recently, Kase (1990) studied the anatomical characters (foot, head, proboscis) of *G.* (*Cernina*) *fluctuata* and stated that the latter should be removed from Naticidae and the Ampullospirinae (another junior synonym of Ampullininae Cossmann, 1919) should be moved closer to the family Campanilidae. Kase and Ishikawa (2003a) confirmed these interpretations showing that *G.* (*C.*) *fluctuata* is an algal grazer, while all naticids are shell-drilling predatory gastropods. Thus, they removed the entire subfamily Ampullospirinae from Naticidae, indicating also their diagnostic shell characters (spire, columellar lip, protoconch). Aronowsky and Leighton (2003) criticised this view, basing their discussion on variation of the diagnostic shell characters and disagreed with Kase and Ishikawa (2003a) on the removal of all fossil ampullinids from Naticidae. In their answer to Aronowsky and Leighton (2003), Kase and Ishikawa (2003b) indicated that they used a "combination of shell characters" in order to justify this removal. We agree with Aronowsky and Leighton (2003) that further study of the morphology of the ampullinids should be the best way to clarify the higher level taxonomic affiliation of fossil ampullinid taxa. Therefore, we present an overview of the residual colour patterns of the Cainozoic ampullinids as an additional and here to date unexploited suite of shell characters useful for delimitation of Ampullinidae from Naticidae. Our aim is to demonstrate the diversity of the residual colour patterns; an exhaustive revision and a cladistic analysis of the family Ampullinidae will be published elsewhere. As many ampullinid species have similar colour patterns, we illustrate the most representative species (including the type species) and those with a large number and/or the best preserved specimens; other species are considered in the SOM 1 and SOM 2.

Institutional abbreviations.—MNHN, Muséum National d'Histoire Naturelle, collection de Paléontologie, Paris (France); MNHN IM, Muséum National d'Histoire Naturelle, collection d'invertébrés marins (mollusques), Paris (France).

Other abbreviations.—AB, Aquitaine Basin, France; HB, Hampshire Basin, England; PB, Paris Basin, France.

Material and methods

We examined a large number of specimens belonging to 83 ampullinid species (including the sole extant species; see SOM 2) stored mainly in the MNHN. The studied material represents about 3100 specimens from 113 fossiliferous sites of the European, mainly French, Mesozoic and Cainozoic (from the Middle Jurassic to the Middle Miocene). Sixty-nine of 81 species listed in European Cainozoic are present in Paris and Aquitaine basins, Loire-Atlantique, Cotentin, Alpes and Aude (France). No residual colour pattern was revealed by the exposure of Mesozoic shells (10 species) under UV light. Forty-six of the 72 Cainozoic species showed residual patterns.

The residual shell pigmentation may be revealed or enhanced by bleaching specimens in sodium hypochlorite (NaClO) then directly exposing those under long-wave UV light (Olsson 1967; Vokes and Vokes 1968; Krueger 1974; Hoerle 1976; Dockery 1980; Swann and Kelley 1985; Pitt and Pitt 1993; Kase et al. 2008). For the UV light observation, the samples were processed using the procedure defined by Merle et al. (2008): (i) they were placed in a bath of concentrated sodium hypochlorite for 24 hours; (ii) they were carefully washed with water to eliminate all traces of dried hypochlorite of sodium; (iii) most of the patterns were revealed by exposure under UV light emitting a wavelength of 3600 Å (Merle 2003). For the UV light photography, the specimens were placed at the intersection of the beams of two UV lamps arranged face to face and emitting the same wavelength. Finally, in order to get the best images, we have undertaken software processing (brightness and contrast adjustment). The photographed specimens are presented as imaged under UV light and not in negative view.

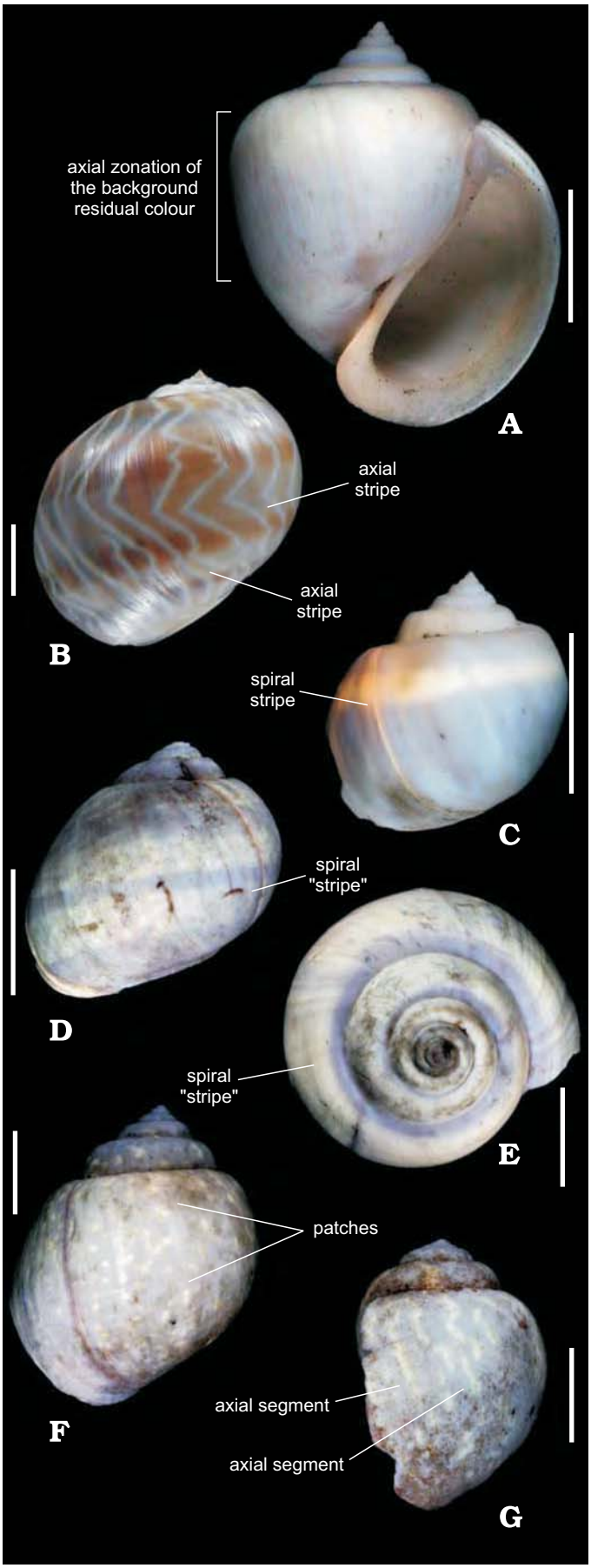
Comments on the relationship between colouration and pigmentation: We observed that the fluorescent regions revealed under UV light on fossil shells correspond to regions with residual pigmentation and that dark regions correspond to "unpigmented" regions. In most cases Recent shells show an inverted contrast: the pigmented regions appear dark and the unpigmented regions appear pale or white. Nevertheless, the shells of *Globularia* appear to present an exception: analogous axial zigzagging stripes observed in several species appear fluorescent, and consequently pigmented, in the fossil record while they are white on the Recent shells. Without chemical analyses, we are unable to determine whether this absence of contrast reversal between the fossil and extant species results from an arrangement of pigments producing a "white colour" in the extant one or from the non-homology of the similar fossil and Recent axial zigzagging stripes. Consequently, we do not know if the use of negative views would permit the observation of colour patterns as they "would have appeared in life" (Hendricks 2009) and prefer to keep the true appearance of the colour patterns as observed under UV light.

Descriptive terminology

Number of levels of residual colouration: the patterns can show from 2 to 4 different colours, called by Meinhardt (1998), levels of pigmentation.

Background relative colouration: a darker or paler background contrasts with the elements producing the different patterns.

Background colour zonation (Fig. 1A): the background can show diffuse colour variations, forming generally some broad stripes or area.



Stripes (Fig. 1B, C): this term applies to any elongated fluorescent colour pattern component which is axially or spirally continuous on the whole shell.

"Stripes" (Fig. 1D, E): the use of quotes illustrates the desire to distinguish the result of a lack of fluorescence from well delineated fluorescent stripes.

Patches (Fig. 1F): this term applies to any small area of a colour contrasting sharply with the background.

Segments (Fig. 1G): the segments are short elongated sections, generally resulting from the coalescence of patches. They are always axially elongated in ampullinids.

A survey of colour patterns according to systematic order

Clade Sorbeoconcha Ponder and Lindberg, 1997

Superfamily Campaniloidea Douvillé, 1904

Family Ampullinidae Cossmann, 1919

Genus *Ampullina* Bowdich, 1822

Type species: *Ampullaria depressa* Lamarck, 1804, Grignon, Lutetian.

Description.—Worldwide, this genus consists of 42 species in the Cainozoic, of which 41 occur in the Palaeogene (SOM 1). 14 of the 34 species observed under UV light reveal a simple and unsophisticated residual colour pattern consisting of fluorescent straight spiral stripes or a diffuse area (SOM 2). However, on the basis of shell morphology, we include in this genus three species previously attributed to *Crommium*, *Ampullina intermedia* (Deshayes, 1832), *Ampullina lignitara* (Deshayes, 1864), and *Ampullina merciniensis* (Deshayes, 1864). They display fluorescent patches or segments, sometimes superimposed on broad spiral stripes.

Ampullina depressa depressa (Lamarck, 1804)

Fig. 2A.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (PB, Loire-Atlantique).

Fig. 1. Descriptive terminology of the residual colour patterns of the Ampullinidae. **A**. *Crommium acutum* (d'Orbigny, 1850), MNHN B58618 (MNHN coll.), Parnes, Oise, France, Lutetian, in ventral view. **B**. *Globularia* (*Cernina*) *fluctuata* (Sowerby, 1825), MNHN IM (Staadt coll.), Banggi Island, Kudat division of Sabah, Malaysia, Recent, in dorsal view. **C**. *Ampullina parisiensis* (d'Orbigny, 1850), MNHN A30403 (MNHN coll.), Villiers-Saint-Frédéric, Yvelines, France, Lutetian, in dorsal view. **D**. *Globularia* (*Deshayesia*) *parisiensis* (Raulin, 1844), MNHN A30892 (Cossmann coll.), Morigny (Château de Brunehaut), Essonne, France, Rupelian (Stampian), in dorsal view. **E**. *Ampullina rustica* (Deshayes, 1864), MNHN A30414 (Ledon coll.), Douains, Eure, France, Lutetian, in apical view. **F**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30416 (MNHN coll.), Cuise-la-Motte, Oise, France, Ypresian (Cuisian), in dorsal view. **G**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30417 (MNHN coll.), Cuise-Lamotte, in labral view. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

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Colour pattern description.—The pattern consists of three levels of residual colouration. The background is heterogeneous with a fluorescent spiral stripe located just below the subsutural step (Fig. $2A_1$). The apex is paler. The diffuse stripe varies in breadth and the whorl is sometimes almost entirely fluorescent (excepting the subsutural step and the base). In the latter case, the stripe may have a different colour (more orange) and is still distinguishable. An additional thin median stripe is seen (Fig. $2A_2$) in several specimens.

Ampullina parisiensis (d'Orbigny, 1850)

Fig. 2B, C.

Stratigraphic and geographic range.—Early Eocene, Ypresian (Cuisian)–Middle Eocene, Bartonian and Priabonian (PB, Cotentin, HB).

Colour pattern description.—The residual pattern is variable and consists of three levels of residual colouration. The background is heterogeneous with one (Fig. 2B, C_1) or two fluorescent spiral stripes and the apex is pale (Fig. $2C_1$). The transition between the two levels of residual colouration of the background is diffuse. There are usually two fluorescent stripes: a broad one on the adapical part and a thinner one on the adbasal part (Fig. $2C_2$). The width of the adapical stripe varies among specimens. Sometimes there are two thin adbasal stripes very close to each other instead of one. The adbasal stripe is sometimes absent and several specimens have an additional thin subsutural fluorescent stripe. Some specimens display a single broad stripe spreading on the major part of the whorl. Although the whorl could be almost entirely fluorescent (excepting the subsutural step and the base), the adapical stripe is sometimes in a different colour (more orange) and remains distinguishable.

Comments on the residual colour pattern of A. depressa depressa *and* A. parisiensis.—Several hypotheses can be advanced to explain the occurrence of two different colours in the background fluorescence: (i) the chemical nature of the incorporated pigments; (ii) the concentration of the incorporated pigments; (iii) the modalities of incorporation. The first two hypotheses appear plausible. Previous studies, chromatographic (Comfort 1949a–c, 1950, 1951; Nicholas and Comfort 1949) and spectrometric (Hedegaard et al. 2006) analyses, have indeed revealed differences in the nature of the substances involved in the pigmentation of gastropod shells. Moreover Hedegaard et al. (2006) also indicated that there is no simple relationship between pigment, colour and taxa: different colours within a single taxon may be due to different pigments or different saturations of colour can be generated by different concentrations of the same pigment.

Ampullina rustica (Deshayes, 1864)

Fig. 2D.

Stratigraphic and geographic range.—Middle Eocene, Lutetian (PB, Cotentin).

Colour pattern description.—The shells show three levels of residual colouration. The background is heterogeneous with a dark subsutural step and a wide fluorescent area covering the major part of the whorl (Fig. $2D_2$). The apex is pale. The transition between the fluorescent area and the darker area of the background is mostly diffuse. The absence of fluorescence on the subsutural step induces a dark straight spiral "stripe" (Fig. $2D_1$). The base of the whorl may be dark too. Sometimes, there are also slightly darker thin and diffuse spiral "stripes" on the last whorl due to a localized lack of fluorescence. These "stripes" are related to obsolete spiral "microlines" and their number and distribution are variable. The residual colour pattern is very similar to that of *A. grossa* (Deshayes, 1864) from the Lutetian–Bartonian of the Paris Basin (Fig. 2E).

Ampullina chenayensis Cossmann, 1892

Fig. 2F.

Stratigraphic and geographic range.—Late Palaeocene, Thanetian (PB).

Colour pattern description.—The pattern consists of three levels of residual colouration: a heterogeneous background with three spiral fluorescent stripes (Fig. 2F) and a pale apex. The transition between the two levels of colouration is diffuse. The median stripe is slightly broader than the two others (Fig. $2F_1$).

Ampullina aizyensis (Bayan, 1870)

Fig. 2G, H.

Stratigraphic and geographic range.—Late Palaeocene, Thanetian–Early Eocene, Ypresian (Cuisian) (PB).

Colour pattern description.—The pattern consists of three levels of residual colouration. The background is heterogeneous with three fluorescent spiral stripes (Fig. 2G, H) and the apex is pale. The transition between the two levels of residual colouration of the background is diffuse. These stripes are located on the shoulder and on the median and adbasal parts of the whorl. Their thickness is not homogeneous on the shell and varies among specimens (Fig. 2G, H_1).

Comments.—The figured shells (Fig. 2G, H) are from the Thanetian of Bachivillers (France, PB) from where this species' occurrence has never been listed. However their shell shape, oblong with slightly elevated and turreted spire and tabulate whorls, differs obviously from the sole previously known Thanetian species *A. chenayensis* (Fig. 2F) which is globose with a low spire and lacks tabulate whorls. We consider that our specimens display the characteristic morphology of the Cuisian species *A. aizyensis* and that they represent the oldest known occurrence of this species.

Ampullina stampinensis (Cossmann and Lambert, 1884)

Fig. 2I.

Stratigraphic and geographic range.—Early Oligocene, Rupelian (Stampian) (PB).

Colour pattern description.—The shells show two levels of residual colouration under UV light (apex absent). The background is dark and heterogeneous with three spiral fluores-

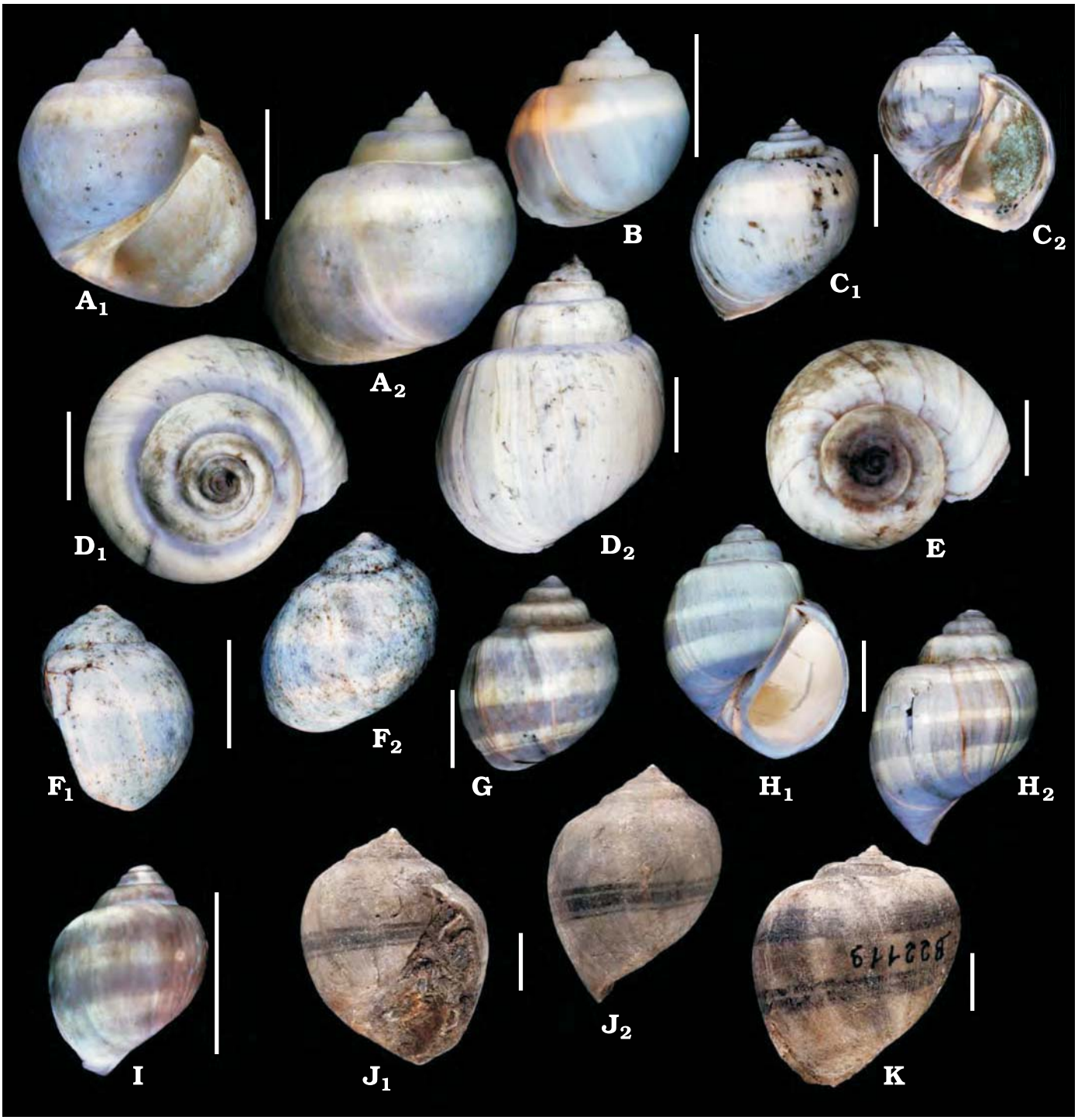

Fig. 2. Species of the genus *Ampullina* Bowdich, 1822, under UV light. **A**. *Ampullina depressa* (Lamarck, 1804), MNHN J02192 (Cossmann coll.), Hérouval, Oise, France, Lutetian, in ventral (A_1) and dorsal (A_2) views. **B**. *Ampullina parisiensis* (d'Orbigny, 1850), MNHN A30403 (MNHN coll.), Villiers-Saint-Frédéric, Yvelines, France, Lutetian, in dorsal view. **C**. *Ampullina parisiensis* (d'Orbigny, 1850), MNHN B58545 (Lhomme coll.), Chavençon (La Tranchée), Oise, France, Priabonian, in abapertural (C_1) and ventral (C2) views. **D**. *Ampullina rustica* (Deshayes, 1864), MNHN A30414 (Ledon coll.), Douains, Eure, France, Lutetian, in apical (D_1) and dorsal (D_2) views. **E**. *Ampullina grossa* (Deshayes, 1864), MNHN B58581 (MNHN coll.), Mont-Saint-Martin, Aisne, France, Bartonian (Auversian), in apical view. **F**. *Ampullina chenayensis* Cossmann, 1892, MNHN A31127 (Faullummel coll.), Chenay, Marne, France, Thanetian, in labral (F_1) and dorsal (F_2) views. **G**. *Ampullina aizyensis* (Bayan, 1870), MNHN A30408 (Ledon coll.), Bachivillers, Oise, France, Thanetian, in dorsal view. **H**. *Ampullina aizyensis* (Bayan, 1870), MNHN A30409 (Ledon coll.), Bachivillers, in ventral (H_1) and abapertural (H_2) views. **I**. *Ampullina stampinensis* (Cossmann and Lambert, 1884), syntype of *Natica stampinensis* MNHN J05147 (Lambert coll.), Saint-Hilaire (Pierrefitte), Essonne, France, Rupelian (Stampian), in dorsal view. **J**. *Ampullina perusta* (Defrance in Brongniart, 1823), MNHN A30821 (MNHN coll.), Ronca, Italy, Lutetian, in ventral (J_1) and abapertural (J_2) views. **K**. *Ampullina perusta* (Defrance in Brongniart, 1823), MNHN A30822 (MNHN coll.), Ronca, in dorsal view. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

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cent stripes (Fig. 2I). The transition between the two levels of colouration is diffuse. The stripes are located on the adapical part, median part and adbasal part of the whorl. Their width is almost equal in the youngest specimens, but the median one becomes broader in most adult specimens. Some young specimens display a fourth spiral stripe around the umbilicus on the base of the shell.

Ampullina perusta (Defrance in Brongniart, 1823)

Fig. 2J, K.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (Italy).

Colour pattern description.—The pattern consists of two levels of residual colouration: a pale heterogeneous background with several dark spiral stripes. Sometimes, there is only a group of two or three thin stripes very close to each other, of a variable width (Fig. 2J), on the median part. There is sometimes an additional broad adapical stripe (Fig. K).

Comments.—The residual colours in this species are observable in natural light and are obviously different from those of the other species. This is the result of a different type of preservation of the colour pattern. It is also interesting to note that this pattern appears as the negative of the residual colour pattern on the other shells and that the dark elements in this species correspond to the fluorescent ones in UV light observations.

Ampullina intermedia (Deshayes, 1832)

Fig. 3A–E.

Stratigraphic and geographic range.—Early Eocene, Ypresian (Cuisian) (PB).

Colour pattern description.—The pattern consists of four levels of residual colouration. The background is heterogeneous with three spiral slightly fluorescent stripes, one on the adapical part, one on the median part and one on the adbasal parts of the whorl (Fig. 3A). The apex is pale and there are small fluorescent patches superimposed on the background (Fig. 3A–C). The transition between the levels of colouration of the background is diffuse. The background is homogeneously dark in some specimens (Fig. 3B–E). The small patches of varying size do not have a definite shape and their distribution is irregular (Fig. 3B). The coalescence of the patches sometimes produces fluorescent sinuous axial segments (Fig. 3D, E). This residual colour pattern is very similar to those of *A. merciniensis* (Deshayes, 1864) (Fig. 3F) from the Ypresian (Cuisian) of the Paris Basin and *Ampullina lignitara* (Deshayes, 1864) from the Ypresian (Sparnacian) of the Paris Basin and Hampshire Basin.

Comments.—Former authors (Cossmann 1888; Wrigley 1946; Glibert 1963) considered the three species *Ampullina intermedia* (Deshayes, 1824), *A. lignitara* (Deshayes, 1864) and *Ampullina merciniensis* (Deshayes, 1824) as belonging to the genus *Crommium*. In the original description of the genus, Cossmann (1888) however stated, that the sheath is absent whereas it occurs in each of the three aforementioned species. Thus, *A. intermedia*, *A. lignitara*, and *A. merciniensis* are, here, no longer considered to belong to the genus *Crommium*. Furthermore, these species with closely related

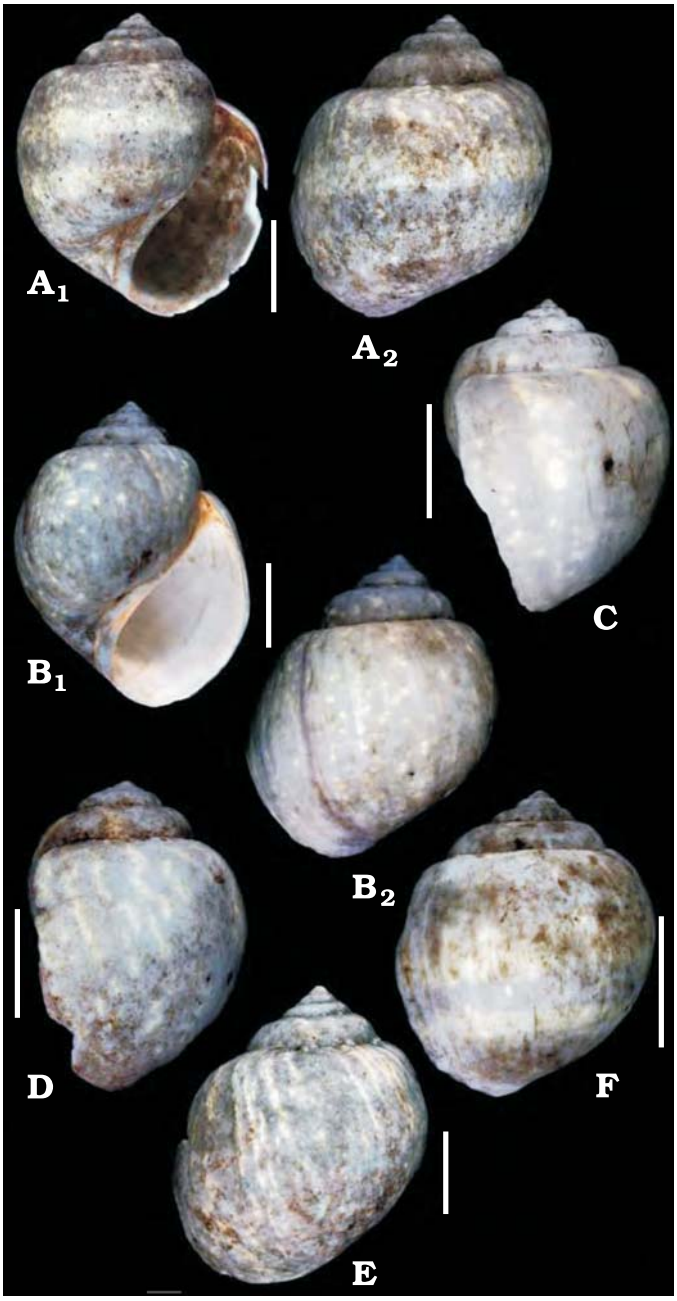

Fig. 3. Species of the genus *Ampullina* Bowdich, 1822, under UV light. **A**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30418 (MNHN coll.), Cuise-la-Motte, Oise, France, Ypresian (Cuisian), in ventral (A_1) and dorsal (A_2) views. **B**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30416 (MNHN coll.), Cuise-la-Motte, in ventral (B_1) and dorsal (B_2) views. **C**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30415 (MNHN coll.), Cuise-la-Motte, in labral view. **D**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30417 (MNHN coll.), Cuise-Lamotte, in labral view. **E**. *Ampullina intermedia* (Deshayes, 1832), MNHN A30422 (d'Orbigny coll.), Cuise-Lamotte, in dorsal view. **F**. *Ampullina merciniensis* (Deshayes, 1864), MNHN J02199 (Cossmann coll.), Mercin-et-Vaulx, Aisne, France, Ypresian (Cuisian), in dorsal view. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

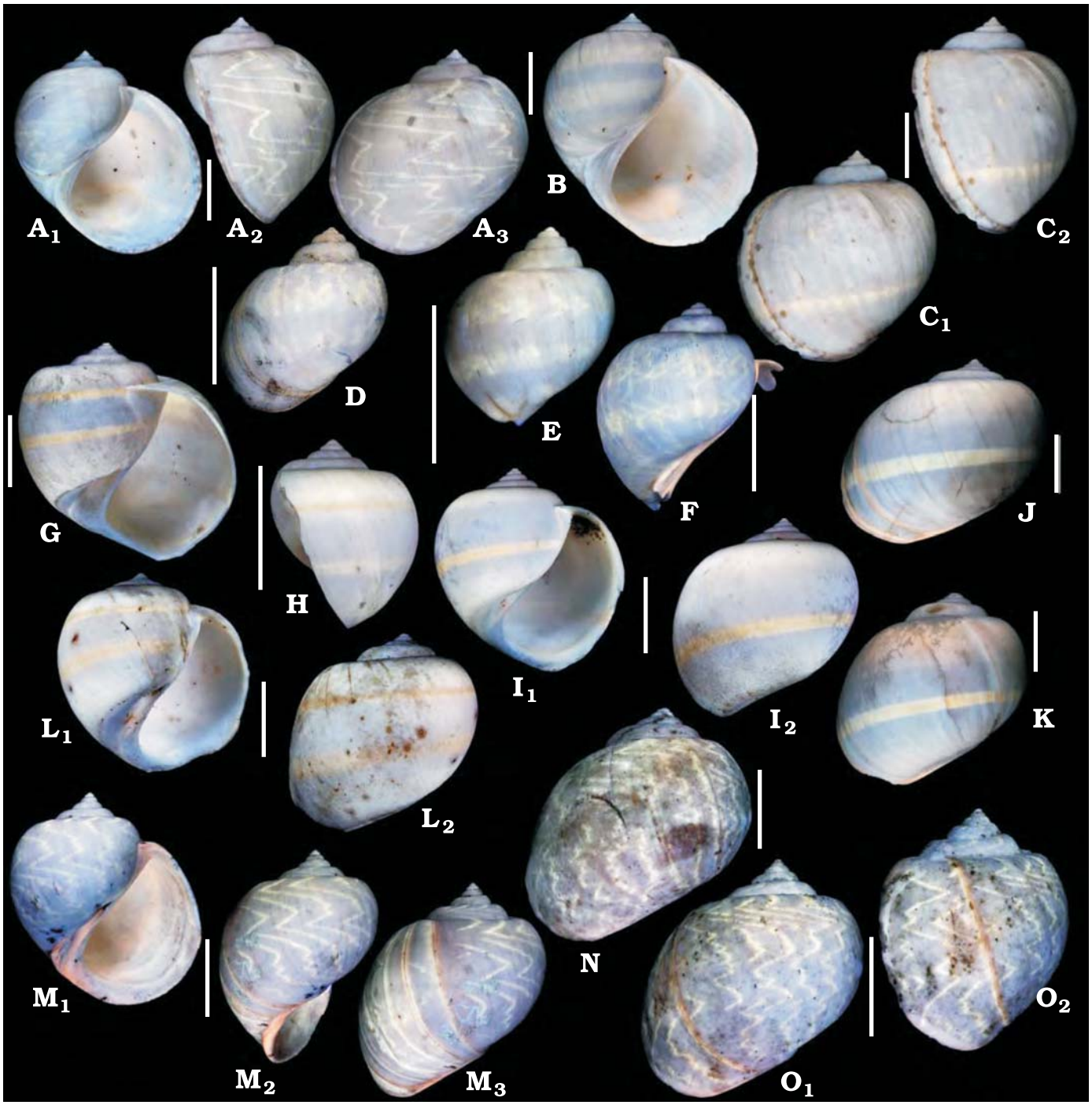

Fig. 4. Species of the genus *Globularia* sensu stricto Swainson, 1840, under UV light. **A**. *Globularia* (s.s.) *sigaretina* (Lamarck, 1804), MNHN A30859 (MNHN coll.), Grignon, Yvelines, France, Lutetian, in ventral (A_1), labral (A_2), and dorsal (A_3) views. **B**. *Globularia sigaretina* (Lamarck, 1804), MNHN A30473 (Lamarck coll.), Parnes (Les Boves), Oise, France, Lutetian, in dorsal view. **C**. *Globularia sigaretina* (Lamarck, 1804), MNHN A30868 (MNHN coll.), Mary-sur-Marne, Seine-et-Marne, France, Bartonian (Auversian), in dorsal (C_1) and labral (C_2) views. **D**. *Globularia berthelini* (Cossmann, 1892), MNHN A30858 (MNHN coll.), Grignon, in dorsal view. **E**. *Globularia berthelini* (Cossmann, 1892), MNHN A30470 (MNHN coll.), Grignon, in dorsal view. **F**. *Globularia berthelini* (Cossmann, 1892), MNHN A30902 (MNHN coll.), Grignon, in abaperural view. **G**. *Globularia patula* (Lamarck, 1804), MNHN A30445 (MNHN coll.), Parnes, Oise, France, Lutetian, in ventral view. **H**. *Globularia patula* (Lamarck, 1804), MNHN A31167 (MNHN coll.), Grignon, in labral view. **I**. *Globularia patula* (Lamarck, 1804), MNHN A31169 (MNHN coll.), Grignon, in ventral (I_1) and dorsal (I_2) views. **J**. *Globularia patula* (Lamarck, 1804), MNHN A30438 (MNHN coll.), Parnes, in dorsal view. **K**. *Globularia patula* (Lamarck, 1804), MNHN A30437 (MNHN coll.), Parnes, in dorsal view. **L**. *Globularia patula* (Lamarck, 1804) MNHN A31168 (MNHN coll.), Grignon, in ventral (L_1) and dorsal (L_2) views. **M**. *Globularia semipatula* (Deshayes, 1864), MNHN A30488 (Faullummel coll.), Cuise-Lamotte, Oise, France, Ypresian (Cuisian), in ventral (M_1), abapertural (M_2), and dorsal (M_3) views. **N**. *Globularia splendida* (Deshayes, 1864), MNHN A30487 (Faullummel coll.), Cuise-Lamotte, in dorsal view. **O**. *Globularia patuloides* (Cossmann and Pissarro, 1902), MNHN A31162 (Faullummel coll.), Le Guépelle, Val d'Oise, France, Bartonian, in dorsal (O_1) and abapertural (O_2) views. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

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shells, display very similar residual patterns. Consequently, our personal opinion is that the discrimination of these three species is probably not justified.

Genus *Globularia* Swainson, 1840

Type species: *Globularia sigaretina* (Lamarck, 1804), Grignon, Lutetian.

Description.—This genus is here considered to comprise three subgenera (*Globularia*, *Deshayesia*, and *Cernina*) with 20 species (16 Palaeogene species, 3 Neogene and one extant; SOM 1). The taxa *Globularia*, *Cernina*, and *Deshayesia* have not always been regarded as congeneric (Wrigley 1946). Nevertheless, the very similar residual colour patterns of 11 of the 15 studied species (zigzagging axial fluorescent stripes; SOM 2; Fig. 4, 5) strengthens the initial impression based on the shell morphology (wide aperture with prosocline outer lip, low spire and expanded sheath delineated by a rim) that they are closely related (Cossmann and Peyrot 1919; Wenz 1941). Thus, thanks to the additional character, all these species are, here, no longer considered to belong to distinct genera but are placed within the genus *Globularia* (senior synonym).

Subgenus *Globularia* Swainson, 1840

Globularia (*Globularia*) *sigaretina* (Lamarck, 1804)

Fig. 4A–C.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (PB, HB).

Colour pattern description.—The shells show four levels of residual colouration. The background is often dark and homogeneous (Fig. 4A, C), but it can be heterogeneous with slightly fluorescent broad spiral stripes (Fig. 4B). The apex is pale and there are fluorescent axial thin zigzagging stripes superimposed on the background (Fig. 4A, C). The transition between the two levels of residual colouration of the background is diffuse. Zigzags occur along the whole height of the stripes and have variable amplitude (Fig. 4A). The density of the zigzags varies with the specimens. One specimen shows an additional fluorescent spiral stripe (Fig. 4C) on the base of the shell. This residual colour pattern is very similar to that of *Globularia* (*G.)* berthelini (Cossmann, 1892) from the Lutetian of the Paris Basin (Fig. 4D–F).

Globularia (*Globularia*) *patula* (Lamarck, 1804)

Fig. 4G–L.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (PB, HB).

Colour pattern description.—The pattern consists of four levels of residual colouration. The background is heterogeneous with two broad slightly fluorescent diffuse spiral stripes on the adapical and adbasal parts of the whorl (Fig. 4I–L). The apex is pale and there are one (Fig. 4I–K) or two (Fig. 4G, H, L) fluorescent sharply delineated spiral stripes superimposed on the background. These two straight fluorescent spiral stripes, superimposed on the dark median "stripe" of the background, are located near its adbasal margin and on its adapical margin. They do not become diffuse through ontogenesis. The adapical one is absent in the shells showing only one stripe (Fig. 4I–K).

Globularia (*Globularia*) *semipatula* (Deshayes, 1864)

Fig. 4M.

Stratigraphic and geographic range.—Late Palaeocene, Thanetian–Middle Eocene, Ypresian (Cuisian) (PB).

Colour pattern description.—This species shows three levels of residual colouration. The background is dark and homogeneous. The apex is pale and there are axial thin fluorescent zigzagging stripes (Fig. 4M). The axial thin stripes present a regular distribution. The zigzags occur along the whole height of the stripes and display variable amplitude. There is intraspecific variability in the number and density of the axial thin stripes. This residual colour pattern is very similar to those of *Globularia* (*G.*) *splendida* (Deshayes, 1864) from the Ypresian of the Paris Basin (Fig. 4N) and *Globularia* (*G.*) *patuloides* (Cossmann, 1902) from the Bartonian of the Paris Basin (Fig. 4O).

Globularia (*Globularia*) *peyreirensis* (Cossmann and Peyrot, 1919)

Fig. 5A.

Stratigraphic and geographic range.—Late Oligocene, Chattian–Early Miocene, Aquitanian (AB).

Colour pattern description.—The shell displays only two levels of residual colouration (apex absent). The background is dark and homogeneous. There are numerous axial fluorescent thin zigzagging stripes (Fig. 5A). The zigzags occur along the whole height of the stripes and have variable amplitude. The thin stripes are not strictly parallel and connect to each other at several points. These connections produce the occurrence of large fluorescent "patches" (Fig. $5A_1$, A_2).

?*Globularia pilula* (Deshayes, 1864)

Fig. 5B, C.

Stratigraphic and geographic range.—Middle Eocene, Lutetian (PB).

Colour pattern description.—The colour pattern consists of three levels of residual colouration: a dark and homogeneous background, a pale apex and some thin fluorescent axial stripes forming zigzags (Fig. $5B_2$, C). The axial thin stripes are not parallel and present an irregular distribution. The zigzags occur along the whole height of the stripes and display variable amplitude. There is intraspecific variability in the density of axial stripes (Fig. $5B_2$, C_2).

Comments.—?*Globularia pilula* has been previously classified in the naticid genus *Euspira.* These shells strongly differ from the type species of the latter genus, *Euspira glaucinoides* (Sowerby, 1812) from the Ypresian of England, in many characters (moderately high and acuminate spire, sutural step, minute umbilicus with no sheath and narrow reflected columellar edge). Furthermore, the colour pattern differs from

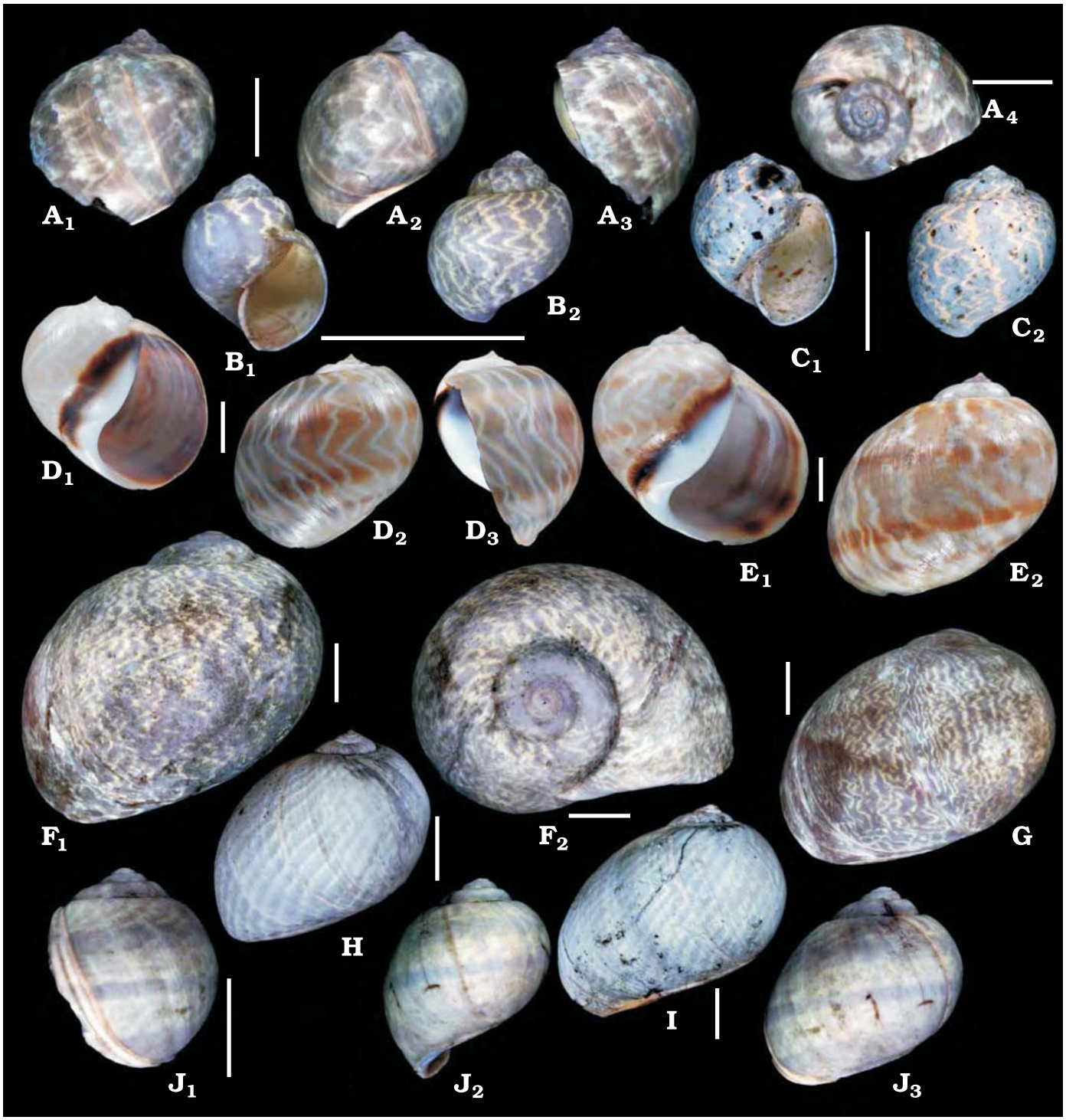

Fig. 5. Species of the genus *Globularia* Swainson, 1840, under UV light. **A**. *Globularia* (*Globularia*) *peyreirensis* (Cossmann and Peyrot, 1919), MNHN Cossmann (A30480 coll.), Peyreire, Gironde; France, Chattian, in dorsal (A_1), abapertural (A_2), labral (A_3), and apical (A_4) views. **B**. ?*Globularia* (*Globularia*) *pilula* (Deshayes, 1864), MNHN J02181 (Cossmann coll.), Villiers-Saint-Frédéric, Yvelines, France, Lutetian, in ventral (B_1) and dorsal (B_2) views. **C**. ?*Globularia* (*Globularia*) *pilula* (Deshayes, 1864), MNHN A30398 (MNHN coll.), Grignon, Yvelines, France, Lutetian, in ventral (C_1) and dorsal (C_2) views. **D**. *Globularia* (*Cernina*) *fluctuata* (Sowerby, 1825), MNHN IM (Staadt coll.), Banggi Island, Kudat division of Sabah, Malaysia, Recent, in ventral (D_1), dorsal (D_2), and labral (D_3) views. **E**. *Globularia* (*Cernina*) *fluctuata* (Sowerby, 1825), MNHN IM (MNHN coll.), Philippines, Recent, in ventral (E_1) and dorsal (E_2) views. **F**. *Globularia* (*Cernina*) *compressa* (Basterot, 1825), MNHN A30399 (MNHN coll.), Mérignac, Gironde, France, Aquitanian, in dorsal (F_1) and apical (F_2) views. **G**. *Globularia* (*Cernina*) *compressa* (Basterot, 1825), MNHN A30400 (MNHN coll.), Mérignac, in dorsal view. **H**. *Globularia* (*Cernina*) sp., MNHN A30459 (Varone coll.), Saint-Martin-d'Oney, Landes, France, Aquitanian, in dorsal view. **I**. *Globularia* (*Cernina*) sp., MNHN A30460 (Varone coll.), Saint-Martin-d'Oney, in dorsal view. **J**. *Globularia* (*Deshayesia*) *parisiensis* (Raulin, 1844), MNHN A30892 (Cossmann coll.), Morigny (Château de Brunehaut), Essonne, France, Rupelian (Stampian), in labral (J_1), abapertural (J_2) and dorsal (J_3) views. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

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those of the fossil naticid shells by converging stripes and numerous zigzags with very variable amplitude as observed in the characteristic colour pattern of genus *Globularia*. Thus, this species is, here, excluded from *Euspira* and is placed within the family Ampullinidae, but only questionably placed in the genus *Globularia*, because of its lack of a sheath.

Subgenus *Cernina* Gray, 1842

Type species: *Natica fluctuata* Sowerby, 1825, Philippines, Recent.

Globularia (*Cernina*) *fluctuata* (Sowerby, 1825)

Fig. 5D, E.

Stratigraphic and geographic range.—Recent (Philippines).

Colour pattern description.—The pattern consists of four levels of colouration. The background is heterogeneous with broad spiral brown stripes. There are four brown stripes on the last whorl (Fig. 5D_2, D_3, E_2): (i) one on the adapical part, (ii) one near the base, and (iii–iv) two stripes, slightly broader, on the median part. The apex is pale and there are white thin axial zigzagging stripes. The transition between the two levels of the background is diffuse. The axial zigzagging stripes are more or less parallel and present an irregular distribution on the shell. Some of these stop on the median part of the whorl (Fig. 5D_2, E_2). The amplitude of the zigzags varies. There is intraspecific variability in the number and density of the axial stripes.

Comment.—The brown (darker) stripes correspond to the fluorescent (paler) stripes revealed under UV light in the fossil shells and the white axial zigzagging stripes are here considered to correspond to the fluorescent zigzagging stripes.

Globularia (*Cernina*) *compressa* (Basterot, 1825)

Fig. 5F, G.

Stratigraphic and geographic range.—Early Miocene, Aquitanian and Burdigalian–Middle Miocene, Langhian (AB, Italy).

Colour pattern description.—This species shows two levels of residual colouration (apex absent). The background is dark and homogeneous. There are thin axial fluorescent stripes. The thin axial stripes are very close to each other, but not parallel and form small zigzags (Fig. 5F_1, G). Their distribution on the shell is variable (Fig. 5G) and the zigzags display variable amplitude. The stripes sometimes branch in a dichotomous manner (Fig. 5F_2).

Globularia (*Cernina*) sp.

Fig. 5H, I.

Stratigraphic and geographic range.—Early Miocene, Aquitanian (AB).

Colour pattern description.—These shells show two levels of residual colouration (apex absent): a dark and homogeneous background and opisthocline thin fluorescent stripes (Fig. 5H, I). These opisthocline stripes are very close to each other, parallel and present a regular distribution. Their thickness is constant on the shell and they are barely sinuous.

Comments.—All three specimens from Saint-Martin-d'Oney (France, AB) display the characteristic morphology of *Globularia* (*Cernina*) *compressa* but the coloured pattern differs by the presence of opisthoclines, barely sinuous, thin stripes instead of axial zigzagging stripes (Fig. 5F, G). In our view, these differences do not result from intraspecific variability and justify these shells as belonging to a species other than *G.* (*C.*) *compressa*.

Subgenus *Deshayesia* Raulin, 1844

Type species: *Deshayesia parisiensis* Raulin, 1844, Morigny, Rupelian (Stampian).

Globularia (*Deshayesia*) *parisiensis* (Raulin, 1844)

Fig. 5J.

Stratigraphic and geographic range.—Early Oligocene, Rupelian (PB).

Colour pattern description.—The shells show three levels of residual colouration (apex absent). The background is heterogeneous with three broad spiral slightly fluorescent stripes and there are some axial and fluorescent thin zigzagging stripes. The spiral stripes are located (i) on the subsutural part, (ii) near the base, and (iii) on the median part. The transition between the two levels of colouration of the background is diffuse. The thin axial zigzagging stripes are superimposed on the background (Fig. 5J_1, J_3). The thin axial stripes connect each other in several points and their distribution on the shell is regular. The zigzags present variable amplitude.

Genus *Crommium* Cossmann, 1888

Fig. 6.

Type species: *Ampullaria willemeti* Deshayes, 1825 (= *A. acutum* Lamarck, 1804), Courtagnon, Grignon, Lutetian.

Description.—The genus *Crommium* comprises 6 exclusively Palaeogene species (SOM 1). Of the 4 species (SOM 2) observed under UV light 2 display the same very simple morphology of the colour pattern with a fluorescent more or less wide area covering the adapical part (Fig. 6).

Crommium acutum (Lamarck, 1804)

Fig. 6A–C.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (PB, HB)

Colour pattern description.—The shells show three levels of residual colouration. The background is heterogeneous with a fluorescent area covering the apical part of the whorl (Fig. 6A, B) (except a thin zone just below the suture). The apex is pale. The transition between the two levels of colouration of the background is diffuse. There is sometimes a second fluorescent diffuse area on the base of the shell. These fluorescent areas cover a smaller or larger part of the whorl. The largest specimens show an entirely fluorescent last whorl (except the subsutural part). The young specimens display three or four thin spiral fluorescent stripes: one on the shoul-

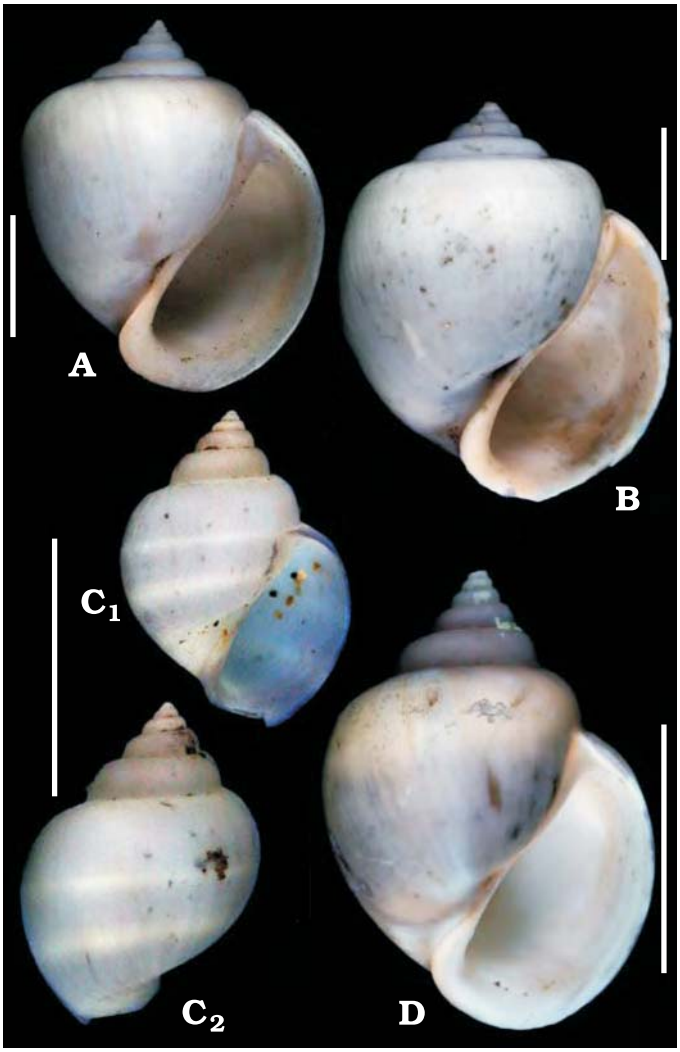

Fig. 6. Species of the genus *Crommium* Cossmann, 1888, under UV light. **A**. *Crommium acutum* (d'Orbigny, 1850), MNHN B58618 (MNHN coll.), Parnes, Oise, France, Lutetian, in ventral view. **B**. *Crommium acutum* (d'Orbigny, 1850), MNHN A30889 (MNHN coll.), Boursault, Marne, France, Lutetian, in ventral view. **C**. *Crommium acutum* (d'Orbigny, 1850), MNHN A30861 (MNHN coll.), Fleury-la-rivière, Marne, France, Lutetian, in ventral (C_1) and dorsal (C_2) views. **D**. *Crommium grignonensis* (d'Orbigny, 1850), type of *Natica heberti* Deshayes, 1864, MNHN J04185 (Hébert coll.), Chaumont-en-Vexin, Oise, France, Lutetian, in ventral view. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

der, one on the base (but often lacking) and two on the median part of the whorl (Fig. 6C). The two median stripes fade with growth until they disappear. The adapical one and the basal one, when present, gradually spread on the whorl.

Crommium grignonensis (d'Orbigny, 1850)

Fig. 6D.

Stratigraphic and geographic range.—Middle Eocene, Lutetian (PB)

Colour pattern description.—This species exhibits three levels of residual colouration. The background is heterogeneous with a slightly fluorescent apical part (Fig. 6D). The transition between the two levels of the background is diffuse.

Genus *Amaurellina* Bayle in Fischer, 1885

Type species: *Amaurellina spirata* Lamarck, 1804, Grignon, Lutetian.

Description.—Worldwide, this genus comprises 8 species in the Cainozoic (SOM 1). 5 of the 6 studied species (SOM 2) display the same simple organisation of residual colouration with one or several fluorescent spiral stripes on a darker background.

Amaurellina spirata Lamarck, 1804

Fig. 7A–C.

Stratigraphic and geographic range.—Middle Eocene, Lutetian (PB, Cotentin)

Colour pattern description.—This species shows three levels of residual colouration. The background is heterogeneous with an almost completely dark whorl except the slightly fluorescent shoulder that forms a spiral stripe (Fig. 7A–C). The apex is pale (Fig. 7A–C). The fluorescent stripe covering the subcarinate shoulder is straight and has a constant width (Fig. $7A_1$, C). This stripe is sometimes also observable on the penultimate whorl (Fig. 7C). The transition between this stripe and the darker colouration of the whorl is diffuse. The base of the whorl can be slightly fluorescent too.

Amaurellina levesquei (d'Orbigny, 1850)

Fig. 7D–F.

Stratigraphic and geographic range.—Early Eocene, Ypresian (Cuisian) (PB)

Colour pattern description.—The shells show two levels of residual colouration: a heterogeneous background with a slightly fluorescent area covering the major part of the shell (apex, spire, last whorl) except two dark "stripes". The adapical one is on the median part of the whorl and is thinner than the other one located on the base of the shell (Fig. 7D, E). On a few well-preserved shells, some slightly fluorescent axial stripes are distinguishable (Fig. 7F). These axial stripes, especially distinguishable on the spire, are slightly prosocline.

Amaurellina sinuosa (d'Orbigny, 1850)

Fig. 7G–I.

Stratigraphic and geographic range.—Early Eocene, Ypresian (Cuisian) (PB).

Colour pattern description.—The residual pattern consists of three levels of residual colouration. The background is heterogeneous with thin fluorescent spiral stripes and the apex is pale. There are two straight stripes and the adapical one is sometimes distinguishable on the penultimate whorl (Fig. $7G_2$, I). Both stripes have constant and similar width.

Amaurellina paludiniformis (d'Orbigny, 1850)

Fig. 7J–K.

Stratigraphic and geographic range.—Early–Middle Eocene, Ypresian (Cuisian)–Lutetian (PB, HB).

Colour pattern description.—The residual pattern consists of three levels of residual colouration. The background is dark and homogeneous, the apex is pale and there are four straight

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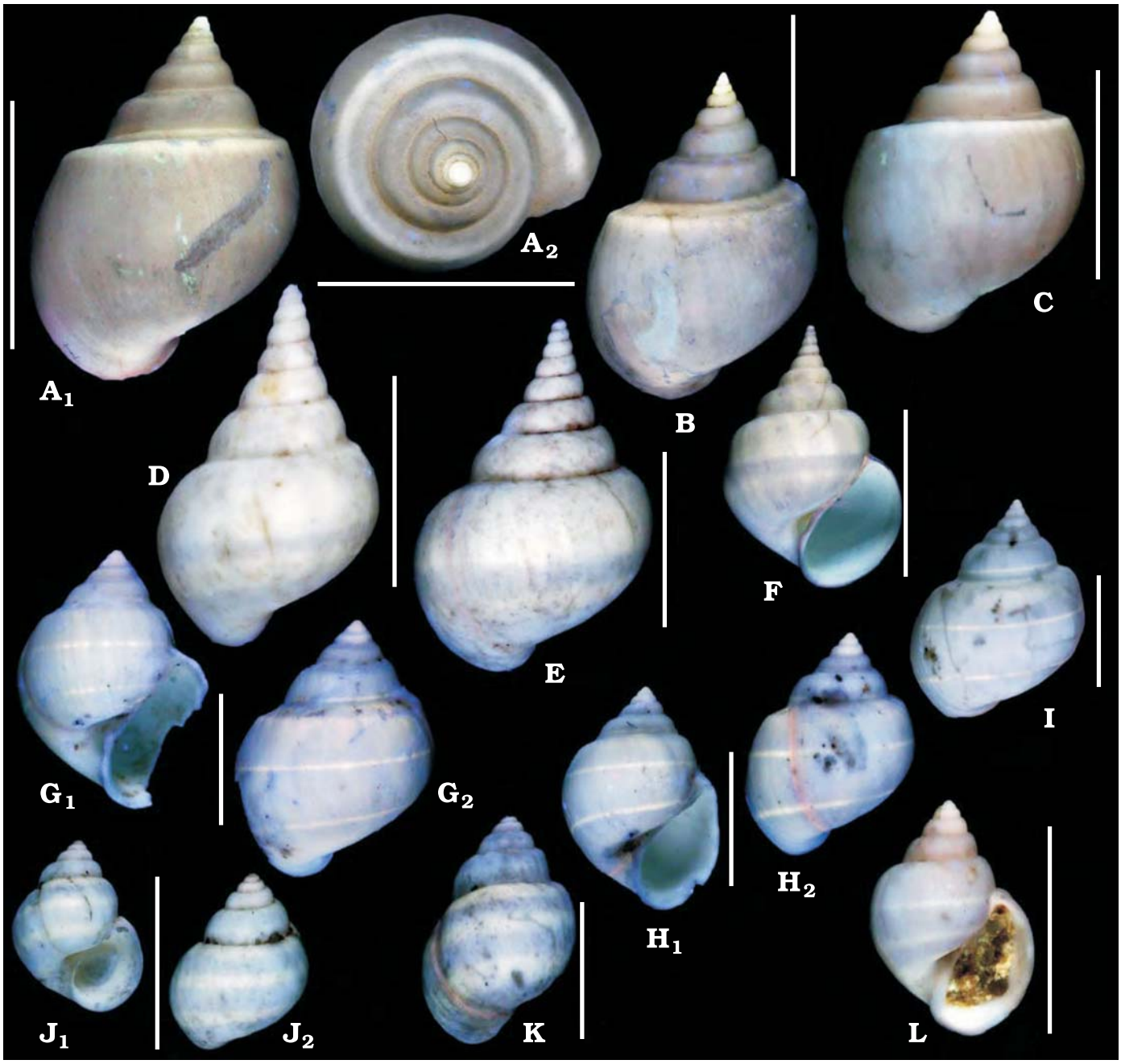

Fig. 7. Species of the genus *Amaurellina* Bayle in Fischer, 1840, under UV light. **A**. *Amaurellina spirata* (Lamarck, 1804), MNHN A30484 (MNHN coll.), Grignon, Yvelines, France, Lutetian, in dorsal (A_1) and apical (A_2) views. **B**. *Amaurellina spirata* (Lamarck, 1804), MNHN A30884 (Faullummel coll.), Fontenay-en-Vexin, Eure, France, Lutetian, in dorsal view. **C**. *Amaurellina spirata* (Lamarck, 1804), MNHN A30485 (MNHN coll.), Grignon, in dorsal view. **D**. *Amaurellina levesquei* (d'Orbigny, 1850), MNHN A30879 (Faullummel coll.), Monampteuil, Aisne, France, Ypresian (Cuisian), in dorsal view. **E**. *Amaurellina levesquei* (d'Orbigny, 1850), MNHN A30878 (Faullummel coll.), Monampteuil, in dorsal view. **F**. *Amaurellina levesquei* (d'Orbigny, 1850), MNHN A30948 (MNHN coll.), Cuise-Lamotte, Oise, France, Ypresian (Cuisian), in dorsal view. **G**. *Amaurellina sinuosa* (d'Orbigny, 1850), MNHN A30432 (Faullummel coll.), Saint-Gobain, Aisne, France, Ypresian (Cuisian), in ventral (G_1) and dorsal (G_2) views. **H**. *Amaurellina sinuosa* (d'Orbigny, 1850), MNHN A30431 (Faullummel coll.), Saint-Gobain, in ventral (H_1) and dorsal (H_2) views. **I**. *Amaurellina sinuosa* (d'Orbigny, 1850), MNHN A30887 (Faullummel coll.), Saint-Gobain, in dorsal view. **J**. *Amaurellina paludiniformis* (d'Orbigny, 1850), MNHN A30490 (Faullummel coll.), Saint-Gobain, in ventral (J_1) and dorsal (J_2) views. **K**. *Amaurellina paludiniformis* (d'Orbigny, 1850), MNHN A30492 (Faullummel coll.), Saint-Gobain, in dorsal view. **L**. *Amaurellina tuba* (Deshayes, 1864), MNHN J02215 (Cossmann coll.), Hermonville, Marne, France, Lutetian, in ventral view. Scale bars 10 mm (A–C), 5 mm (D–L). Photographs by C. Lemzaouda and P. Loubry (MNHN).

fluorescent spiral stripes (Fig. $7J_1$): one is located on the subsutural part of the whorl, one is on the base, circling the umbilicus, and two are on the median part. These stripes present a similar and constant width and are slightly thinner than the space between. The two adapical stripes are sometimes distinguishable on the penultimate whorl. This residual colour

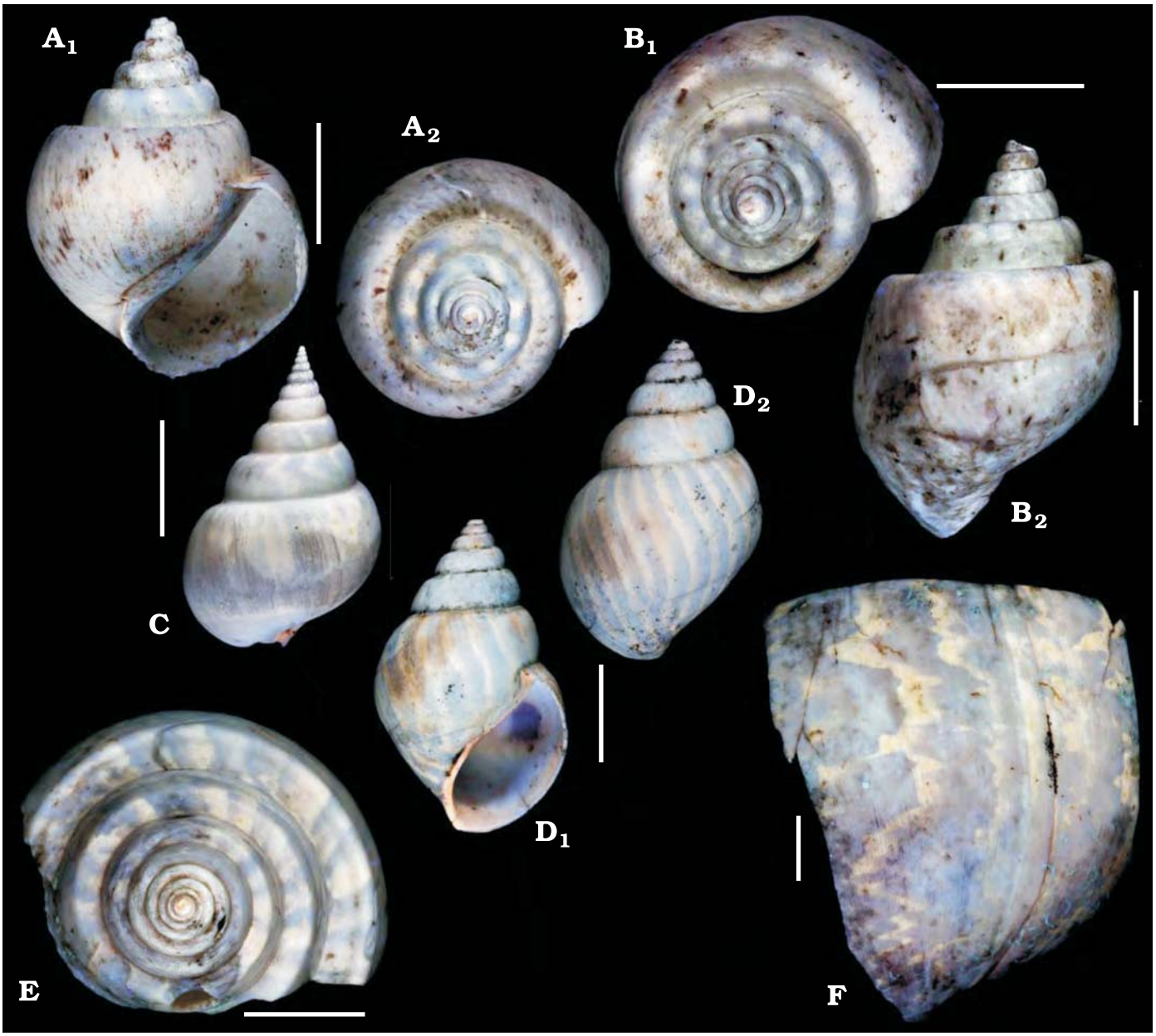

Fig. 8. Species of the genus *Pachycrommium* Woodring, 1928, under UV light. **A**. *Pachycrommium suessoniensis* (d'Orbigny, 1850), MNHN A30881 (Pacaud coll.), Celles-sur-Aisne, Aisne, France, Ypresian (Cuisian), in ventral (A_1) and apical (A_2) views. **B**. *Pachycrommium suessoniensis* (d'Orbigny, 1850), MNHN A30882 (Pacaud coll.), Celles-sur-Aisne, in apical (B_1) and dorsal (B_2) views. **C**. *Pachycrommium productum* (Deshayes, 1864), MNHN A30945 (Pacaud coll.), Chaussy, Val d'Oise, France, Lutetian, in dorsal view. **D**. *Pachycrommium* sp., MNHN A30482 (Pacaud coll.), Monampteuil, Aisne, France, Ypresian (Cuisian), in ventral (D_1) and dorsal (D_2) views. **E**. *Pachycrommium scalariformis* (Deshayes, 1825), MNHN A30401 (Ledon leg.), Fontenay-en-Vexin, Lutetian, in apical view. **F**. *Pachycrommium scalariformis* (Deshayes, 1825), MNHN A30402 (Ledon leg.), Fontenay-en-Vexin, view of a shell fragment. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

pattern is very similar to that of *Amaurellina tuba* (Deshayes, 1864) from the Lutetian of the Paris Basin (Fig. 7L).

Genus *Pachycrommium* Woodring, 1928

Type species: *Amaura guppyi* Gabb, 1873, Dominican Republic, Miocene.

Description.—Among the 8 Cainozoic species in the genus *Pachycrommium* known worldwide (with one present in the Neogene; SOM 1), 7 have been examined (SOM 2). All the species reveal some fluorescent axial, or opisthocline for *Pachycrommium acuminatum* (Lamarck, 1804), stripes or segments on a darker background (Figs. 8, 9).

Pachycrommium suessoniensis (d'Orbigny, 1850)

Fig. 8A, B.

Stratigraphic and geographic range.—Early Eocene, Ypresian (Cuisian) (PB)

Colour pattern description.—The pattern consists of three

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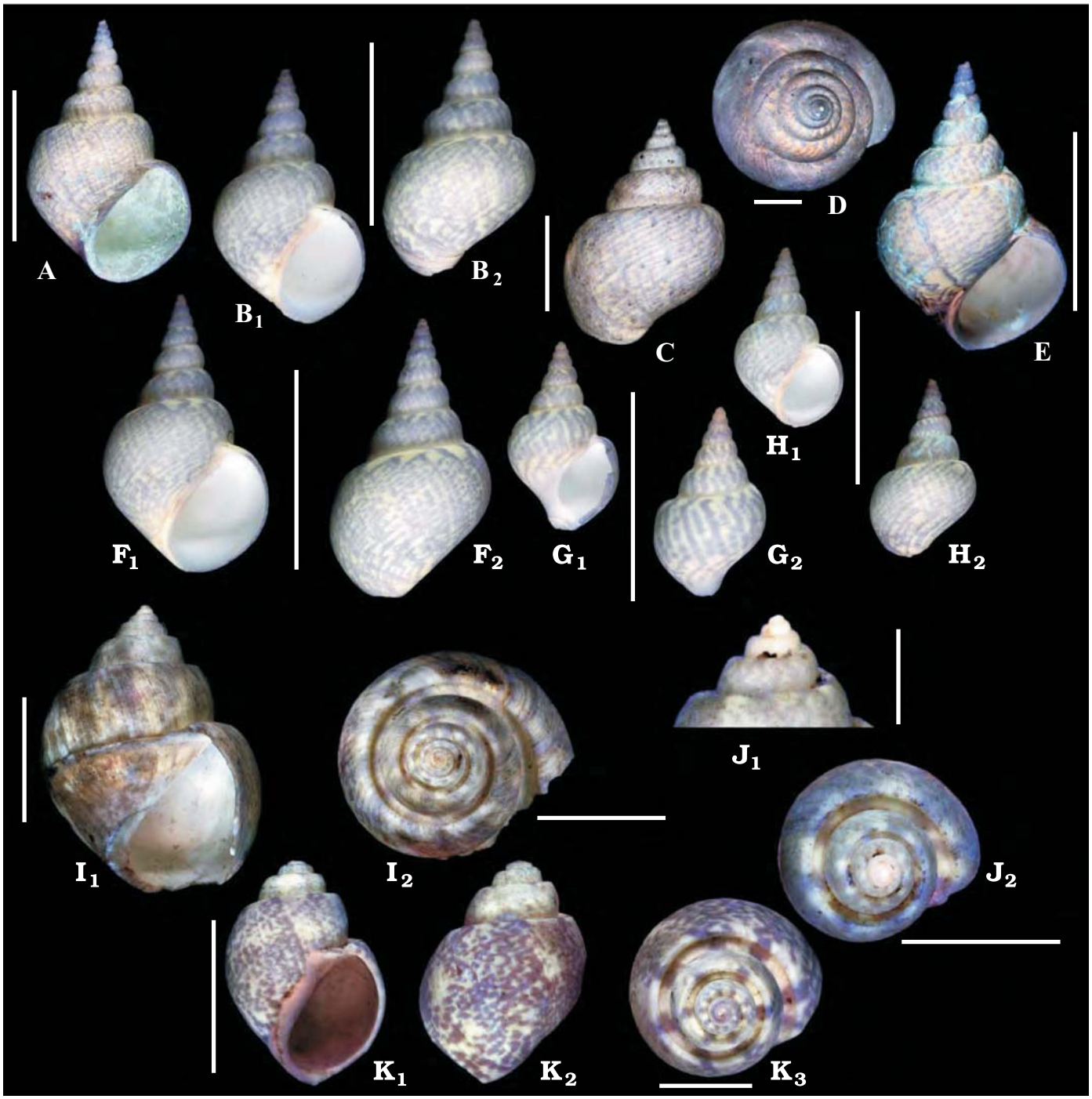

Fig. 9. Species of the genus *Pachycrommium* Woodring, 1928, under UV light. **A**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A30476 (Faullummel coll.), Chaussy, Val d'Oise, France, Lutetian, in ventral view. **B**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A30874 (Faullummel coll.), Fontenay-en-Vexin, Eure, France, Lutetian, in ventral (B_1) and dorsal (B_2) views. **C**. *Pachycrommium acuminatum*, MNHN A25003 (Faullummel coll.), Chaussy, in dorsal view. **D**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A25004 (Faullummel coll.), Villiers-Saint-Frédéric, Yvelines, France, Lutetian, in apical view. **E**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A30479 (Faullummel coll.), Chaussy, in ventral view. **F**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A30875 (Faullummel coll.), Fontenay-en-Vexin, in ventral (F_1) and dorsal (F_2) views. **G**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A30872 (Faullummel coll.), Fontenay-en-Vexin, in ventral (G_1) and dorsal (G_2) views. **H**. *Pachycrommium acuminatum* (Lamarck, 1804), MNHN A30873 (Faullummel coll.), Fontenay-en-Vexin, in ventral (H_1) and dorsal (H_2) views. **I**. *Pachycrommium eburnoides* (Grateloup, 1847), MNHN A30405 (Faullummel coll.), Saint-Paul-lès-Dax, Landes, France, Burdigalian, in ventral (I_1) and apical (I_2) views. **J**. *Pachycrommium eburnoides* (Grateloup, 1847), MNHN A30411 (Cossman coll.), Dax, Landes, France, Early Miocene, in detailed view of the first whorls (J_1) and apical (J_2) view. **K**. *Pachycrommium eburnoides* (Grateloup, 1847), MNHN A30410 (Cossmann coll.), Dax, in ventral (K_1), dorsal (K_2), and apical (K_3) views. Scale bars for all 10 mm, except 5 mm (I_3, J_2), 2 mm (J_1). Photographs by C. Lemzaouda and P. Loubry (MNHN).

levels of residual colouration. The background is dark and homogeneous, the apical whorls appear paler than the rest of the spire but are rarely preserved and there are some axial fluorescent stripes (Fig. 8A, B). The axial stripes, straight to sinuous and slightly prosocline (Fig. 8A_1, B_2), are only observable on the spire. The width of the stripes is equivalent to that of their interspaces and their distribution is regular. This residual colour pattern is very similar to those of *Pachycrommium productum* (Deshayes, 1864) from the Lutetian of the Paris Basin (Fig. 8C), *Pachycrommium* sp. from the Ypresian of the Paris Basin (Fig. 8D) and *Pachycrommium hybridum* (Lamarck, 1804) from the Bartonian (Auversian) of the Paris Basin.

Pachycrommium scalariformis (Deshayes, 1825)

Fig. 8E, F.

Stratigraphic and geographic range.—Middle Eocene, Lutetian (PB, HB).

Colour pattern description.—The colour pattern consists of a dark and homogeneous background and broad axial slightly fluorescent stripes (Fig. 8E, F). These stripes appear straight on the spire but present saw-tooth edges. They actually form zigzags spreading over the whole height of the whorl. Their width is not constant (Fig. 8F).

Pachycrommium acuminatum (Lamarck, 1804)

Fig. 9A–H.

Stratigraphic and geographic range.—Middle Eocene, Lutetian (PB).

Colour pattern description.—This species show three levels of residual colouration: a dark and homogeneous background, a pale apex and fluorescent rows of small axial coalescent segments. These fluorescent and thin segments very close to each other form small zigzags and are more or less elongated. Their width is not constant (Fig. 9B_2, F_2, G_2). The coalescence produces, on the subsutural step, broad triangular fluorescent patches. The segments are often opisthocline and the frequency of the zigzags varies among individuals (Fig. 9B_2, C, G_2, H_2).

Pachycrommium eburnoides (Grateloup, 1847)

Fig. 9I–K.

Stratigraphic and geographic range.—Oligocene, Chattian–Miocene, Burdigalian (AB).

Colour pattern description.—The pattern consists of three levels of residual colouration. The background is dark and homogeneous, the apex is pale and there are broad axial fluorescent stripes (Fig. 9I, J, K_3). The stripes are broader than the interspaces and their width increases with growth (Fig. 9I_2). Their distribution is regular and they may be straight (Fig. 9I_1) or sinuous (Fig. 9J_1). Some specimens from Dax (Fig. 9J, K) display an additional level of colouration: some patches much darker than the background, more or less axially compressed, with irregular distribution and often coalescent (Fig. 9J_2, K).

Ampullinid-like gastropods of uncertain affinity

Genus *Ampullonatica* Sacco, 1890

Type species: *Ampullaria ambulacrum* Sowerby, 1822, Barton, Bartonian.

Description.—No residual colour pattern is observed under UV light.

Remarks.—This genus comprises 5 worldwide Cainozoic species (SOM 1). Two of the studied species of *Ampullonatica*, *A. ambulacrum* (Sowerby, 1822), and *A. brongniarti* (Deshayes, 1864) from the Bartonian of England and France (HB, PB; SOM 2), are characterised by an acuminate and moderately high spire turreted by a deeply canaliculated suture, a large and deep umbilicus with an undistinguishable sheath and a thin and narrow columellar edge. This shell morphology is similar to the shell morphology of the enigmatic taxon *Amauropsina*.

?*Ampullonatica gouberti* (Deshayes, 1864), described on the basis of a unique specimen from the Bartonian of France, displays unusual shell morphology (very strong shoulder, very low spire) and might be a teratological specimen of an already known species (e.g., *Ampullina parisisiensis*).

Genus *Amauropsina* Bayle in Chelot, 1885

Type species: *Ampullaria canaliculata* Lamarck, 1804, Grignon, Lutetian.

Description.—The two Palaeogene species of this genus (SOM 1, 2) display various morphologies of the colour pattern varying from fluorescent patches more or less regularly positioned on a darker background to axial fluorescent segments formed by coalescence of these patches.

Remarks.—The morphology of the species of *Amauropsina* (elevated and acuminate spire, large umbilicus without sheath, narrow columellar edge somewhat reflected and, in the type species a narrowly canaliculated suture) is not representative of the Naticidae. This rather resembles the shell morphology of the ampullinid genus *Ampullonatica* (no residual pattern under UV light). However, the colour pattern of *A. arenularia* is similar to that revealed in Eocene naticids (Le Meur 2009) and that of *A. canaliculata* displays sparse small fluorescent patches, unknown from other naticids and even from other ampullinids. Interpretations of the systematic affinity of this genus derived from shell morphology and colour pattern data differ and so the genus *Amauropsina* remains an enigmatic taxon.

Amauropsina canaliculata (Lamarck, 1804)

Fig. 10A–D.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (Auversian) (PB, HB).

Colour pattern description.—The pattern consists of three levels of residual colouration: a dark and homogeneous background, a pale apex and small fluorescent patches (Fig. 10A–C). The small patches are of variable size and shape and present an irregular distribution (Fig. 10B_1, C). There is

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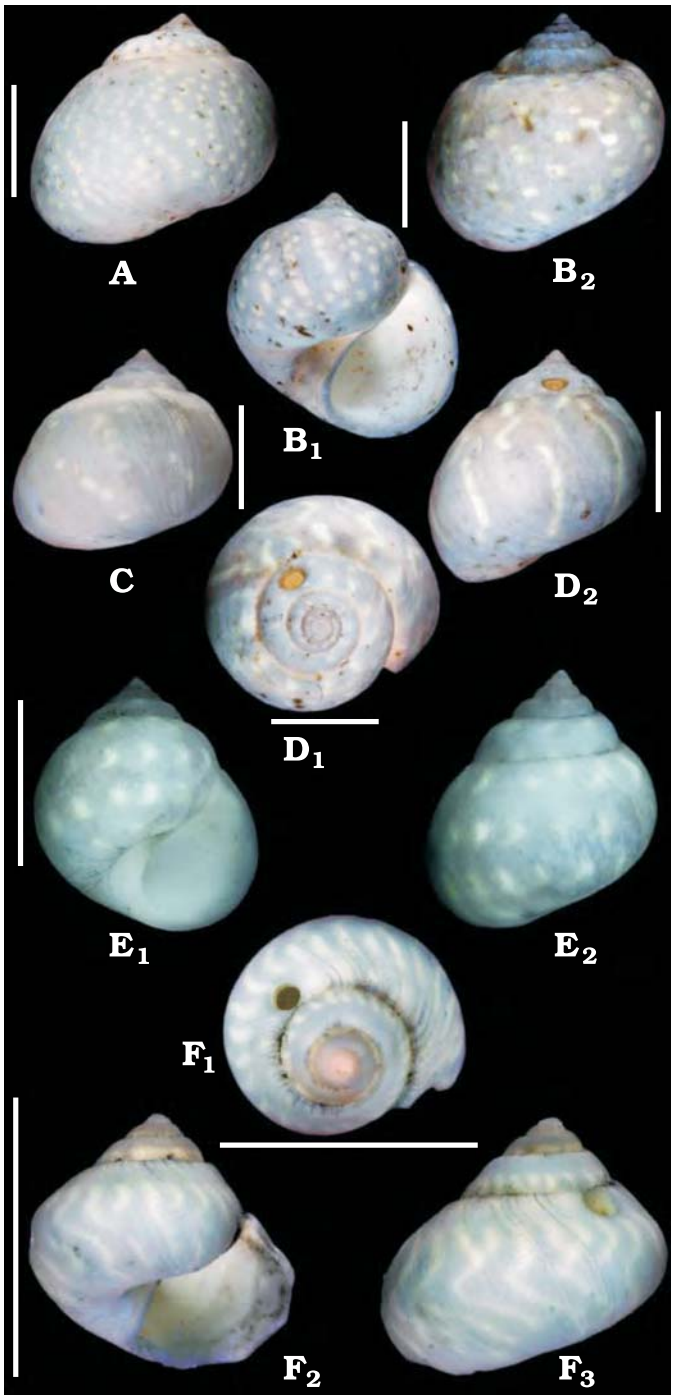

Fig. 10. Species of the genus *Amauropsina* Bayle in Chelot, 1885, under UV light. **A**. *Amauropsina canaliculata* (Lamarck, 1804), MNHN A30469 (MNHN coll.), Grignon, Yvelines, France, Lutetian, in dorsal view. **B**. *Amauropsina canaliculata* (Lamarck, 1804), MNHN A30468 (MNHN coll.), Grignon in ventral (B_1) and dorsal (B_2) views. **C**. *Amauropsina canaliculata* (Lamarck, 1804), MNHN J02165 (Cossmann coll.), Grignon, in dorsal view. **D**. *Amauropsina canaliculata* (Lamarck, 1804), MNHN A30467 (MNHN coll.), Grignon, in apical (D_1) and dorsal (D_2) views. **E**. *Amauropsina arenularia* (Vasseur, 1882), MNHN A30465, Villliers-Saint-Frédéric, Yvelines, France, Lutetian, in ventral (E_1) and dorsal (E_2) views. **F**. *Amauropsina arenularia* (Vasseur, 1882), MNHN A30471 (Vaquez coll.), Saffré (Bois-Gouët), Loire-Atlantique, France, Bartonian, in apical (F_1), ventral (F_2), and dorsal (F_3) views. Scale bars 10 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

intraspecific variability in the density and coalescence of the patches. The coalescence sometimes produces fluorescent sinuous axial segments (Fig. 10D).

Amauropsina arenularia (Vasseur, 1882)

Fig. 10E, F.

Stratigraphic and geographic range.—Middle Eocene, Lutetian–Bartonian (PB, Loire-Atlantique).

Colour pattern description.—This species exhibits three levels of residual colouration. The background is dark and homogeneous. The apex is pale and there are three spiral rows of fluorescent patches. The patches are variable in shape and they are axially and spirally aligned (Fig. 10E). A specimen from Saffré (Loire-Atlantique) displays some sinuous axial segments (Fig. 10F). Depending on the part of the shell, there may be only axial elongated sinuous segments or alternating elongated and short straight segments (Fig. $10F_2$). In the latter case the two types of segments are sometimes connected (Fig. $10F_3$).

Discussion

Classification of the ampullinid colour patterns.—The different residual colour patterns can be organised into four distinct classes, each containing possible homologues in regard to the modalities of pigments incorporation during shell growth:

– one to three spiral stripes or a wide fluorescent diffuse area (colour zonation of the background);
– axial fluorescent zigzagging stripes;
– axial, sometimes opisthocline, straight or slightly sinuous stripes or segments;
– fluorescent patches sometimes forming axial segments through coalescence.

Class I contains the most common patterns (Figs. 2–7) within the Ampullinidae and occurs in most of the genera except *Pachycrommium* (Figs. 8, 9). The survey of a large number of specimens, particularly in the genera *Ampullina* and *Crommium*, shows that spiral stripes can diffuse and spread through ontogenesis, thus forming a wide diffuse area. We therefore include these two colour patterns in Class I. We believe that they both result from variation of the background colouration.

The three other Classes: II (*Globularia* including the extant species), III (*Pachycrommium*), and IV (three species of *Ampullina*) are easily distinguishable and occur less commonly within the Ampullinidae.

Taxonomic implications of the patterns.—Class I: The residual patterns of this class are very common within the Ampullinidae and also in numerous superfamilies of gastropods (e.g., Caenogastropods: Naticoidea, Cerithioidea, Littorinoidea, Muricoidea, Triphoroidea, Epitonioidea, Conoidea; Heterobranchia: Pyramidelloidea). They also occur in the Recent terrestrial Ampullarioidea, that have very similar overall

shell morphology. As a corollary we regard them as general within the Ampullinidae and, whether plesiomorphic or resulting from convergence, they do not appear to be systematically informative. Consequently, in this case, the residual patterns of the Class I do not reliably discriminate ampullinid gastropods from naticids, although this pattern morphology is rarely encountered in fossil Naticidae (Le Meur 2009). Some species, e.g., *Globularia* (*G.*) *patula* (Lamarck, 1804) and *Amaurellina sinuosa* (d'Orbigny, 1850), display sharply delineated spiral stripes, which never diffuse with growth. Thus, these peculiar stripes do not appear as a result from variation of the background. They might be real elements of pattern, as in the Recent helicid land snail *Cepaea nemoralis* (Linnaeus, 1758). In this case, there would be a transition from background variation to real elements of patterns in the genera *Globularia* and *Amaurellina*.

Class II: All the species of *Globularia*, excepting *Globularia* (*G.*) *patula*, reveal patterns of Class II, alone or superimposed on a pattern of Class I (Figs. 4, 5). The absence of this pattern in the other genera of the family makes us consider it as probably more derived. Thus the striking similarity of the pattern between the various fossil species of *Globularia* (Figs. 4, 5) and with the sole extant species, *G.* (*Cernina*) *fluctuata,* suggests a close relationship. This type of thin axial fluorescent zigzagging stripes is absent in naticids (Fig. 11; Table 1) allowing an easy distinction of all the species of *Globularia* from those of the Naticidae and supporting their inclusion to Ampullinidae.

Class III: Our observations demonstrated that the species of *Pachycrommium* reveal similar patterns of Class III (Fig. 8, 9). This class of pattern is absent in all other Ampullinidae with the exception of rare specimens of *Amaurellina levesquei*. Thus this character, almost unique to *Pachycrommium*, can be regarded as a second probable derived pattern within the Ampullinidae suggesting a certain unity within this genus. Furthermore, this class of pattern is never observed in Naticidae and allows this genus of Ampullinidae to be distinguished from the Naticidae. Besides, the similarity between the pattern morphology of *P. acuminatum* and *G.* (*Cernina*) sp. indicates that both genera, *Pachycrommium* and *Globularia*, seem phylogenetically not very distant.

Class IV: Three species of *Ampullina* (*Ampullina. intermedia*, *A. merciniensis*, and *A. lignitara*; Fig. 3) display fluorescent poorly organised elements and sometimes thin sinuous axial segments. Among the studied taxa, this pattern is more similar to the peculiar pattern of the Class II of *Globularia* than any other known from the other genera. This suggests that *Ampullina* and *Globularia* seem phylogenetically not very distant too.

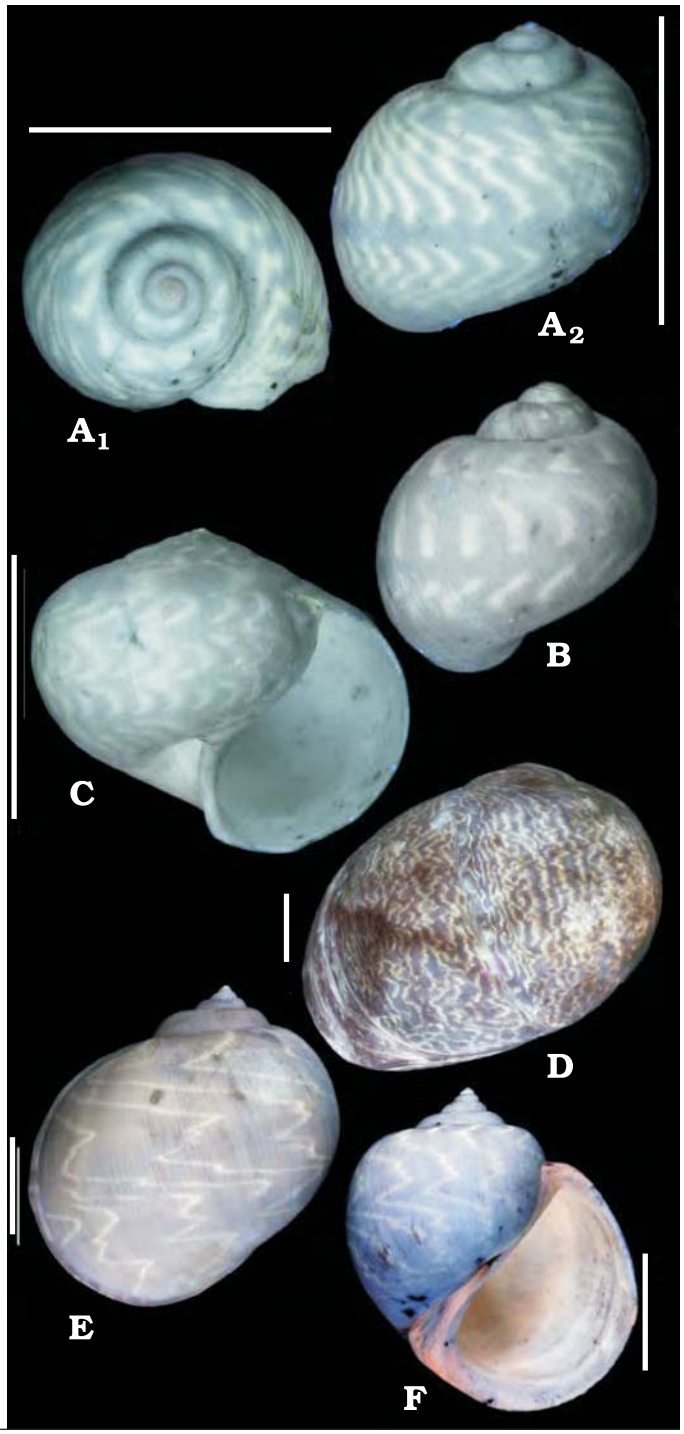

Fig. 11. Comparisons of residual colour patterns between Naticidae and Ampullinidae under UV light. **A**–**C**. Naticidae. Indeterminate class: parallel zigzagging stripes, few zigzags per stripes, homogeneous zigzags' amplitude. **A**. *Natica stoppanii* Deshayes, 1864, MNHN A42002 (MNHN coll.), Cuise-Lamotte, Oise, France, Ypresian (Cuisian), in apical (A_1) and dorsal (A_2) views. **B**. *Payraudeautia perforata* (Deshayes, 1864), MNHN A31803 (MNHN coll.), Grignon, Yvelines, France, Lutetian, in dorsal view. **C**. *Cepatia cepacea* (Lamarck, 1804), MNHN B58269 (MNHN coll.), Croix-Blanche, France, Lutetian, in ventral view. **D**–**F**. Ampullinidae. Class II: non-parallel zigzagging stripes, numerous zigzags per stripes, heterogeneous zigzags' amplitude. **D**. *Globularia* (*Cernina*) *compressa* (Basterot, 1825), MNHN A30400 (MNHN coll.), Mérignac, Gironde, France, Aquitanian, in dorsal view. **E**. *Globularia* (s.s.) *sigaretina* (Lamarck, 1804), MNHN A30859 (MNHN coll.), Grignon, Yvelines, France, Lutetian, in dorsal view. **F**. *Globularia* (s.s.) *semipatula* (Deshayes, 1864), MNHN A30488 (Faullummel coll.), Cuise-Lamotte, Oise, France, Ypresian (Cuisian), in ventral view. Scale bars 10 mm for all, except 5 mm (B, C). Photographs by C. Lemzaouda and P. Loubry (MNHN).

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Table 1. Summary comparative table of the diagnostic characters to discriminate ampullinids and naticids (considering anatomical and morphological characters from Kase 1990, and Kase and Ishikawa 2003a) supplemented with colour pattern features (this paper).

	Ampullinidae	Naticidae
Feeding habits	Algal grazer	Carnivorous predator
Anatomical features	– foot with small, flat, quadrangular propodium and massive, short metapodium; – wide, flat, bipartite and snoutless head without extensible proboscis	– foot with a large plow-like propodium; – head with a long extensible proboscis containing the radula
Morphological features	– highly elevated and pointed spire; – tabulate whorls; – columellar lip lined abaxially with a sheath; – anterior tip of the columellar lip often expanding abaxially into a round lobe; – species with small protoconch have protoconch consisting of 1.2–1.5 helicoidal, smooth and inflated whorls.	– low spire with obtusely pointed apical whorls; – devoid of a sheath and developing instead one or more funicles; – species with small protoconch have protoconch consisting of 2.2–3.5 planispirally and ornamented whorls.
Colour pattern features	– Classes II, III, IV; Class II – non-parallel zigzagging stripes; – numerous zigzags per stripe; – very heterogeneous zigzags' amplitude.	– Classes II, III, IV not observed; – parallel zigzagging stripes; – few zigzags per stripe; – homogeneous zigzags' amplitude.

Conclusions

The study of the residual colour patterns provides much new morphological information on fossil Cainozoic species of the family Ampullinidae. The testing on Mesozoic species provided up to now only negative results. Future observations of very well preserved material (e.g., Cretaceous from Northern America, Jurassic from Eastern Europe) nevertheless may complete the present study. The diversity of Cainozoic colour patterns appears to a greatest magnitude during the Middle Eocene, when the specific richness of the family is most pronounced, as observed in the stromboid family Seraphsidae (Caze et al. 2010).

Firstly, we demonstrated that there is an obvious similarity between the residual pattern of fossil *Globularia* and that of the extant *Globularia* (*Cernina*) *fluctuata*. Secondly, in the other studied genera, some species display intermediate patterns suggesting a transition between *Globularia* and *Ampullina* (*A. intermedia*; Fig. 3) and between *Globularia* and *Pachycrommium* (*Globularia* (*C.*) sp.; Fig. 5).

Otherwise the colour patterns of fossil ampullinids and naticids appear easily distinguishable (Le Meur 2009; Fig. 11) and can be used as an additional diagnostic character to discriminate the two families (Table 1). Thus, although the request of Aronowsky and Leighton (2003) for more detailed morphological studies was correct, we can safely confirm the suggestion of Kase and Ishikawa (2003a) that fossil, or at least Cainozoic, and Recent ampullinids should be removed from Naticidae. Nevertheless, we should urge caution because the species with the general colour pattern of class I are difficult to adjudicate. Finally, we believe that molecular sequence data analyses would be helpful to resolve this question definitively and thus test the relevance of the use of UV light in such cases. Despite the existence of only a single living representative, we can assert that the colour patterns of *Globularia* remain almost unchanged from the Early Palaeogene to the Recent, the other patterns disappearing with the extinction of the other ampullinid genera.

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