First systematic study using the variability of the residual colour patterns: the case of the Paleogene Seraphsidae (Mollusca, Gastropoda, Stromboidea)

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ABSTRACT
This work presents for the first time the application of the residual colour patterns revelead under UV light for the systematic study on Caenozoic seraphsids. The seraphsids species have been previously distinguished on the basis of the shell shape, but this generally bear few diagnostic characters. This study concerns 14 European Palaeogene species belonging, in the previous classification, to the following taxa *Seraphs* (*s.s.*) Montfort, 1810, *S.* (*Diameza*) Deshayes, 1865, *S.* (*Miniseraphs*) Jung, 1974 and *Paraseraphs* Jung, 1974. The observation of 1400 specimens under UV light allows integrating intraspecific variability. Except for *P. praecedens* n. sp. (Thanetian, oldest occurrence of the genus) and *S. subconvolutus* (d'Orbigny, 1852) (Rupelian), all species show colour patterns. The bauplan of the fossil colour patterns is very similar to that of the single extant *Terebellum terebellum* (Linnaeus, 1758), except for *Diameza* Deshayes, 1865. Taking into account their peculiar pattern and shell shape, *Diameza* and *Miniseraphs* are here excluded from *Seraphs* and raised to genus level, and *Miniseraphs* is regarded as a subgenus of *Diameza*. At specific level, the similarity of the colour patterns of *S. volutatus* (Solander *in* Brander, 1766), *S. olivaceus* (Cossmann, 1889) and *S. sopitus* (Solander *in* Brander, 1766), do not justify their distinction based on close shell shapes. Considering the colour patterns, we demonstrate that several shell characters, previously used to distinguish *Paraseraphs* species, are no longer useful for diagnose. *Seraphs peterjungi* n. sp. (Lutetian, Paris Basin) is distinguished on the basis of the colour pattern and two *Seraphs* species are in open nomenclature. As for *T. terebellum*, the colour patterns of *S. chilophorus* (Cossmann, 1889) and *P. tetanus* Jung, 1974 are highly variable. Thus, taking into account intraspecific variability, the residual colour patterns represent an important taxonomic tool in addition to the traditional study of the shell shape.

KEY WORDS
Mollusca,
Gastropoda,
Stromboidea,
Seraphsidae,
residual colour patterns,
UV light,
Palaeogene,
Europe,
intraspecific variability,
new species.

RÉSUMÉ
Première étude systématique fondée sur la variabilité des motifs colorés résiduels : le cas des Seraphsidae paléogènes (Mollusca, Gastropoda, Stromboidea)
Ce travail propose pour la première fois l'utilisation d'une analyse descriptive des patrons de coloration résiduels révélés sous lumière UV pour le traitement systématique des Seraphsidae cénozoïques. Par le passé, celles-ci avaient été uniquement distinguées à partir de la coquille, bien qu'elle présente assez peu de caractères diagnostiques. Cette étude porte sur 14 espèces du Paléogène d'Europe appartenant, dans la classification précédente, aux taxons *Seraphs* (*s.s.*) Montfort, 1810, *S.* (*Diameza*) Deshayes, 1865, *S.* (*Miniseraphs*) Jung, 1974 et *Paraseraphs* Jung, 1974. Plus de 1400 spécimens ont été étudiés sous lumière ultraviolette ce qui a permis de bien prendre en compte la variabilité intraspécifique. Exceptés *P. praecedens* n. sp. (Thanétien, plus ancien représentant du genre) et *S. subconvolutus* (d'Orbigny, 1852) (Rupélien), toutes les espèces montrent des motifs colorés. Le plan d'organisation des patrons de coloration fossiles est très similaire de celui de l'espèce actuelle *Terebellum terebellum* (Linnaeus, 1758), sauf chez *Diameza* Deshayes, 1865. Considérant ce motif particulier et la forme de la coquille, *Diameza* est, ici, exclu du genre *Seraphs*. Au niveau spécifique, la forte similitude du patron de coloration de *S. volutatus* (Solander *in* Brander, 1766), *S. olivaceus* (Cossmann, 1889) et *S. sopitus* (Solander *in* Brander, 1766), aux coquilles très proches, ne justifie pas leur distinction. Plusieurs caractères morphologiques de la coquille, utilisés habituellement pour distinguer les espèces de *Paraseraphs*, ne peuvent plus être considérés comme diagnostiques au regard des patrons de coloration. *Seraphs peterjungi* n. sp. (Lutétien, bassin de Paris) est exclusivement décrit grâce au patron et deux espèces de *Seraphs* sont en nomenclature ouverte. Comme chez *T. terebellum*, les patrons de coloration de *S. chilophorus* (Cossmann, 1889) et *P. tetanus* Jung, 1974 sont très variables. Ainsi, en tenant compte de la variabilité intraspécifique, les patrons de coloration représentent un outil taxonomique important en complément de l'étude traditionnelle de la forme de la coquille.

MOTS CLÉS
Mollusca,
Gastropoda,
Stromboidea,
Seraphsidae,
patrons de coloration
résiduels,
lumière UV,
Paléogène,
Europe,
variabilité intraspécifique,
espèces nouvelles.

INTRODUCTION

Many Recent gastropod families are represented by species having various colour patterns. These patterns can be used as a discriminating criterion for specific recognition or identification (Cox 1969) as for the Cypraeidae Rafinesque, 1815, the Triviidae Troschel, 1863 (Dommergues *et al.* 2006), the Naticidae Guilding, 1834, the Conidae Fleming, 1822, the Marginellidae Fleming, 1828, the Columbellidae Swainson, 1840, the Volutidae Rafinesque, 1815 (Dockery 1980), the Olividae Latreille, 1825, etc. In the fossil record, shells usually do not show visible colour patterns, because the pigments have disappeared or are deteriorated. However, an approach initiated by Olsson in the 1960's (Krueger 1974) enables observation of residual colour patterns on fossil marine shells (Vokes & Vokes 1968; Cate 1972; Krueger 1974; Hoerle 1976; Hoerle & Vokes 1978; Dockery 1980; Bouniol 1982; Swann & Kelley 1985; Kelley & Swann 1988; Pitt & Pitt 1992,1993; Merle 2003; Pacaud 2003, 2007; Cluzaud & Cahuzac 2006a, b; Kase *et al.* 2008; Merle *et al.* 2008). These hidden patterns are revealed or enhanced by bleaching the shells in sodium hypochlorite and photographing them under long wave ultraviolet light. Subsequently,

Fig. 1. — Variability of the extant species *Terebellum terebellum* (Linnaeus, 1758) in dorsal view and normal light: **A**, *T. terebellum* form *delicatum* Kuroda & Kawamoto, 1961, MNHN IM, Segond Channel, Santo, Vanuatu; **B**, **H**, **I**, *T. terebellum* form *punctulorum* (Röding, 1798); **C**-**G**, *T. terebellum* form *lineatum* (Röding, 1798); **B**, MNHN IM, Grand Récif Sud, New Caledonia; **C**, MNHN IM, Lagon Nord, New Caledonia; **D**, MNHN IM, unknown locality; **E**, MNHN IM, New Caledonia; **F**, MNHN IM, Grand Récif Sud, New Caledonia; **G**, MNHN IM, Atoll de Surprise, New Caledonia; **H**, MNHN IM, Grand Récif Sud, New Caledonia; **I**, MNHN IM, Grand Récif Sud, New Caledonia. Scale bars: 10 mm. Photographs by C. Lemzaouda (MNHN).

this method has been used by a few authors for the study of Caenozoic gastropods. Most of them only illustrated one or two specimens of some species (e.g., Wilson 1975; Dockery 1977; Swann & Kelley 1985) and described the residual patterns "as an additional point of interest" (Hoerle 1976) in the framework of the study of a given fauna. Some authors (Krueger 1974; Swann & Kelley 1985; Kelley & Swann 1988; Pitt & Pitt 1993) asserted like Dockery (1980: 3) that "Color patterns in Tertiary molluscs may be a basis for establishing lineages and identifying new species or subspecies". However, they did not use the residual patterns as a taxonomic tool excepting Cate (1972) for the American volutids (Lyriinae Pilsbry & Olsson, 1954) and recently Kase (2008) for Asiatic potamidids (genus *Vicarya* d'Archiac & Aime, 1854). Thus, the use of the residual patterns, as taxonomic tool including the intraspecific variabilty, remains a largely unexplored field for palaeontologists. The present study of the Seraphsidae Jung, 1974 is the first approach using the full potential of this method in order to investigate the systematics of the fossils in this family.

THE CASE OF SERAPHSIDAE

The Seraphsidae are represented by Caenozoic taxa and by a single extant species *Terebellum terebellum* (Linnaeus, 1758), living in the Indo-Pacific province. The shells have a smooth surface and few diagnostic characters allowing a distinction between different species. Thus, the fossil species have often been distinguished considering the differences in the shell shape, but, unfortunately, without a study based on modern morphometric methods allowing access to shape variability. Moreover, investigations into the residual colour patterns have never been carried out.

The sole extant species, *Terebellum terebellum*, could be regarded as the single point of reference in order to better understand the variablility of colour pattern within the family. This species is so variable (Figs 1; 2) that ancient authors distinguished nine species. However, Jung & Abbott (1967) did not recognize these species as valid and individualised only four morphological types. According to Jung (1974), intermediary specimens show that it is impossible to separate one type from another, as distinct species (Figs 1; 2).

In the fossil record, traces of pigmentation are usually not preserved, except on rare perfectly preserved shells of *Seraphs volutatus* (Solander *in* Brander, 1766) from the Lutetian of the Paris basin, showing remnants of the colour patterns. Thus, as the distinction of the species is very difficult based on the shell characters, the study of the residual colour patterns using UV light provides an additional complex of characters for the identification of fossil species. However, as seen above with *Terebellum terebellum*, it is necessary to consider the intraspecific variability of the studied species. Our study is the first one integrating the intraspecific variability of the residual colour patterns thanks to the observation of a huge number of specimens.

DESCRIPTIVE TERMINOLOGY

The terminology defined by Meinhardt (1998) for the descriptions of the colour patterns of the Recent molluscs has also been used for the descriptions of the fossil residual patterns. In order to clarify these descriptions, a definition of different terms is given below.

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

Background relative pigmentation: a darker or paler background contrasts with other elements (making) resulting in different morphologies.

Nature of the pattern: the elements constituting the patterns, fluorescent or not, can show various morphologies having different distribution and density.

Patches-Dots (Fig. 3A, B, E): both terms apply to a small area of a colour contrasting sharply with the background. The distinction between the patches and the dots is essentially based on the relative size of the elements. We consider here that patches are larger than dots (see Figure 3).

Spots (Fig. 3C, D): the dots are composed of one or two coloured parts. These parts are called spots.

FIG. 2. — Variability of the extant species *Terebellum terebellum* (Linnaeus, 1758) in dorsal view and normal light: **A**-**D**, *T. terebellum* form *punctulorum* (Röding, 1798); **E**, *T. terebellum* form *delicatum* Kuroda & Kawamoto, 1961, MNHN IM, Segond Channel, Santo, Vanuatu; **F**-**J**, *T. terebellum* form *nebulosum* (Röding, 1798); **A**, MNHN IM, Grand Récif Sud, New Caledonia; **B**, MNHN IM, Grand Récif Sud, New Caledonia; **C**, MNHN IM, Secteur de Balabio, New Caledonia; **D**, MNHN IM, Grand Récif Sud, New Caledonia; **F**, MNHN IM, Plateau des Chesterfield; **G**, MNHN IM, Plateau des Chesterfield); **H**, MNHN IM, Aésé Island, Santo, Vanuatu; **I**, MNHN IM, Baie des Citrons, Nouméa, New Caledonia; **J**, MNHN IM, Quatre Bancs de l'Ouest, lagoon of Nouméa, New Caledonia; **K**, *T. terebellum*, MNHN IM, Plateau des Chesterfield. Scale bars: 10 mm. Photographs by C. Lemzaouda (MNHN).

Lines-Stripes (Fig. 4A, B): both terms apply to any elongated (object) area or space which is axially or spirally continuous on the whole shell. The distinction between lines and stripes is based on the relative width of these elements. We consider that lines are narrower than stripes. Both elements can be spiral or axial (Fig. 4A, B) and often result from the coalescence of dots or patches.

Segments (Fig. 4D): the segments are short elongated strokes, generally resulting from the coalescence of dots or patches. They can be spiral or axial.

Rows (Fig. 4C): the rows are axial or spiral alignments of dots, patches or segments.

MATERIAL

The studied material represents about 1400 specimens from 61 fossiliferous sites of the French Palaeogene (Paris and Aquitan basins, Loire-Atlantique and Cotentin). It mainly comes from the Collection de Paléontologie and from the Collection de Malacologie of the Muséum national d'Histoire naturelle of Paris. The detailed list is given in Appendices 1, 2.

METHOD

As mentioned above, the residual shell pigmentation may be revealed or enhanced by bleaching specimens in sodium hypochlorite then directly exposing those under long wave UV light (Vokes & Vokes 1968; Dockery 1980; Swann & Kelley 1985). In this study, the residual patterns have been observed thanks to the procedure defined by Merle *et al.* (2008). First, the samples are placed in a bath of concentrated sodium hypochlorite for 24 hours. After the bath, they are carefully washed with water. Second, most of the patterns are revealed by an exposure under UV light emitting a wavelength of 3600 Å (Merle 2003).

According to Krueger (1974) refering to Olsson: "When colour patterns fluoresce under UV light, they appear to the human eye as photographic negatives of the colour pattern on a modern shell". Thus, a negative of the picture may give information about the true relationship between a residual colour pattern and a live animal's shell. The negative has a dark colour pattern on a lighter background and can be used as a lantern slide to demonstrate how the fossil shell looked when the animal was alive (Fig. 5C, F). In the present work, the shells illustrated under UV light are generally presented without negative treatment. In order to show how the colour pattern was when the animal was alive, a negative treatment is sometimes given (Figs 5C, F; 11F; 16K; 30C).

ABBREVIATIONS

BMNH	The Natural History Museum, Department of Palaeontology, London;
MHNG	Muséum d'Histoire Naturelle, département de Géologie et de Paléontologie, Geneva;
MHNN	Muséum d'Histoire naturelle de Nantes;
MNHN	Muséum national d'Histoire naturelle, collection de Paléontologie, Paris;
IM	Muséum national d'Histoire naturelle, collection d'invertébrés marins (mollusques), Paris;
NMB	Naturhistorisches Museum, Basel;
UBT	université Bordeaux1, Talence;
UCBL	université Claude Bernard, UFR Sciences de la Terre, Lyon 1.

RESULTS

Before presenting the systematic treatment, it is important to stress that the inovation of this work is to have a sufficiently abundant material displaying residual colour pattern to allow the study of the intraspecific variability. Based on 1400 specimens, almost 90% of the material show positive results under UV light (Table 1). For the various species, the number of specimens observed differs considerably. Among the 14 fossil species, six species are represented by more than 30 specimens, among which four are represented by more than 100 specimens (between 117 and 494 specimens). These samples allow a precise and faithful idea of real variability. For the other species, the number of specimens is lower.

SYSTEMATIC PALEONTOLOGY

Order LITTORINIMORPHA
Golikov & Starobogatov, 1975
Superfamily STROMBOIDEA Rafinesque, 1815

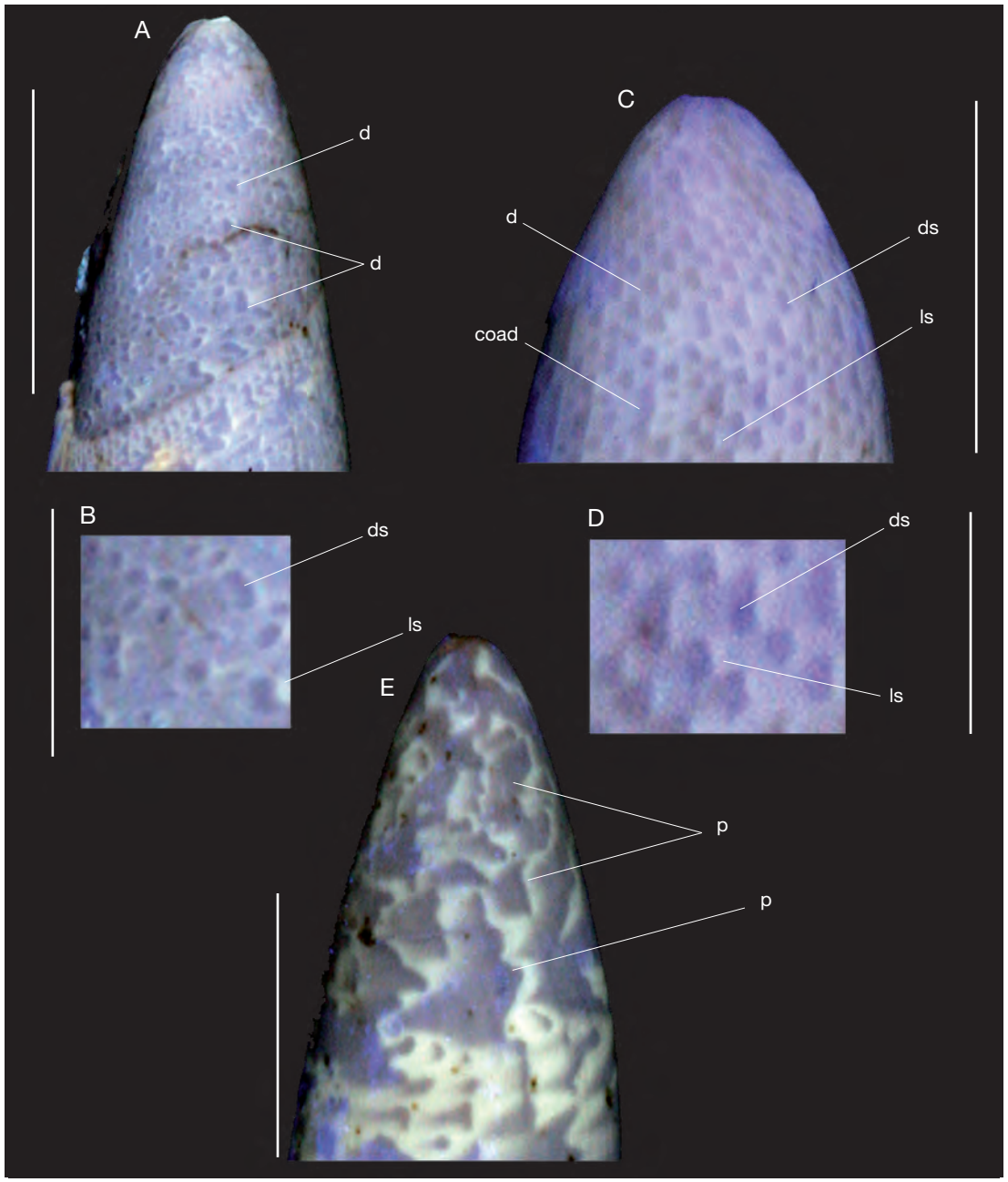

FIG. 3. — Descriptive terminology of the residual colour patterns of the Seraphsidae Jung, 1974: **A**, **B**, *Paraseraphs placitus* Jung, 1974, MNHN A28963 (Ballot coll.), Grignon, Yvelines, France, Lutetian; **A**, apical part; **B**, detailed view of the dots; **C**, **D**, *Seraphs volutatus* (Solander *in* Brander, 1766), MNHN A28873, Grignon, Lutetian; **C**, apical part; **D**, detailed view of the dots; **E**, *S. chilophorus* (Cossmann, 1889), MNHN A28922 (leg. Pacaud), Fercourt, Oise, France, Lutetian (apical part). Abbreviations: **coad**, coalescence of dots; **d**, dot; **ds**, darker spot; **ls**, lighter spot; **p**, patch. All pictures taken under UV light. Scale bars: A, C, E, 5 mm; B, D, 2 mm. Photographs by C. Lemzaouda (MNHN).

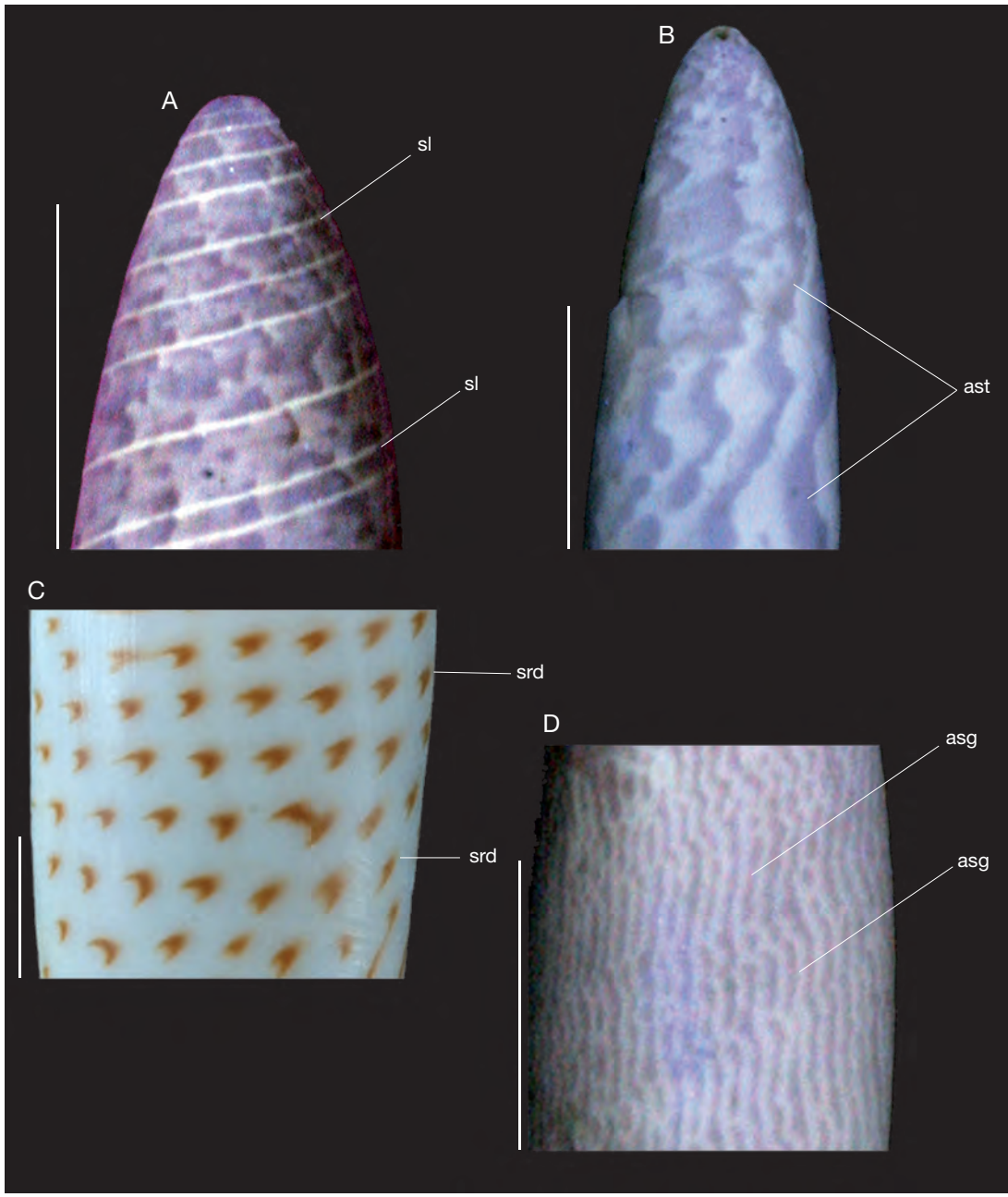

FIG. 4. — Descriptive terminology of the residual colour patterns of the Seraphsidae Jung, 1974: **A**, paratype of *Seraphs peterjungi* n. sp. (apical part), MNHN A28931 (leg. Pacaud), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **B**, *Paraseraphs tetanus* Jung, 1974 (apical part), MNHN A28958 (Faullummel coll.), Saint-Gobain, Aisne, France, Ypresian (Cuisian); **C**, *Terebellum terebellum* (Linnaeus, 1758) (median part), MNHN IM, Atoll de Surprise, New Caledonia, Recent; **D**, *Paraseraphs tetanus* (median part), MNHN A28943, Cuise-Lamotte (Butte-des-Usages), Oise, France, Ypresian (Cuisian); **A**, **B**, **D**, under UV light; **C**, in normal light. Abbreviations: **asg**, axial segment; **ast**, axial stripes; **sl**, spiral line; **srd**, spiral row of dots. Scale bars: 5 mm. Photographs by C. Lemzaouda (MNHN).

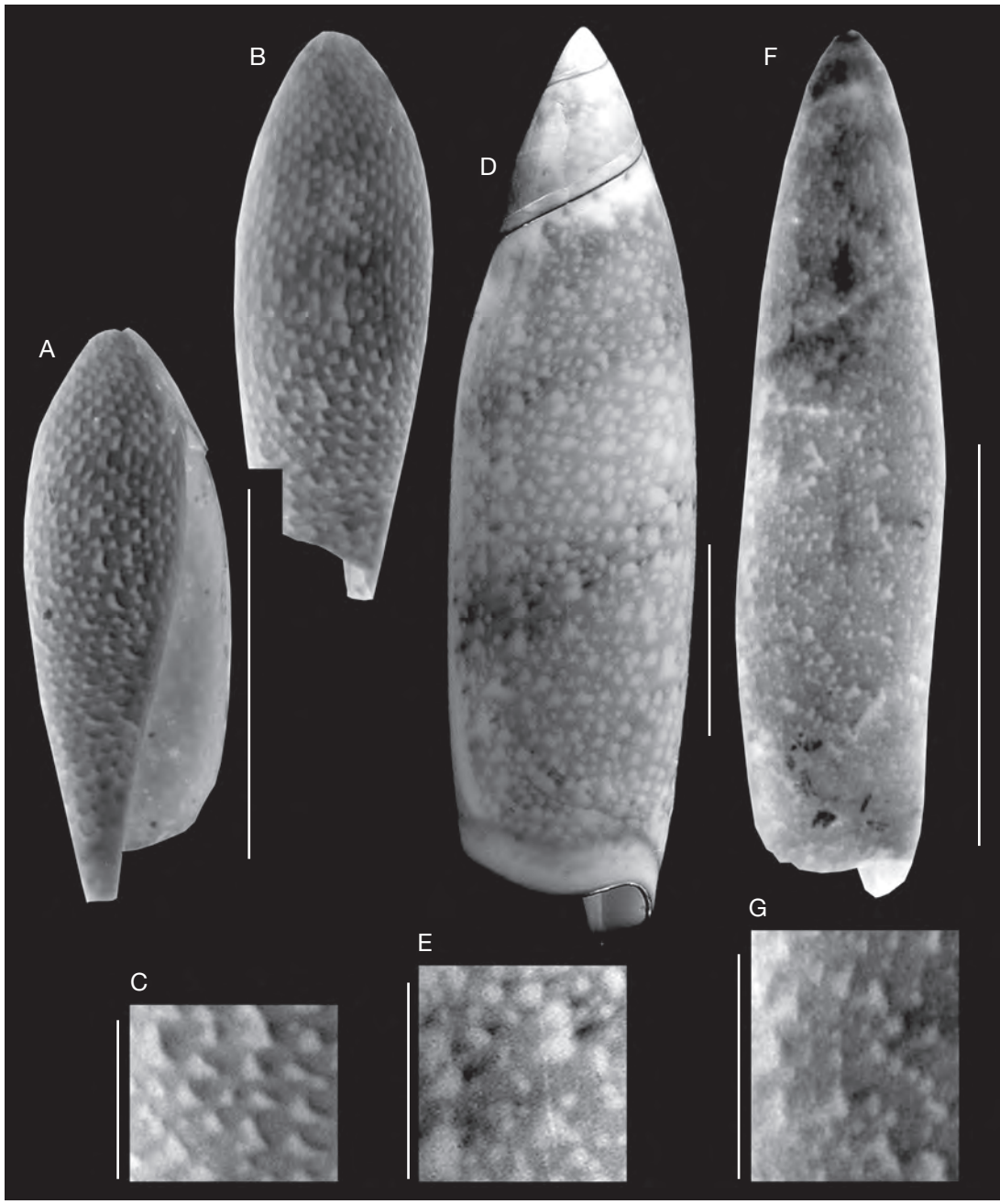

FIG. 5. — Comparison between the colour patterns of fossil and Recent Seraphsidae Jung, 1974: **A**-**C**, *Seraphs volutatus* (Solander *in* Brander, 1766), MNHN A28873, Grignon, Yvelines, France, Lutetian; **A**, ventral view; **B**, dorsal view; **C**, detailed view of the dots; **D**, **E**, *Terebellum terebellum* (Linnaeus, 1758), MNHN IM, Baie des Citrons, Nouméa, New Caledonia, Recent; **D**, dorsal view; **E**, detailed view of the dots; **F**, **G**, *Paraseraphs placitus* Jung, 1974, MNHN A29168 (leg. Pacaud), Chaussy, Val d'Oise, France, Lutetian; **F**, dorsal view; **G**, detailed view of the dots; **A**-**C**, **F**, **G**, under UV light in negative view; **D**, **E**, in normal light. Scale bars: A, B, D, F, 10 mm; C, G, 2 mm; E, 5 mm. Photographs by C. Lemzaouda (MNHN).

TABLE 1. — Comparison between positive and negative results among the studied material.

Species	Total number of specimens	Positive under UV light	Negative under UV light	Percentages
Seraphs volutatus (Solander *in* Brander, 1766)	562	494	68	87.9
Seraphs sopitus (Solander *in* Brander, 1766)	15	11	4	73.3
Seraphs olivaceus (Cossmann, 1889)	22	20	2	90.9
Seraphs leukoleptus Jung, 1974	5	4	1	80
Seraphs chilophorus (Cossmann, 1889)	163	160	3	98.16
Seraphs peterjungi n. sp.	24	24	0	100
Seraphs subconvolutus (d'Orbigny, 1852)	14	0	14	0
Diameza (*Miniseraphs*) *eratoides* (Cossmann, 1889)	36	28	8	77.8
Diameza (*Miniseraphs*) *isabella* (Bernay *in* Deshayes, 1865)	132	117	15	88.6
Diameza (*s.s.*) *fragilis* (Defrance, 1825)	41	31	10	75.6
Paraseraphs tetanus Jung, 1974	319	304	15	95.3
Paraseraphs placitus Jung, 1974	77	66	11	85.7
Paraseraphs armoricus (Vasseur, 1882)	4	4	0	100
Paraseraphs praecedens n. sp.	1	0	1	0
Total	1415	1263	152	89.3

Family SERAPHSIDAE Jung, 1974

Genus *Seraphs* Montfort, 1810

TYPE SPECIES. — *Terebellum convolutum* Lamarck, 1802 (= *Bulla volutata* Solander *in* Brander, 1766) by original designation. Lutetian, Paris Basin.

Seraphs volutatus
(Solander *in* Brander, 1766)
(Figs 5A, B, E; 6A-E; 7; 8)

Bulla volutata Solander *in* Brander, 1766: 34, pl. 6, fig. 75.

Terebellum convolutum Lamarck, 1798: pl. 360, fig. 2 (*nomen nudum*).

Terebellum convolutum Lamarck, 1802: 390, no. 1, vélin 2, fig. 7a, b; 1805: 225, 226, pl. 2 [44], fig. 3a, b; 1810: 302, no. 2; 1816: pl. 360, fig. 2; 1822: 411, no. 2; 1823: pl. 2, fig. 3a, b. — de Roissy 1804: 425-426. — Bory de Saint-Vincent 1826: 165, pl. 360, fig. 2; 1827: 165, pl. 360, fig. 2. — de Blainville 1827: pl. 27, fig. 2, 2a. — Deshayes & Milne-Edwards 1844: 585, no. 2. — Pictet 1855: pl. 64, fig. 1.

Terebellum sopitum – d'Orbigny 1850: 352, no. 263 *partim*. — Lowry *et al.* 1866: pl. 3. — Cossmann 1907: 254, fig. 3. — Bosatta *et al.* 1973: 190, pl. 1, figs 8, 9. Non *Bulla sopita* Solander *in* Brander, 1766.

Terebellum (*Seraphs*) *sopitum* – Cossmann 1901: 89, pl. 15, fig. 5. — Glibert 1933: 58; 1963: 40. — Korobkov 1955: 260, pl. 57, fig. 4. Non *Bulla sopita* Solander *in* Brander, 1766.

Seraphs convolutus – de Montfort 1810: 375, 376, 1 fig. — Defrance 1827: 490. — Wood 1829: 7, pl. 6, fig. 75.

Terebellum (*Seraphs*) *convolutum* – Fischer 1884: 673, fig. 433. — Cossmann 1904: 46, pl. 1, fig. 1. — Cossmann & Pissarro 1911: pl. 31, fig. 158-2. — Wenz 1940: 938, fig. 2742.

Terebellum (*Seraphs*) *sopitum* var. *convoluta* – Cossmann 1889: 96-97; 1898: 341, pl. 7, fig. 35.

Seraphs sopitus – Jung 1974: 16-21, pl. 1, figs 1-19; pl. 2, figs 1-8; pl. 3, figs 1-9; pl. 4, figs 1-13, text-fig. 11. — Dolin *et al.* 1980: 28. — Savazzi 1991: 324, fig. 13F. Non *Bulla sopita* Solander *in* Brander, 1766.

Seraphs volutatus – Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162. — Pacaud 2008: 724, fig. 2E, F.

TYPE LOCALITY. — Hordwell (England), Bartonian (Middle Eocene).

TYPE MATERIAL. — *Bulla volutata* Solander *in* Brander, 1766: the single preserved syntype (BMNH GG 21010) has been selected unambiguously by Jung (1974: 18) as lectotype: "the type specimen of *Bulla volutata* Solander *in* Brander (1766, p. 34, pl. 6, fig. 75)". According to article 74.5 of the ICZN (1999) this mention, made before 2000, constitutes a valid lectotype designation.

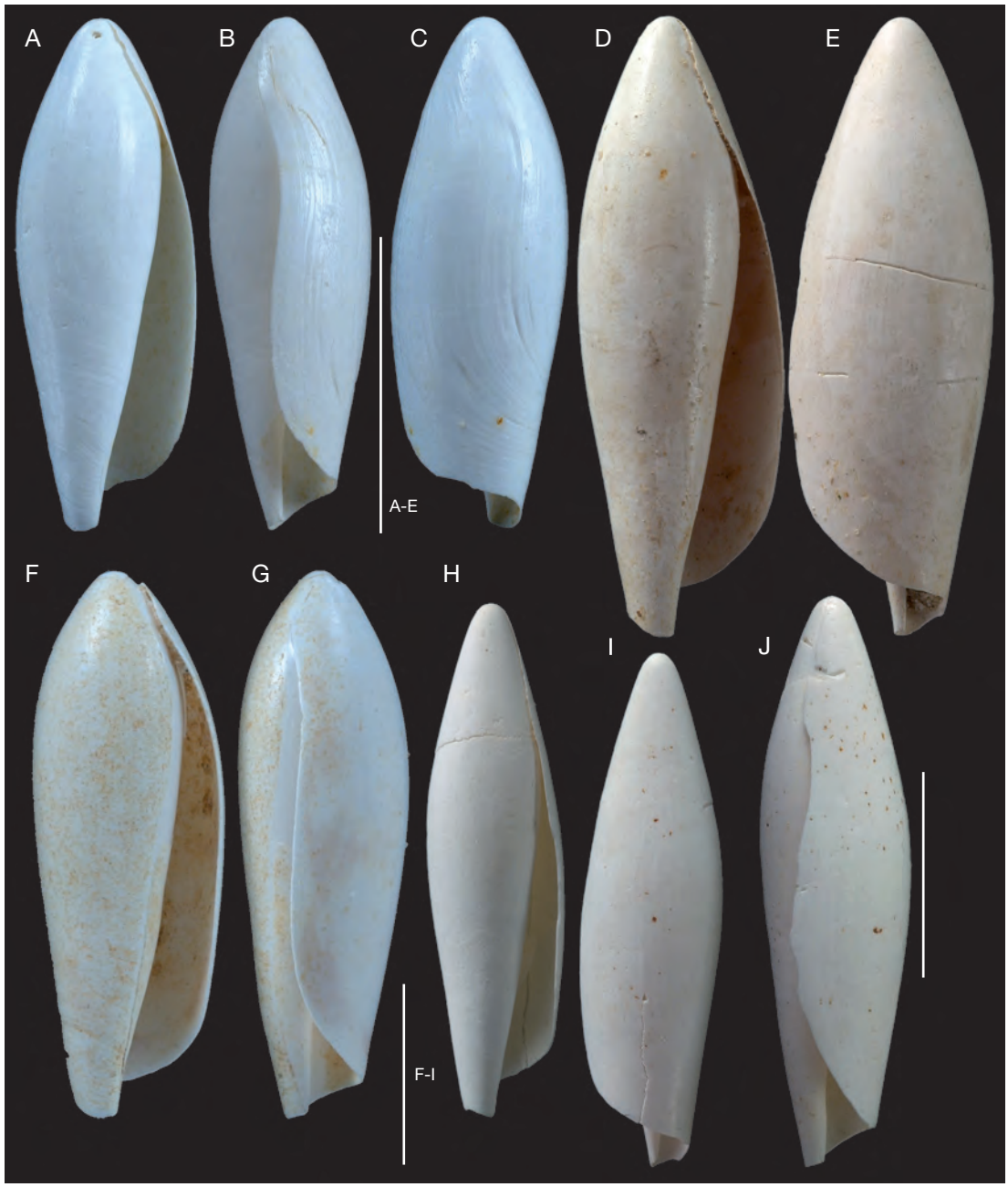

FIG. 6. — *Seraphs* Montfort, 1810 shells in normal light: **A**-**E**, *S. volutatus* (Solander *in* Brander, 1766); **A**-**C**, MNHN A28776 (ex Galerie de Zoologie coll.), Grignon, Yvelines, France, Lutetian; **A**, ventral view; **B**, labral view; **C**, dorsal view; **D**, **E**, lectotype of *Terebellum convolutum* Lamarck, 1802, MNHN B70325 (Lamarck coll.), Grignon, Lutetian; **D**, ventral view; **E**, dorsal view; **F**, **G**, *S. sopitus* (Solander *in* Brander, 1766), MNHN A28778 (Faullummel coll.), Le Limon, Seine-et-Marne, France, Bartonian; **F**, ventral view; **G**, labral view; **H**-**J**, *S. olivaceus* (Cossmann, 1889); **H**, **I**, MNHN A28577 (Ledon coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **H**, ventral view; **I**, dorsal view; **J**, MNHN A29225, labral view (Ledon coll.), Chaussy (Les Garennes), Lutetian. Scale bars: 10 mm. Photographs by C. Lemzaouda (MNHN).

Terebellum convolutum Lamarck, 1802: lectotype (MNHN B70325, Lamarck coll.) selected here from 3 syntypes from the Lutetian of Grignon (Yvelines); 2 paralectotypes (MNHN A28775, Lamarck coll.).

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shells

Shell up to 75 mm in height and 22 mm in diameter, slightly inflated with short and blunt to somewhat acute apex (Jung 1974). Aperture long and narrow. Callus of the inner lip very thin and rarely preserved except on some "gerontic" shells. Columella almost straight near the base, or rarely bent in some big shells. Outer lip very thin, not thickened, sinuous for the whole height and extending to the apex (Fig. 6B). Siphonal notch moderately deep on the dorsal side of the shell. No sculpture on the surface of the shell.

Colour pattern

According to Jung (1974), perfectly preserved specimens from the Lutetian of Paris Basin show, in normal light, many small and irregular dots which compose the residual colour pattern.

Under UV light, the colour pattern consists of numerous small dots on a lighter background (Fig. 7). These dots, variable in size, show two levels of residual pigmentation (Fig. 7G). The first one consists of triangle-like spots, darker than the background. The apex of these spots is directed towards the growing edge. The second one consists of spots with a fuzzy border, white, fluorescent under UV light and directed towards the inner lip. They are adjacent to the base of the dark spots. Light spots are variable in shape and size, but they are usually narrower than the dark spots (Fig. 7A-D, G-I). These two components form the dots. Dot density is generally more important on the apical part of the shell. They often form sinuous, axial rows nearly parallel to the edge of growth (Fig. 7A, B). The space between these rows is narrow on the apex and broader on the median and basal parts of the shell.

VARIABILITY OF THE COLOUR PATTERN

The background is generally light, but sometimes shows large and diffuse darker areas (Fig. 7H, I). The density of dots is very variable. Some shells have a few large dots and their axial rows are not clearly defined. On other shells, the density of dots is so great that their coalescence may hide the original background. Some specimens strongly coalescent show very few isolated dots. Juvenile specimens often show proportionally bigger dots (Fig. 7E, F). Sometimes the relative size of the light spot is greater than the dark triangular spot (Fig. 7E, F).

STRATIGRAPHIC EXTENSION

Several specimens (Fig. 8) collected in Sapicourt (Marne, France) constitute the new oldest occurence of the species (Ypresian [Cuisian]).

Seraphs sopitus (Solander *in* Brander, 1766) (Figs 6F, G; 9)

Bulla sopita Solander *in* Brander, 1766: 19, pl. 1, fig. 29a.

Seraphs convolutus Wood, 1829: 7, pl. 1, fig. 29a. Non *Terebellum convolutum* Lamarck, 1802.

Terebellum sopitum – d'Orbigny 1850: 352, no. 263 *partim*. — Newton 1894: 98.

Terebellum (*Seraphs*) *sopitus* – Cossmann 1889: 96, 97.

Terebellum (*Seraphs*) *sopitum* – Cossmann 1904: 46.

Seraphs sopitus – Jung 1974: 16-21 *partim*, pl. 1, figs 1-3.

TYPE LOCALITY. — Hordwell (England), Bartonian (Middle Eocene).

TYPE MATERIAL. — Lectotype (BMNH GG21010) designated by Jung (1974).

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Shell up to 40 mm in height and 14 mm in diameter, inflated with short and blunt apex (Fig. 6F, G). Aperture long and narrow. Callus of the inner lip thin and rarely preserved, except on the largest shell. Columella mainly straight but bent back, near the base. Outer lip very thin, not thickened and sinuous for the whole height in labral view

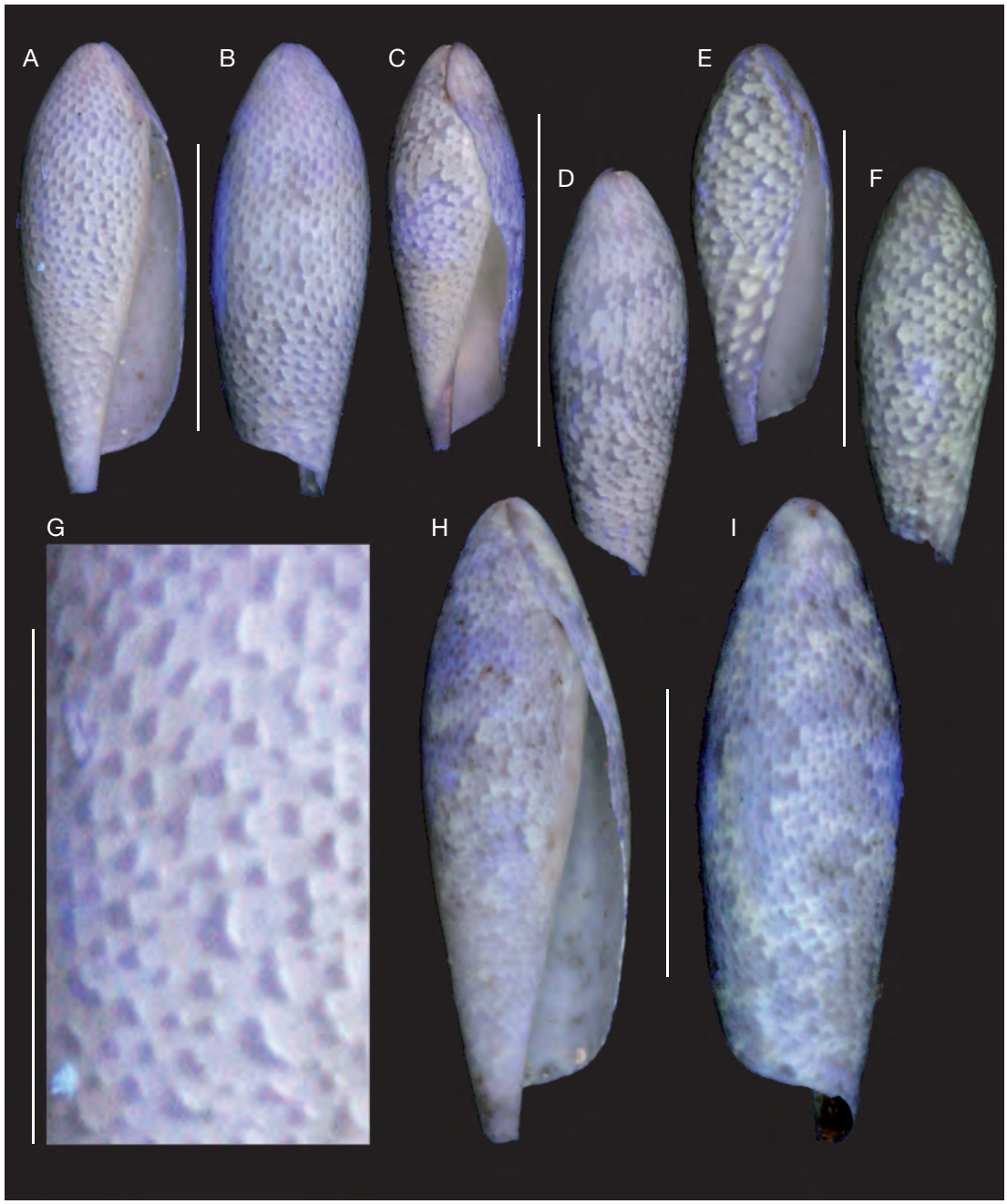

FIG. 7. — *Seraphs volutatus* (Solander *in* Brander, 1766) under UV light: **A**, **B**, **G**, MNHN A28873, Grignon, Yvelines, France, Lutetian; **A**, ventral view; **B**, dorsal view; **G**, detailed view of the dots; **C**, **D**, MNHN A28876, Grignon, Lutetian; **C**, ventral view; **D**, dorsal view; **E**, **F**, MNHN A28875 (Valenciennes coll.), Fontenay-en-Vexin, Eure, France, Lutetian; **E**, ventral view; **F**, dorsal view; **H**, **I**, MNHN A28874, Grignon, Lutetian; **H**, ventral view; **I**, dorsal view. Scale bars: A-F, H, I, 10 mm; G, 5 mm. Photographs by C. Lemzaouda (MNHN).

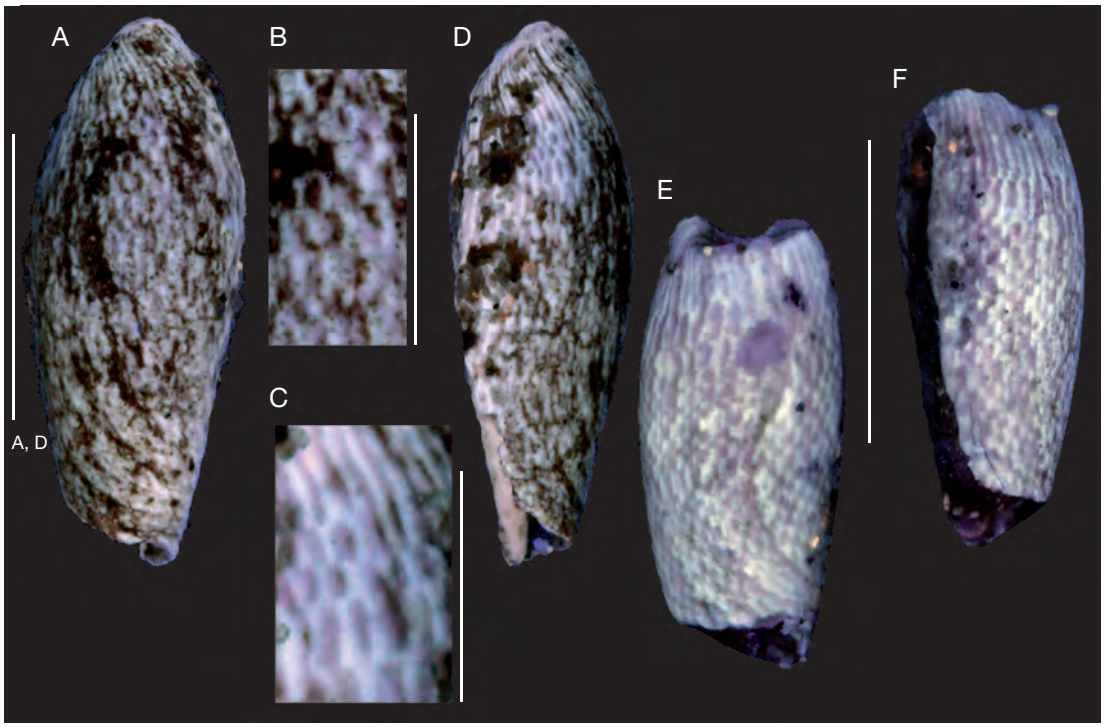

Fig. 8. — Oldest known specimens of *Seraphs volutatus* (Solander *in* Brander, 1766) under UV light: **A**-**D**, MNHN A30419, Sapicourt, Marne, France, Ypresian (Cuisian); **A**, dorsal view; **B**, **C**, detailed view of the dots; **D**, labral view; **E**, **F**, MNHN A30420, Sapicourt, Ypresian (Cuisian); **E**, dorsal view; **F**, labral view. Scale bars: A, D, E, F, 5 mm; B, C, 2 mm. Photographs by C. Lemzaouda (MNHN).

(Fig. 6G). Siphonal notch moderately deep on the dorsal side of the shell. No sculpture on the surface of the shell.

Colour pattern

The colour pattern consists of numerous small and irregular dots on a lighter background (Fig. 9). These dots show two levels of residual pigmentation (Fig. 9C, D, H, J, K): triangular spots, darker than the background, with the apex orientated towards the outer lip and diffuse, fluorescent spots lighter than the background and orientated towards the inner lip. These white fluorescent spots, adjacent to the base of the triangles, are variable in shape. They can be narrower than the dark triangles (Fig. 9C, D, J, K) or bigger and ovoid to almost circular (Fig. 9H). These two components form the dots. The dots are of various sizes. They are more distorted and axially elongated on the shell extremities (Fig. 9A, C). When they coalesce, these dots form sinuous axial nearly collabral rows (Fig. 9A, E, F).

Seraphs olivaceus (Cossmann, 1889) (Figs 6H-J; 10)

Terebellum (*Seraphs*) *olivaceum* Cossmann, 1889: 97, 98, pl. 3, figs 1, 2.

Terebellum (*Seraphs*) *olivaceus* – Cossmann 1904: 46. — Cossmann & Pissarro 1911: pl. 31, fig. 158-4.

Seraphs olivaceus – Jung 1974: 21, pl. 5, fig. 5-11, text-fig. 15. — Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162.

Type locality. — Chaussy (Val d'Oise, France), Lutetian (Middle Eocene).

Type material. — The illustrated syntype of Cossmann (1889) has been selected unambiguously by Jung (1974:

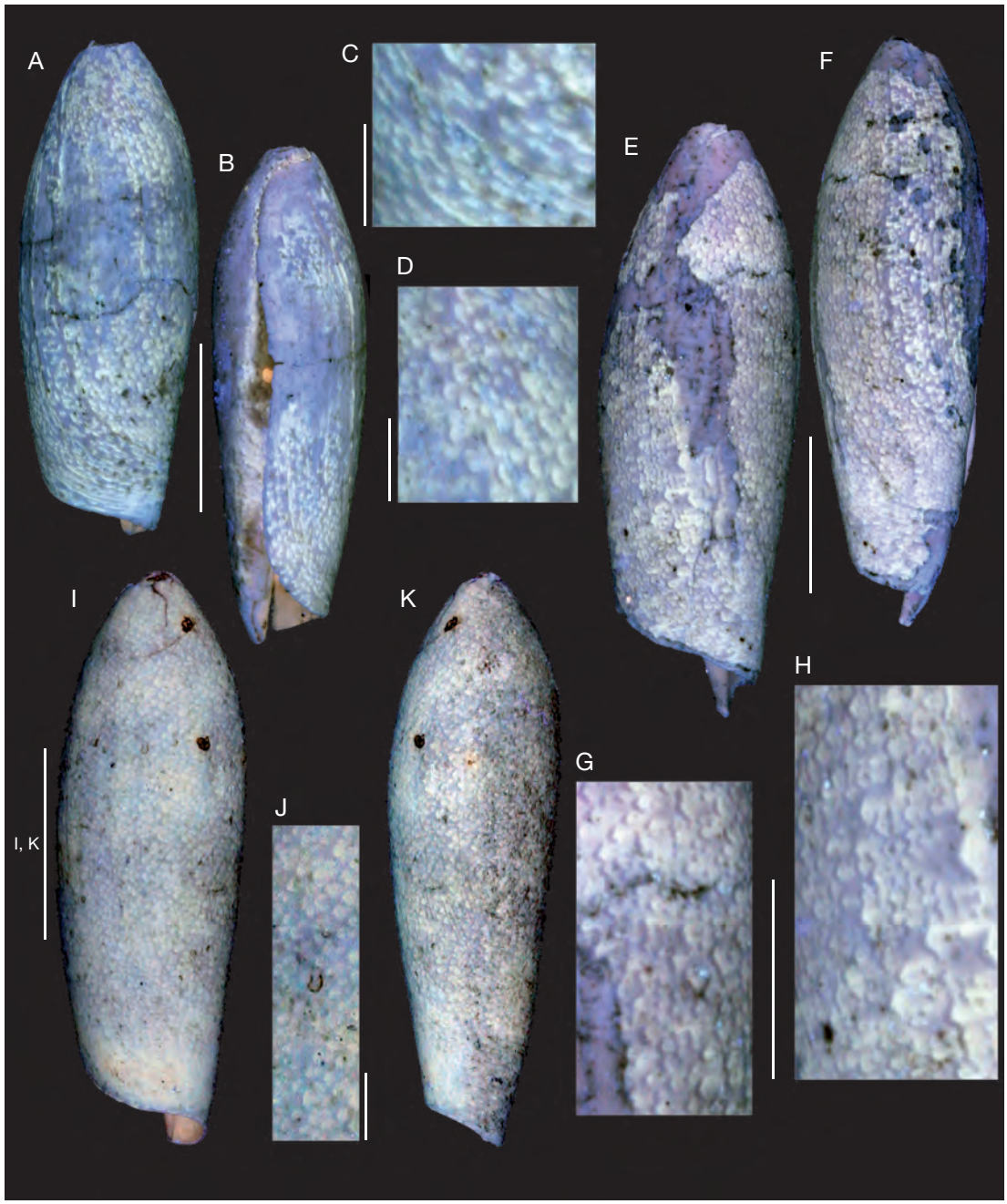

Fig. 9. — *Seraphs sopitus* (Solander *in* Brander, 1766) under UV light: **A**-**D**, MNHN A28884, Saint-Witz (Le Guépelle), Val d'Oise, France, Bartonian; **A**, dorsal view; **B**, labral view; **C**, **D**, detailed views of the dots; **E**-**H**, MNHN A27526, Saint-Witz (Le Guépelle), Bartonian; **E**, dorsal view; **F**, abapertural view; **G**, **H**, detailed views of the dots; **I**-**K**, MNHN A28778, Le Limon, Seine-et-Marne, France, Bartonian; **I**, dorsal view; **J**, detailed view of the dots; **K**, abapertural view. Scale bars: A, B, E, F, I, K, 10 mm; C, D, J, 2 mm; G, H, 5 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

21) as lectotype, using wrongly the term holotype: "Cossmann's figure […]. This specimen is the holotype". According to article 74.5 of the ICZN (1999), this mention, made before 2000, constitutes a valid lectotype designation. Unfortunately, the type material of this species has not been found in the Bourdot collection, deposited at University of Lyon 1 (UCBL). A neotype designation is needed to clarify the taxonomic status of this species. A neotype from the type locality (MNHN A28885, leg. Pacaud, Fig. 10F-H) is accordingly chosen here. This initiative is in conformity with the rules specified by the ICZN (1999: art. 75), as regards the designation of a neotype.

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Shell up to 28 mm in height and 7 mm in diameter, moderately slender with elongated and pointed apex (Fig. 6H). Aperture long and narrow. Callus of the inner lip very thin, inconspicuous and rarely preserved. Straight columella near the base. Outer lip not thickened, reaching the apex and sinuous for the whole height in labral view, i.e. outer lip prosocyrt on the anterior part and opisthocyrt on the posterior part of the shell (Fig. 6J). Siphonal notch moderately deep on the dorsal side of the shell. No sculpture on the surface of the shell.

Colour pattern

The shells show small and irregular dots on a lighter background. These dots are composed of two levels of residual pigmentation (Fig. 10E, H). The first one consists of triangular spots, darker than the background. These small triangles are pointed towards the growing edge. The second one consists of white fluorescent fuzzy-bordered spots directed towards the inner lip. They are adjacent to the base of the dark triangles. White fluorescent spots are generally narrower than the dark spots (Fig. 10E, H). These two components form the dots. These dots, variable in size and sometimes coalescent (Fig. 10H), form sinuous axial nearly collabral rows (Fig. 10C, D, F, G). The space between these rows is narrow on the apex and broader on the median and basal parts of the shell.

VARIABILITY OF THE COLOUR PATTERN

The background is generally uniform and can bear large and diffuse darker areas (Fig. 10F-H). The density of the dots varies. When the density is high the axial rows are clearly defined, whereas they are less clearly or not defined when it decreases.

COMPARISONS OF THE THREE SPECIES OF *SERAPHS*: *S. VOLUTATUS*, *S. SOPITUS* AND *S. OLIVACEUS*

Shell

Among the representatives of *Seraphs*, the adult shell shape of *S. volutatus*, *S. sopitus* and *S. olivaceus* is very similar (Fig. 6). Moreover, these shells share a lack of sculpture. *Seraphs volutatus* generally has a straight columella, while it is bent in the two other species. Jung (1974) regarded *Bulla volutata* as a synonym of *Bulla sopitus*. However, according to Le Renard (1992), *S. sopitus* differs from *S. volutatus* by its short and blunt apex. For Jung (1974), *S. olivaceus* is distinguished from *S. volutatus* (= *S. volutatus* + *S. sopitus* sensu Jung [1974]) by an elongated and acute apical part (Fig. 6H). According to Jung (1974), *S. volutatus* shows a gradual change in the shell shape during ontogeny, and we observed some very large specimens similar to *S. olivaceus* and some small specimens similar to *S. sopitus*.

Residual colour pattern

Dots on a light background are common to *S. volutatus* (Fig. 8), *S. sopitus* (Fig. 9) and *S. olivaceus* (Fig. 10). These species show the same type of dots with two levels of residual pigmentation: 1) dark triangular spots orientated towards the growing edge; and 2) white fluorescent spots towards the inner lip. Furthermore, they have sinuous rows, almost parallel to the line of growth. In the studied material (22 ex.) of *S. olivaceus*, the dots are always small and less numerous than in the two other species.

DISCUSSION

After study of 15 specimens of *S. sopitus*, 22 of *S. olivaceus*, 562 of *S. volutatus*, the colour patterns of each species appear variable, but very similar and no distinction can be made. According to Jung (1974) and Le Renard (1992), the main differences result from shell characters (the morphology of the apex and the columella). However, these differential characters, which vary during ontogeny and even in adulthood, were not defined considering variability. In conclusion, our personal opinion is that,

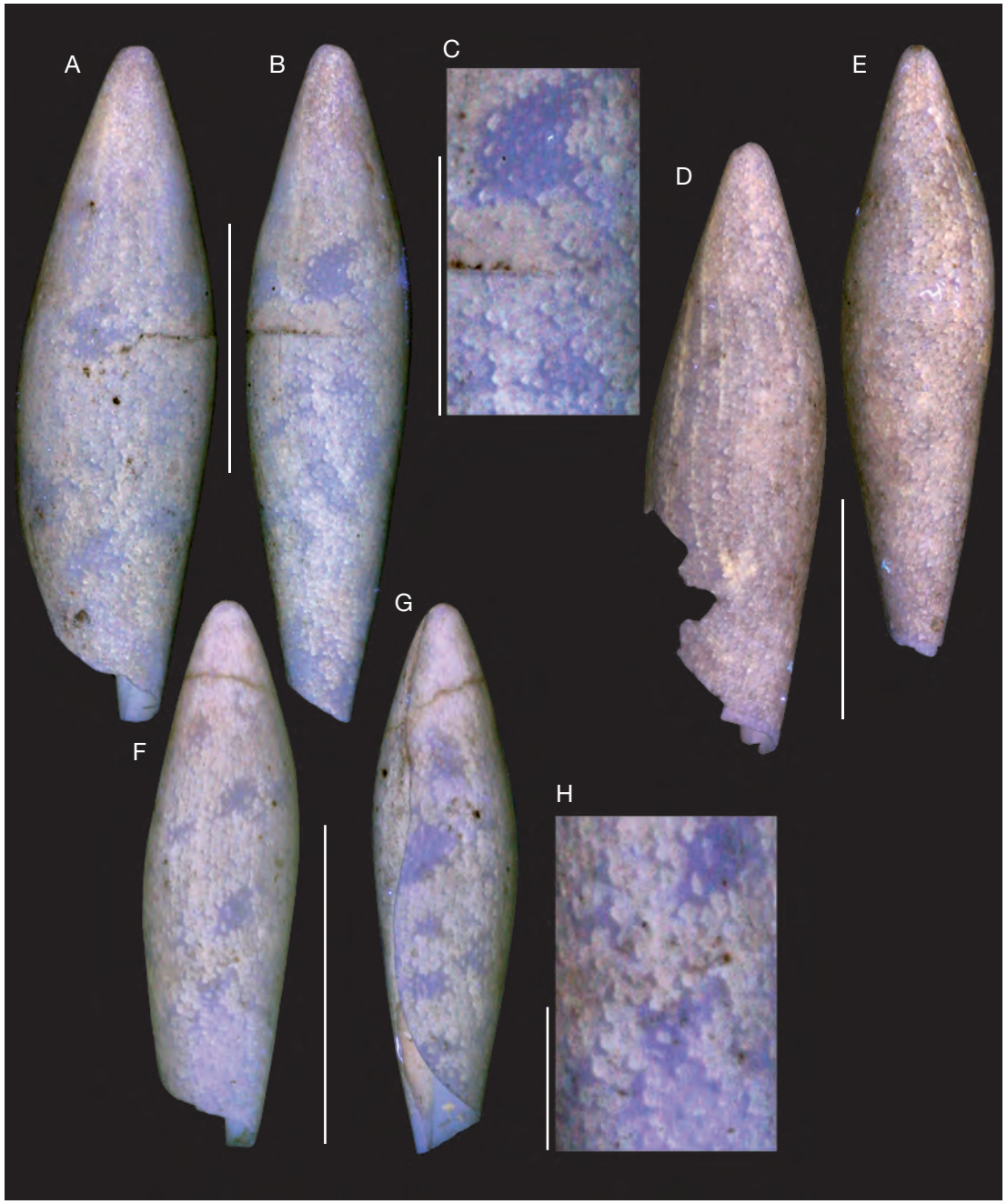

FIG. 10. — *Seraphs olivaceus* (Cossmann, 1889) under UV light: **A**-**C**, MNHN A28560 (leg. Pacaud), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, dorsal view; **B**, abapertural view; **C**, detailed view of the dots; **D**, **E**, MNHN A29057 (Houdas coll.), Chaussy (Les Garennes), Lutetian; **D**, dorsal view; **E**, abapertural view; **F**-**H**, neotype, MNHN A28885 (leg. Pacaud), Chaussy (Les Garennes), Lutetian; **F**, dorsal view; **G**, labral view; **H**, detailed view of the dots. Scale bars: A, B, D-G, 10 mm; C, 5 mm; H, 2 mm. Photographs by C. Lemzaouda (MNHN).

following the colour patterns, the discrimination of these three species is not justified. In order to know if it is necessary to continue to distinguish them, it would be rewarding to study the shell using modern morphometric methods.

Seraphs sp. 1
(Figs 11A-C; 12A-C)

Seraphs sp. – Merle *et al.* 2008: 200, pl. 25, fig. 3.

MATERIAL EXAMINED. — Lutetian, Chaussy (Les Garennes), Val d'Oise, 1 ex. (MNHN A25011, Faullummel coll.).

DESCRIPTION

Shell

Shell 13 mm in height and 4 mm in diameter, slightly inflated with short and blunt apex. Aperture long and narrow. Callus of the inner lip not preserved. Straight columella near the base. Outer lip very thin, not thickened and extending to the apex (Fig. 11A, B). Siphonal notch moderately deep on the dorsal side of the shell. No sculpture on the surface of the shell.

Colour pattern

The residual pattern is only composed of two levels of residual pigmentation: fluorescent axial stripes on a darker background. The stripes, sinuous overall, include some zigzags on short segments (Fig. 12A-C). They are rarely continuous on the whole height of the shell. Their width is variable.

COMPARISONS

The shell shape is indistinguishable from that of young *S. volutatus* and they share the lack of sculpture. However, the residual pattern of *Seraphs* sp. 1 is very different from that of all other *Seraphs* in showing axial sinuous stripes. Moreover, it is the only pattern showing light elements on a darker background.

DISCUSSION

Although the residual colour pattern of *Seraphs* sp. 1 is clearly distinct (no intermediate pattern) from that of *S. volutatus* and even from that of the other *Seraphs*, we believe that it is preferable to avoid the description of a new species, because of the strong intrageneric variability and the occurence of only one specimen having this pattern.

Seraphs sp. 2
(Figs 11D, E; 12D-F)

MATERIAL EXAMINED. — Lutetian, Fresville (Coteau de Vauville), Manche, 2 ex. (MNHN A28577, de Morgan coll.).

DESCRIPTION

Shell

Shell 18 mm in height and 6 mm in diameter, slightly inflated with short and blunt apex. Aperture long and narrow. Callus of the inner lip not preserved. Straight columella near the base. Outer lip extending to the apex but broken in labral view (Fig. 11D). Siphonal notch not observable (Fig. 10E). No sculpture on the surface of the shell.

Colour pattern

On the best preserved specimen, the residual pattern is only composed of two levels of residual pigmentation: dark spiral stripes on a lighter background. The stripes are broad and have marked borders (Fig. 12D-F). They are continuous and each stripe has the same width on the whole of the last whorl. The width of the different stripes is variable. On the less well-preserved specimen, a dark spiral stripe is present with dots, like in *S. volutatus*.

COMPARISONS

The shell shape of *Seraphs* sp. 2 is similar to that of young *S. volutatus* (Fig. 6A-C) and both species lack sculpture. Under UV light, the best preserved specimen is very different from the other *Seraphs* in showing thick and dark spiral stripes. The less well-preserved specimen is slightly similar, but bears dots as in *S. volutatus*.

DISCUSSION

If the best preserved specimen bears this peculiar pattern, the less well-preserved specimen suggests continuity between this pattern and that of *S. volutatus*, because of the occurrence of dots. Thus, as for *Seraphs* sp. 1, we prefer to avoid describing a new species, based on a small number of specimens.

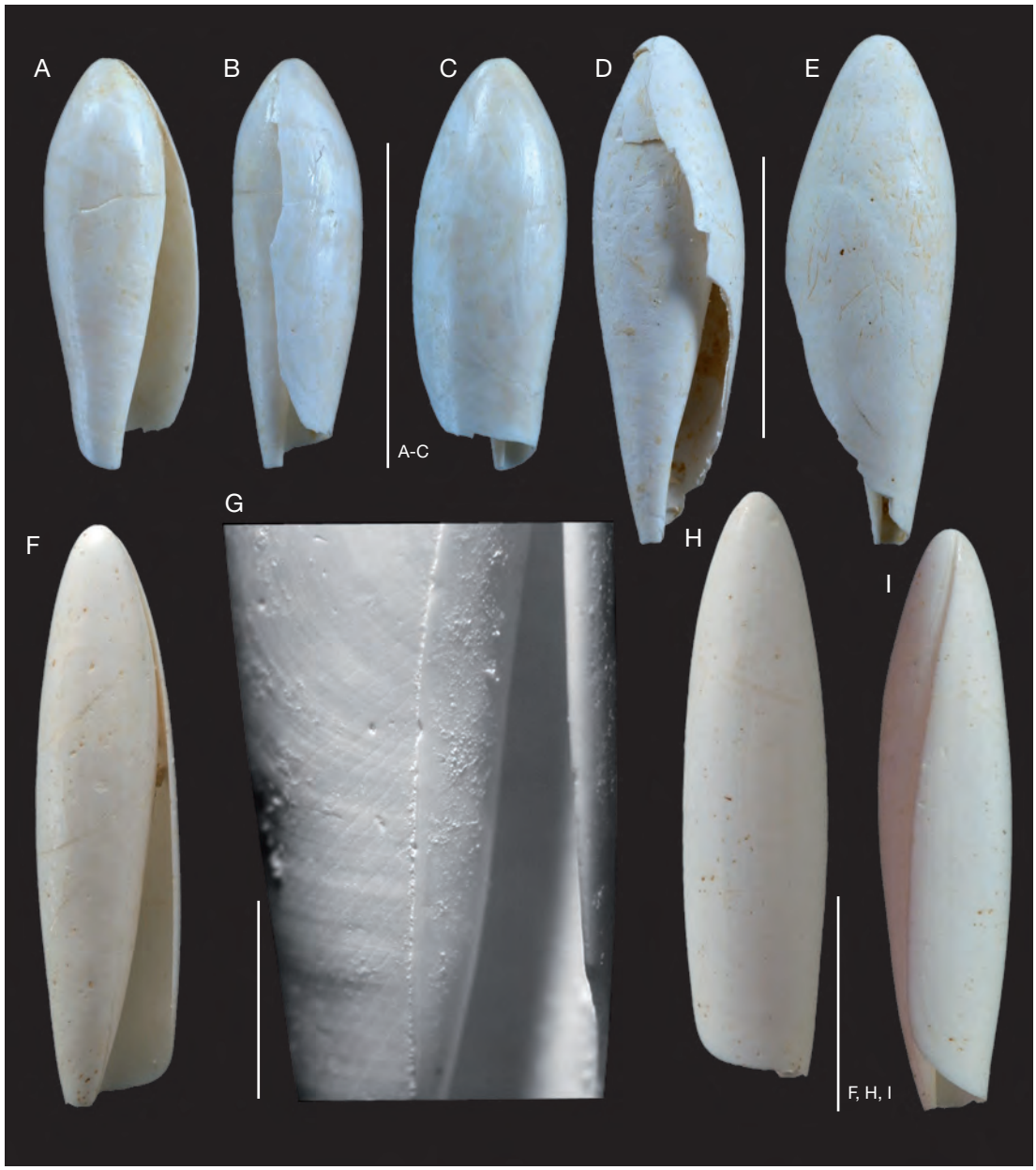

FIG. 11. — *Seraphs* Montfort, 1810 shells in normal light: **A**-**C**, *Seraphs* sp. 1, MNHN A25011 (Faullummel coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, ventral view; **B**, labral view; **C**, dorsal view; **D**, **E**, *Seraphs* sp. 2, MNHN A28887 (de Morgan coll.), Fresville (Coteau de Vauville), Manche, France, Lutetian; **D**, labral view; **E**, dorsal view; **F**-**I**, *S. leukoleptus* Jung, 1974; **F**, **H**, **I**, neotype, MNHN A28781 (Ledon leg.), Chaussy (Les Garennes), Lutetian; **F**, ventral view; **H**, dorsal view; **I**, labral view; **G**, MNHN A28968 (Houdas coll.), Chaussy, Lutetian, detailed view of the oblique grooves. Scale bars: A-F, H, I, 10 mm; G, 5 mm. Photographs by C. Lemzaouda (MNHN).

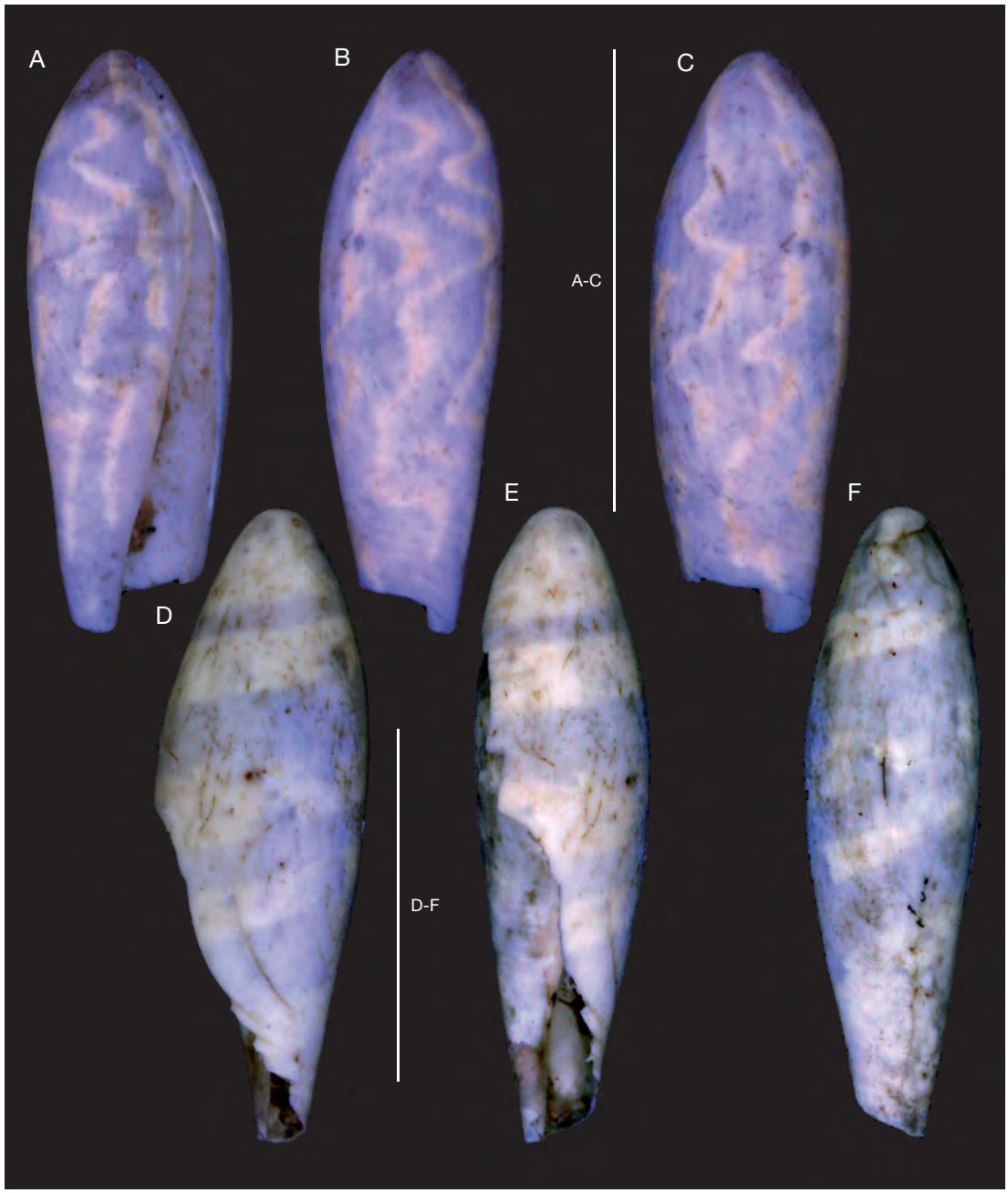

Fig. 12. — *Seraphs* Montfort, 1810 shells under UV light: **A**-**C**, *Seraphs* sp. 1, MNHN A25011 (Faullummel coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, ventral view; **B**, abapertural view; **C**, dorsal view; **D**-**F**, *Seraphs* sp. 2, MNHN A28887 (de Morgan coll.), Fresville (Coteau de Vauville), Manche, France, Lutetian; **D**, ventral view; **E**, labral view; **F**, abapertural view. Scale bars: 10 mm. Photographs by C. Lemzaouda (MNHN).

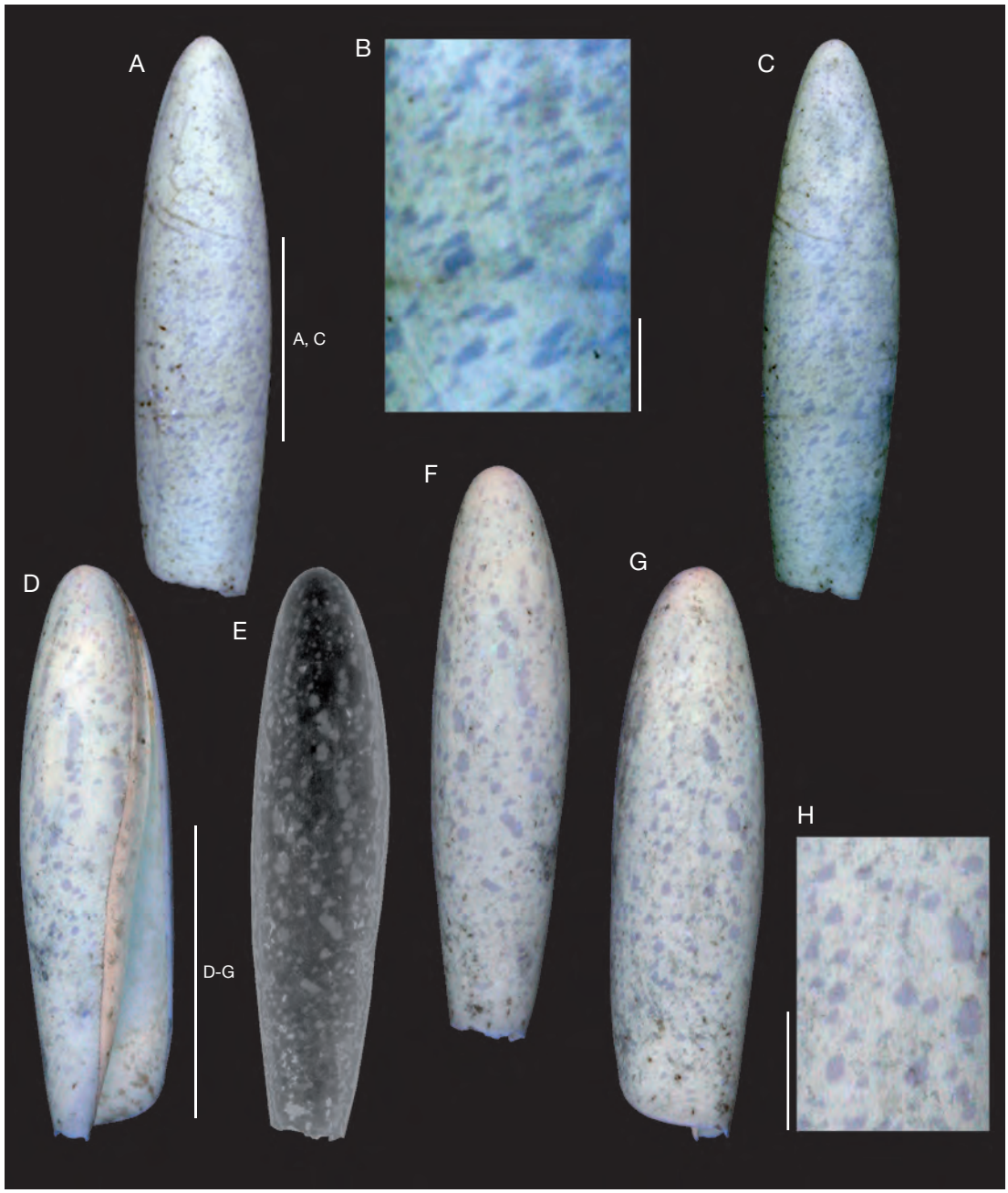

FIG. 13. — *Seraphs leukoleptus* Jung, 1974, under UV light: **A**-**C**, neotype, MNHN A28781 (Ledon leg.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, dorsal view; **B**, detailed view of the dots; **C**, abapertural view; **D**-**H**, MNHN A28968 (Houdas coll.), Chaussy (Les Garennes), Lutetian; **D**, ventral view; **E**, **F**, abapertural views (**E** negative view); **G**, dorsal view; **H**, detailed view of the dots. Scale bars: A, C-G, 10 mm; B, H, 2 mm. Photographs by C. Lemzaouda and P. Loubry (MNHN).

Seraphs leukoleptus Jung, 1974
(Figs 11F-I; 13)

Seraphs leukoleptus Jung, 1974: 23, 24, pl. 6, figs 1-3, text-fig. 17.

Terebellum (*Seraphs*) *fusiformopse* – Cossmann 1889: 97, pl. 3, figs 3, 4; 1904: 46 *partim*. — Cossmann & Pissarro 1911: pl. 31, fig. 158-3. Non *Terebellum fusiformopse* de Gregorio, 1880.

Seraphs leukoleptus – Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162.

Type locality. — Chaussy, Les Garennes (Val d'Oise, France), Lutetian (Middle Eocene).

TYPE MATERIAL. — Holotype (Deshayes coll.); 1 paratype (Deshayes coll., Les Garennes, Chaussy). Unfortunately, the type material of this species has not been found in the Deshayes collection, deposited at the UCBL. A neotype designation is needed to clarify the taxonomic status of this species. A neotype from the type locality (MNHN A28781, Ledon leg.; Figs 11F, H, I; 13A-D) is thus chosen here. This initiative conforms to the rules specified by the ICZN (1999: art. 75), as regards the designation of a neotype.

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Shell up to 36 mm in height and 8 mm in diameter, very slender and elongated, with straight and almost parallel sides (Fig. 11F, H). Aperture long and narrow. Callus of the inner lip very thin, but well delineated, continuing adapically on the spire and forming a narrow band parallel to the outer lip. Columella slightly bent backwards near the base. Outer lip thickened, almost straight in labral view, opisthocline and extending to the apex (Fig. 11I). Shallow siphonal notch on the dorsal side of the shell (Fig. 11H). Few oblique faint grooves near the base (Fig. 11G).

Colour pattern

The residual pattern is only composed of 2 levels of residual pigmentation: dark dots on a lighter background (Fig. 13). The dark dots are small and spirally elongated forming narrow triangles (Fig. 13B-C, I). These triangles, orientated towards the outer lip, are irregularly spread over the whole surface.

COMPARISONS

Seraphs leukoleptus is the only species having a shell with straight and almost parallel sides. Moreover, it is easily distinguished from the other species by a shallow siphonal notch. The pattern of *S. leukoleptus* is distinguishable from the other patterns by its dots. They do not form rows, as observed in *S. volutatus* and *S. olivaceus*. Moreover, these dots are composed of only one level of residual pigmentation, while the other species have dots composed of two levels of residual pigmentation.

Seraphs subconvolutus (d'Orbigny, 1852)
(Fig. 14)

Terebellum subconvolutum d'Orbigny, 1852: 9, no. 140.

Terebellum convolutum – Grateloup 1834: 314, no. 604; 1846: pl. 1 [42] fig. 1. Non Lamarck, 1802.

Terebellum fusiforme – Grateloup 1834: 315, no. 605; 1846: pl. 1 [42] figs 2, 3. Non Lamarck, 1802.

Terebellum subfusiformis d'Orbigny, 1852: 9, no. 141.

Terebellum (*Seraphs*) *subconvolutum* – Cossmann 1904: 46.

Terebellum (*s.s.*) *subconvolutum* – Magne 1940: 33.

Terebellum subconvolutum – Vergneau 1967: 203, 206. — Bosatta *et al.* 1973: 190.

Seraphs subconvolutus – Jung 1974: 26, 27, pl. 8, figs 1-10, text-fig. 18.

TYPE LOCALITY. — Gaas (Landes, France), Rupelian (Oligocene).

TYPE MATERIAL. — *Seraphs subconvolutus*: the illustrated syntype (UBT 65-2-120, Grateloup. coll.) of Grateloup (1834) has been selected unambiguously by Jung (1974 :26) as lectotype, using wrongly the term of holotype: "They therefore represent the holotypes of *S. subconvolutus*...". But in the original work of d'Orbigny (1852), no holotype was designated for the taxon. In accordance with article 74.6 of the ICZN (1999), Jung's stipulation constitutes a lectotype fixation.
Terebellum subfusiformis: the illustrated syntype (UBT 65-2-121, Grateloup coll.) of Grateloup (1834) has been selected unambiguously by Jung (1974: 26) as lectotype, using wrongly the term of holotype: "They therefore represent the holotypes of *S. subconvolutus* and *S. subfusiformis* respectively". But in the original work

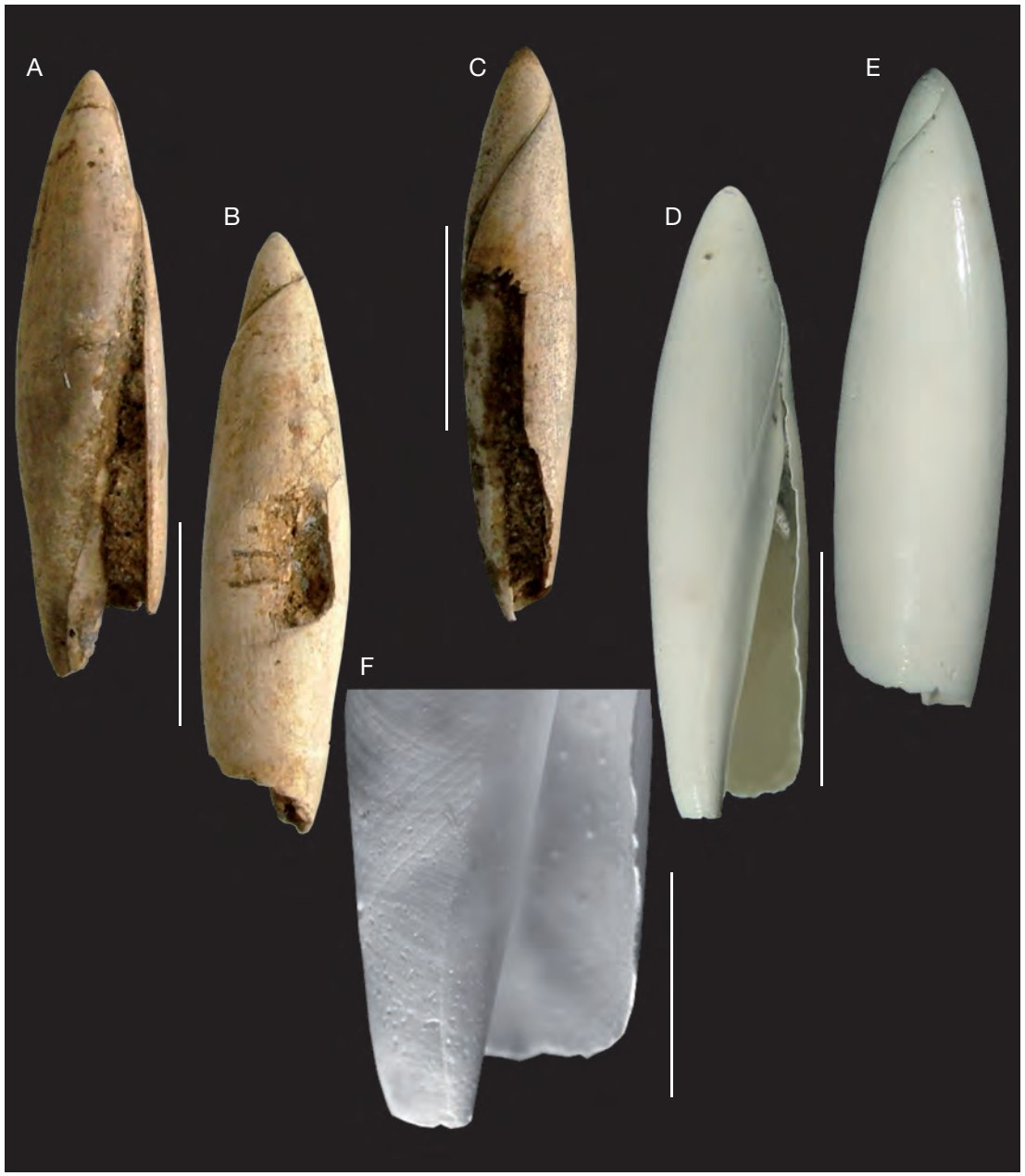

FIG. 14. — *Seraphs* Montfort, 1810 shells in normal light: **A**, **B**, holotype of *S. subconvolutus* (d'Orbigny, 1852), UBT 65-2-120 (Grateloup coll.), Gaas (Lesbarritz), Landes, France, Rupelian; **A**, ventral view; **B**, dorsal view; **C**, holotype of *S. subfusiformis* d'Orbigny, 1852 (labral view), UBT 65-2-121 (Grateloup coll.), Gaas (Lesbarritz), Rupelian; **D**-**F**, MNHN A28967 (Aucoin coll.), Gaas (Espibos), Rupelian; **D**, ventral view; **E**, dorsal view; **F**, detailed view of the oblique grooves. Scale bars: A-E, 10 mm; F, 5 mm. Photographs by C. Lemzaouda (MNHN).

of d'Orbigny (1852), no holotype was designated for the taxon. In accordance with article 74.6 of the ICZN (1999), the Jung stipulation that the illustrated specimen is the holotype constitutes a lectotype fixation.

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Shell up to 31 mm in height and 8 mm in diameter moderately slender with acute apical part. Aperture long and narrow. Callus of the inner lip thin, but well delineated, extending towards the apex and forming a narrow band parallel to the outer lip. Columella slightly bent backwards near the base of the shell. Outer lip slightly thickened and somewhat prosocyrt, in labral view, below the adapical end of the aperture (Jung 1974). Outer lip extending onto the posterior part of the shell, but bent towards the dorsal side (Fig. 14B, C, E) and "reaching the apex after about half a volution" (Jung 1974). Siphonal notch moderately deep. Surface sculpture of narrow oblique grooves observable on the ventral side near the base (Fig. 14F).

Colour pattern

No residual pattern is observed under UV light. Nevertheless, the studied specimens seem slightly corroded and we cannot preclude the possibility that the species originally had a colour pattern.

COMPARISONS OF THE SHELL MORPHOLOGY

Seraphs subconvolutus is similar to *S. chilophorus* and *S. peterjungi* n. sp. (Fig. 15) in sharing an abapical part of the columella slightly bent backwards, narrow oblique grooves on the ventral side near the base and a well delineated callus (Fig. 14D) of the inner lip forming adapically a narrow band parallel to the outer lip. However, this species is the only *Seraphs* having an opisthocline extension of the outer lip on the posterior part of the shell. The outer lip does not continue directly to the apex, but is bent towards the dorsal side reaching the apex after about half a volution (Fig. 14B, C, E). This feature of *S. subconvolutus* resembles that of members of *Paraseraphs* (Jung 1974), but the shell is involute as in other *Seraphs*.

Seraphs chilophorus (Cossmann, 1889) (Figs 15A-I; 16; 17)

Terebellum (*Seraphs*) *chilophorum* Cossmann, 1889: 98, pl. 3, figs 5, 6;

Terebellum (*Seraphs*) *chilophorum* – Cossmann 1904: 45, pl. 2, fig. 6. — Cossmann & Pissarro 1911: pl. 32, fig. 158-5. — Korobkov 1955: 260, pl. 57, fig. 3. — Glibert 1963: p. 39.

Seraphs chilophorus – Jung 1974: 22, pl. 5, figs 12-21, text-fig. 15-16. — Dolin *et al.* 1980: 28. — Savazzi 1991: 324, fig. 13I, J. — Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162. — Merle *et al.* 2008: 198, pl. 25, figs 1a, b, 2.

TYPE LOCALITY. — Fontenay-en-Vexin, Bois du But (Eure, France), Lutetian (Middle Eocene).

TYPE MATERIAL. — The illustrated syntype (Bourdot coll., sample Bernay) of Cossmann (1889) has been selected unambiguously by Jung (1974: 22) as lectotype, using wrongly the term holotype: "Cossmann's original figure […]. This specimen is the holotype". In accordance with article 74.5 of the ICZN (1999) this mention, made before 2000, constitutes a valid lectotype designation. Unfortunately, the type material of this species has not been found in the Bourdot collection, now deposited at UCBL. A neotype designation is needed to clarify the taxinomic status of this species. A neotype from the locality of Fontenay-en-Vexin (MNHN A25009, Fig. 16C-E) is accordingly chosen here. This initiative conforms to the rules specified by the ICZN (1999: art. 75), as regards the designation of a neotype.

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Shell up to 28 mm in height and 8 mm in diameter, moderately slender with acute apical part. Aperture long and narrow. Callus of the inner lip well developed and well delineated, continuing adapically on the spire and forming a narrow band parallel to the outer lip (Fig. 15C). Columella bent backwards near the base. Outer lip, slightly thickened and sinuous in labral view, near the adapical end of the aperture. Outer lip extending to the apex and continuing on the opposite side of the apex for a short distance (Fig. 15G, I). Jung called this apical part of the outer lip, the apical canal. Siphonal notch moderately deep on the dorsal side. Surface sculpture of narrow oblique grooves near the base (Fig. 15H).

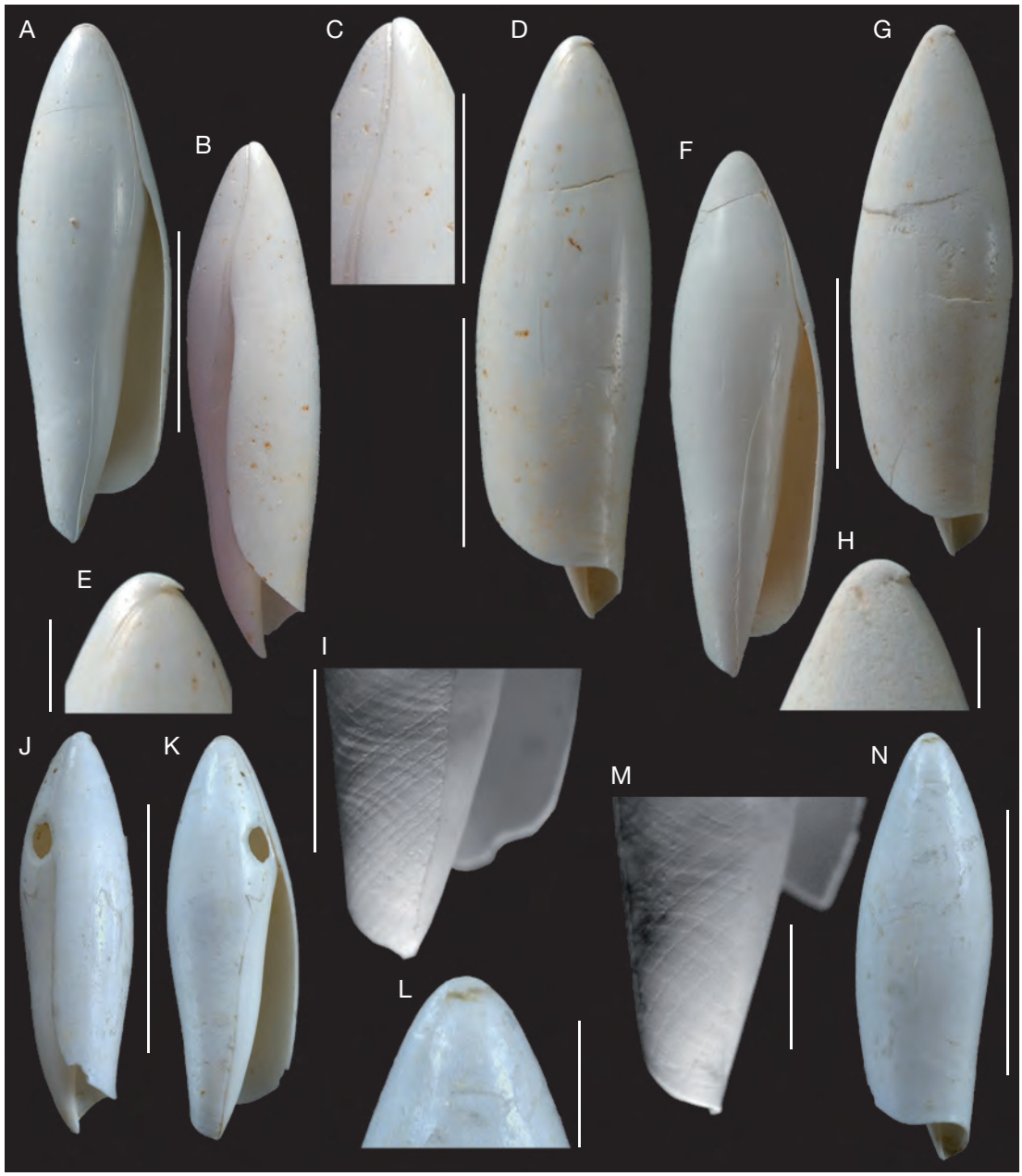

FIG. 15. — *Seraphs* Montfort, 1810 shells in normal light; **A**-**I**, *S. chilophorus* (Cossmann, 1889); **A**-**E**, MNHN A28779 (Ledon coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, ventral view; **B**, labral view; **C**, detailed view of the apical part; **D**, dorsal view; **E**, detailed view of the apical part; **F**-**H**, MNHN A28780 (Ledon coll.), Chaussy (Les Garennes), Lutetian; **F**, ventral view; **G**, dorsal view; **H**, detailed view of the apical part; **I**, MNHN A27783, detailed view the oblique grooves (leg. Pacaud), Saint-Lubin-de-la-Haye, Eure-et-Loir, France, Lutetian; **J**-**N**, *S. peterjungi* n. sp., holotype MNHN A28578 (Pacaud leg.), Chaussy (Les Garennes), Lutetian; **J**, ventral view; **K**, labral view; **L**, detailed view of the apical part; **M**, detailed view the oblique grooves; **N**, dorsal view. Scale bars: A-B, D, F-G, J-K, N, 10 mm; C, I, 5 mm; E, H, L, M, 2 mm. Photographs by C. Lemzaouda (MNHN).

Colour pattern

The colour pattern is composed of two different dark elements on a lighter background: thick rows of patches nearly perpendicular to the line of growth and tiny dots located between these rows.

The rows are composed of dark triangular patches (7-8). The apex of each of is orientated towards the outer lip. The patches are usually disconnected and separated by a small white fluorescent patch. This morphology is called a fishbone pattern (Fig. 16I, J) by Meinhardt (1998: fig. 4.10). The distance between the rows and their width are variable. Sometimes, several rows are adjacent to one another (Fig. 16F). The dots are small and more or less triangular (Fig. 16E). As for the patches, the apex is always directed towards the outer lip. Their size, distribution and shape are heterogenous and irregular. Above the most adapical row, the density and the size of dots are often greater as is the degree of coalescence (Fig. 16H).

COMPARISONS OF THE SHELL MORPHOLOGY

The morphologies of *S. chilophorus* and *S. peterjungi* n. sp (Fig. 15J-N) are very similar with their thickened callus of the inner lip and their narrow band on the adapical part of the shell. Moreover, they share an apical canal (Fig. 15G, I, L), lacking in the other *Seraphs*.

The shell of *S. chilophorus* is more slender than those of *S. volutatus* (Fig. 6A-E) and *S. sopitus* (Fig. 6F, G). This species is generally more slender than *S. olivaceus*, although both can have an acute apex. Also, *S. chilophorus* clearly differs from *S. olivaceus*, *S. volutatus* or *S. sopitus* by the morphology of its outer lip and its callus of the inner lip.

VARIABILITY OF THE COLOUR PATTERN

Among 163 specimens from various localities (11 from the Lutetian and 1 from the Bartonian), 160 (98.16%) show a residual colour pattern under UV light (Table 1). Accordingly, these observations provide a good general survey of the intraspecific variability.

The residual pattern of *S. chilophorus* is quite variable (Fig. 17) and is often subject to significant distortion of the elements on the shell extremities, especially the apical one (Fig. 17C-F).

The huge variability is visible on every element of the residual pattern. The number of spiral rows varies from 0 to 6. Several shells show partially or totally connected rows (Fig. 17B, D). The shape of the dark patches can show important variations from triangular (Fig. 17A, C) to completely distorted or shapeless (Fig. 17F, J). Although they are usually separated by a small fluorescent patch, they may be connected with each other (Fig. 17E). The density of dots fluctuates from low values (Fig. 17A, D-F) to very high ones (Fig. 17K). In this case, the dots form axial rows more or less coalescent (Fig. 17K-N). This coalescence sometimes increases until the dots disappear and only axial segments are observable (Fig. 17H, M, N). There are often some large triangular and coalescent patches near the edge of the outer lip. Finally, there are sometimes small axial segments between the dark patches of the rows (Fig. 17J).

In spite of this variability, we can distinguish three morphological types. The most abundant an representative type 1 is composed of spiral rows of dark triangles directed towards the outer lip and small dots between them (Fig. 17A-C, I). The type 2 shows some thin and tightened axial segments with, often, remnants of spiral rows of triangular patches (Fig. 17H, N, O). The type 3 shows only large and more or less coalescent dark triangles (Fig. 17D, E). Several shells bear a morphology intermediate (Fig. 18) between types 1 and 2 (Fig. 17J-M), between types 1 and 3 (Fig. 17F), between types 2 and 3 (Fig. 17G). The relative abundance of these morphologies is given in Figure 18. Figure 17 illustrates this variability with a certain disparity, but the observation of numerous intermediate specimens suggest that it is impossible to separate one type from another, as different species.

COMPARISONS OF THE COLOUR PATTERN

Seraphs chilophorus (Fig. 16) bears dots, as *S. volutatus*, *S. sopitus*, *S. olivaceus* and *S. leukoleptus* (Figs 7-10). The pattern of *S. chilophorus* is, however, easily distinguishable as the dots are composed of only one residual colour and by the occurrence of broad spiral rows of dark patches.

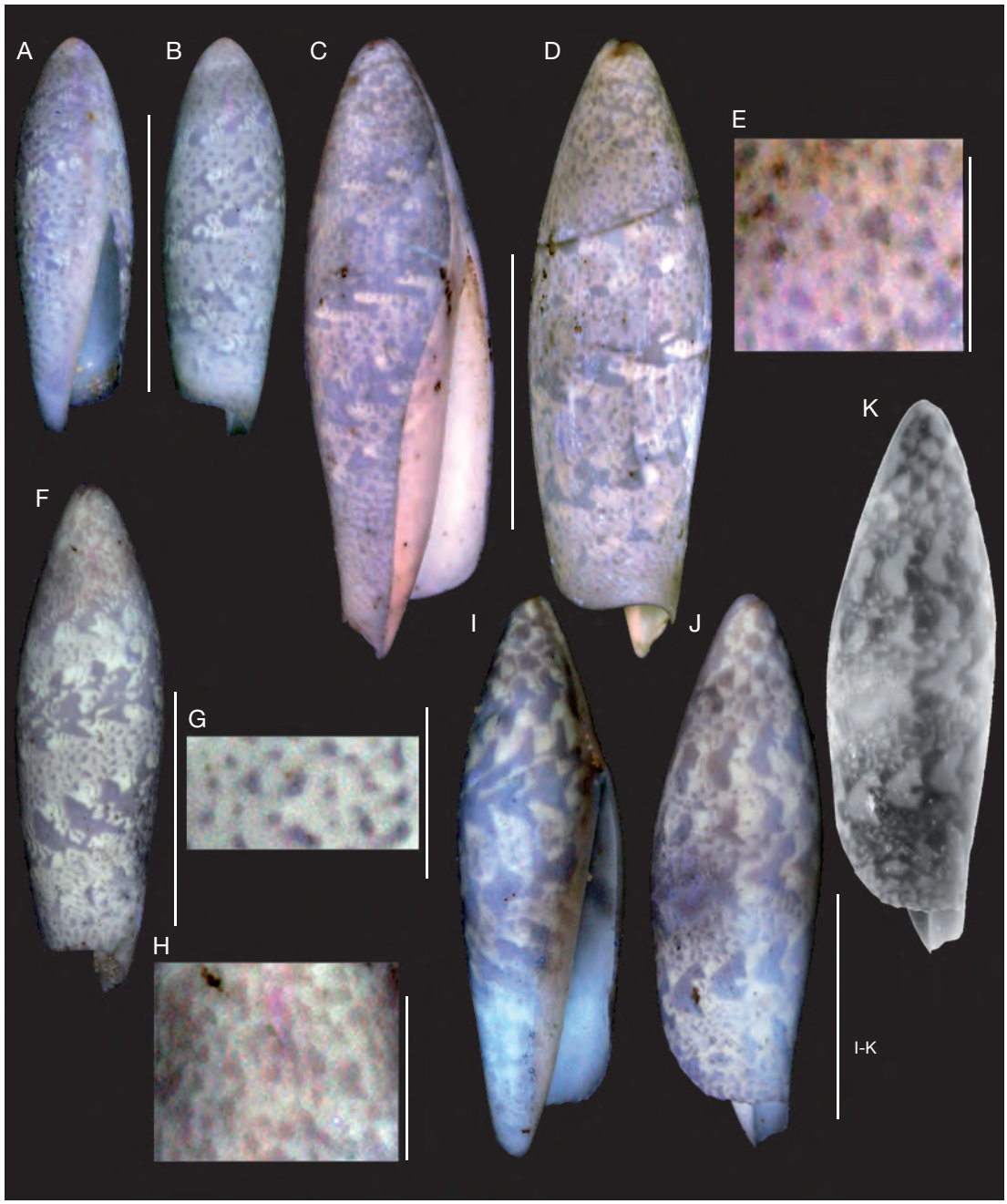

FIG. 16. — *Seraphs chilophorus* (Cossmann, 1889) under UV light: **A**, **B**, MNHN A28927 (Roissy coll.), Parnes, Oise, France, Lutetian; **A**, ventral view; **B**, dorsal view; **C**-**E**, neotype MNHN A25009, Fontenay-en-Vexin, Eure, France, Lutetian; **C**, ventral view; **D**, dorsal view; **E**, detailed view of the dots; **F**-**H**, MNHN A28924 (leg. Pacaud), Fercourt, Oise, France, Lutetian; **F**, dorsal view; **G**, **H**, detailed views of the dots; **I**-**K**, MNHN A28928 (leg. Pacaud), Parnes, Oise, France, Lutetian; **I**, ventral view; **J**, **K**, dorsal views (**K** negative view). Scale bars: A-D, F, I-K, 10 mm; E, G, H, 2 mm. Photographs by C. Lemzaouda (MNHN).

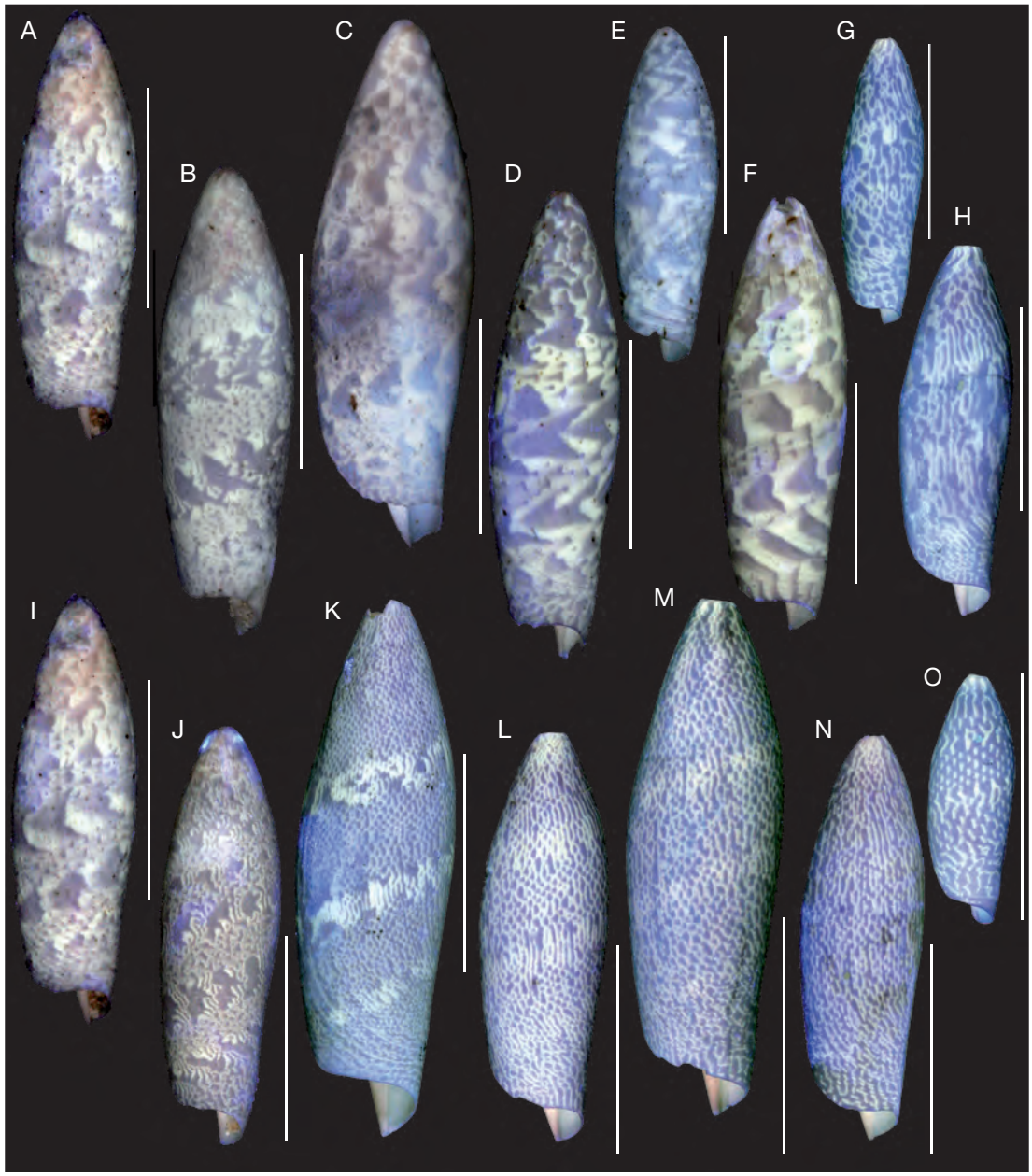

Fig. 17. — Variability of *Seraphs chilophorus* (Cossmann, 1889) in dorsal view and under UV light: **A**, **I**, MNHN A28926 (leg. Pacaud), Fercourt, Oise, France, Lutetian; **B**, MNHN A28924 (leg. Pacaud), Fercourt, Lutetian; **C**, MNHN A28928 (leg. Pacaud), Parnes, Oise, France, Lutetian; **D**, MNHN A28922 (leg. Pacaud), Fercourt, Lutetian; **E**, MNHN A28921 (1965-11 coll.), Saulxmarchais, Yvelines, France, Lutetian; **F**, MNHN A28923 (leg. Pacaud), Fercourt, Lutetian; **G**, MNHN A28919 (leg. Pacaud), Parnes, Lutetian; **H**, MNHN A28891 (leg. Pacaud), Parnes, Lutetian; **J**, MNHN A28925 (leg. Pacaud), Fercourt, Lutetian; **K**, MNHN A28888 (leg. Pacaud), Parnes, Lutetian; **L**, MNHN A28929 (leg. Pacaud), Parnes, Lutetian; **M**, MNHN A28889 (leg. Pacaud), Parnes, Lutetian; **N**, MNHN A28890 (leg. Pacaud), Parnes, Lutetian; **O**, MNHN A28920 (leg. Pacaud), Parnes, Lutetian; **A**-**C**, **I**, Type 1; **H**, **N**, **O**, Type 2; **D**, **E**, Type 3; **J**-**M**, intermediaries 1-2; **F**, intermediary 1-3; **G**, intermediary 2-3. Scale bars: 10 mm. Photographs by C. Lemzaouda (MNHN).

Seraphs peterjungi n. sp.
(Figs 15J-N; 19)

TYPE LOCALITY. — Chaussy, Les Garennes (Val d'Oise), France, Lutetian (Middle Eocene).

TYPE MATERIAL. — Holotype: MNHN A28578, leg. Pacaud.
Paratypes: Chaussy (Les Garennes), Val d'Oise, 2 ex., MNHN A27613 (1965-11 coll.); 1 ex., MNHN A28506 (Morlet coll.); 1 ex., MNHN A28931 (leg. Pacaud); 1 ex., MNHN A27273 (leg. Pacaud); 1 ex. MNHN A28537 (Faullummel coll.); 1 ex., MNHN A28538 (Faullummel coll.); 1 ex., MNHN A27550 (Schtrock coll.); 1 ex., MNHN A28550 (leg. Pacaud); 1 ex., MNHN A28559 (Ledon coll.);
Beynes, Yvelines, 1 ex., MNHN A28789;
Fercourt, Oise, 5 ex., MNHN A27634 (leg. Pacaud);
Grignon, Yvelines, 1 ex., MNHN A27632 (ex Galerie de Zoologie coll.); 1 ex., MNHN A28512 (leg. Caze); 1 ex., MNHN A28530 (Ballot coll.);
Parnes, Oise, 1 ex., MNHN A11186 (d'Orbigny coll.); 1 ex., MNHN A28511 (Roissy coll.);
Parnes (Grande Cronière), Oise, 1 ex., MNHN A28521 (leg. Pacaud);
Saulx-Marchaix, Yvelines, 1 ex., MNHN A28520 (1965-11 coll.).

ETYMOLOGY. — Dedicated to Peter Jung for his work on the Seraphsidae.

DESCRIPTION OF THE HOLOTYPE
Shell 23 mm in height and 7 mm in diameter, slender with acute apical part. Aperture long and narrow. Callus of the inner lip well developed and delineated, continuing adapically on the spire and forming a narrow band parallel to the outer lip. Columella bent backwards near the base (Fig. 15K). Outer lip slightly thickened and, in labral view, sinuous near the adapical end of the aperture. Outer lip extending to the apex and continuing on the opposite side for a short distance (Fig. 15K, L, N). Siphonal notch moderately deep on the dorsal side of the shell. Surface sculpture of narrow oblique grooves near the base (Fig. 15M).

COLOUR PATTERN DESCRIPTION
The colour pattern shows two different and superimposed levels of residual pigmentation: a dark one and a white and fluorescent one. The background displays an intermediate colour between these two levels. The darker elements correspond to several thick spiral rows of patches. The lighter fluorescent elements, overlaid on the darker, consist of narrow spiral lines. The morphology of the dark elements is similar to the pattern of *S. chilophorus*: several spiral rows of dark triangles of which the apex is directed towards the outer lip. Their width, depending on the size of the patches, is variable (Fig. 19A, B). In addition, some tiny and isolated triangles, orientated towards the outer lip, are visible between the rows (Fig. 19G, H). Their size, distribution and shape are heterogenous and irregular (Fig. 19G, H). On the apical part of the shell, the elements are more dense and coalescent, tending to be shapeless.

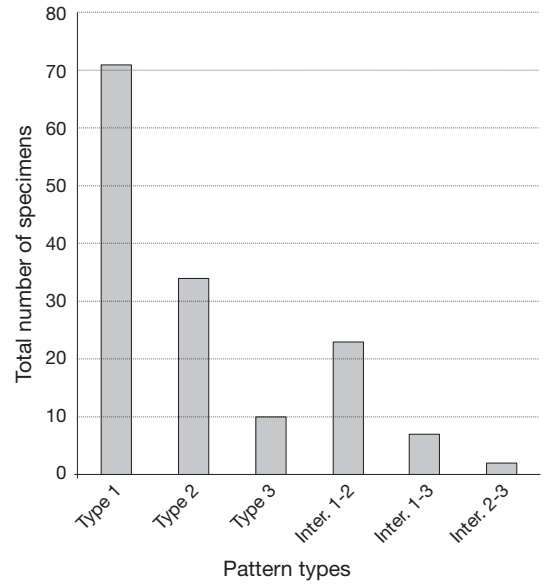

FIG. 18. – Distribution of the pattern types with their intermediaries (**Inter.**) in *Seraphs chilophorus* (Cossmann, 1889).

VARIABILITY
The variability is only observable on the darker elements of the residual pattern. The rows can be more or less distant, from widely spaced to contiguous (Fig. 19A, E, F). Dark patches can show considerable shape variation from triangular to completely distorted (Fig. 19E, F). They can be well separated or connected. The fluorescent elements, narrow spiral lines, do not show perceptible variation except in their number: between 16 and 20.

Shell and colour pattern comparisons

The shell of *Seraphs peterjungi* n. sp. is indistinguishable from that of *Seraphs chilophorus*. Accordingly, for shell comparison with the other species, see *S. chilophorus*.

The dark underlying elements of *S. peterjungi* n. sp. resemble the colour pattern of *S. chilophorus*, but it appears to be less variable. *Seraphs chilophorus* never has fluorescent narrow lines.

Discussion

The comparisons between *S. peterjungi* n. sp. and *S. chilophorus* are respectively based on 24 specimens and 163 specimens (Table 1). Using the shell shape, no distinction can be made between the two populations. Using the residual pattern, we can observe a strong similarity in the dark component, suggesting a close relationship. However, *S. peterjungi* n. sp. shows an additional element with some light and fluorescent spiral lines (Fig. 19), lacking in all examined *S. chilophorus* (Fig. 16) and suggesting a morphological discontinuity. Considering the number of specimens studied and the lack of intermediaries between the two colour patterns, we cannot regard both populations as a single species. In this case, the residual pattern does seem to be a unique discriminating criterion enabling the differentiation of fossil species.

Genus *Diameza* Deshayes, 1865

Type species. — *Ovula media* Deshayes & Milne-Edwards, 1844 (= *Ovula fragilis* Defrance, 1825) by monotypy. Lutetian, Paris Basin.

Generic discussion

Jung (1974) considered *Diameza* and *Miniseraphs* Jung, 1974, as two subgenera of *Seraphs*. Nevertheless, *S.* (*Diameza*) *fragilis* (Defrance, 1825), *S.* (*Miniseraphs*) *eratoides* (Cossmann, 1889) and *S.* (*Miniseraphs*) *isabella* (Bernay *in* Deshayes, 1865) have very small and inflated shells with a large apical angle (Fig. 20) which are obviously different from those of *Seraphs* (*s.s.*) (Figs 6; 11; 15) which are larger, slender and more elongated. Thus, these species are, here, no longer considered to belong to the genus *Seraphs* and are placed together within *Diameza*, which is here raised to the generic level. The name *Diameza*, older than the name *Miniseraphs*, is selected for this genus including two subgenera: *Diameza* and *Miniseraphs*.

Under UV light, these three species show very similar patterns (Figs 21-23). They bear sinuous or wavy axial lines which are lacking in *Seraphs* (Figs 7-10; 12; 13; 16; 18), in *Paraseraphs* (Figs 26; 28; 30) and *Terebellum* (Figs 1; 2). These observations strengthen the initial interpretation based on the shell morphology: *Diameza* (*s.s.*) *fragilis*, *D.* (*Miniseraphs*) *eratoides* and *D.* (*Miniseraphs*) *isabella* are closely related and very different from all other fossil and Recent species.

Subgenus *Diameza* Deshayes, 1865

Diameza (*s.s.*) ***fragilis*** (Defrance, 1825) (Figs 20A-E; 21)

Ovula fragilis Defrance, 1825: 132.

Rostellaria macroptera Lamarck, 1803: 220, no. 1 *partim* (testa junior, incompleta), vélin 4, fig. 5a-c. — Palmer 1977: 15, vélin 4, fig. 5a-c.

Ovula intermedia Deshayes, 1835: 718, pl. 95, fig. 34-37. Non Sowerby, 1830.

Ovula media Deshayes & Milne-Edwards, 1844: 479, 480 (*nomen novum pro Ovula intermedia* Deshayes, 1835 non Sowerby, 1830). — Deshayes 1865: 572.

Ovula (*Diameza*) *media* – Fischer 1884: 665.

Diameza media – Cossmann 1889: 99, pl. 3, fig. 16. — Cossmann & Pissarro 1911: pl. 32, fig. 159-1.

Terebellum (*Diameza*) *media* – Cossmann 1904: 48, pl. 3, figs 9-12.

Terebellum (*Diameza*) *medium* – Wenz 1940: 939, fig. 2744. — Glibert 1963: 40.

Seraphs (*Diameza*) *intermedius* – Jung 1974: 30, pl. 9, figs 10-12, text-figs 19, 20. — Savazzi 1991: 324, fig. 13L. — Le Renard 1992: 6.

Seraphs (*Diameza*) *fragilis* – Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162. — Le Renard 2001: 17, 18.

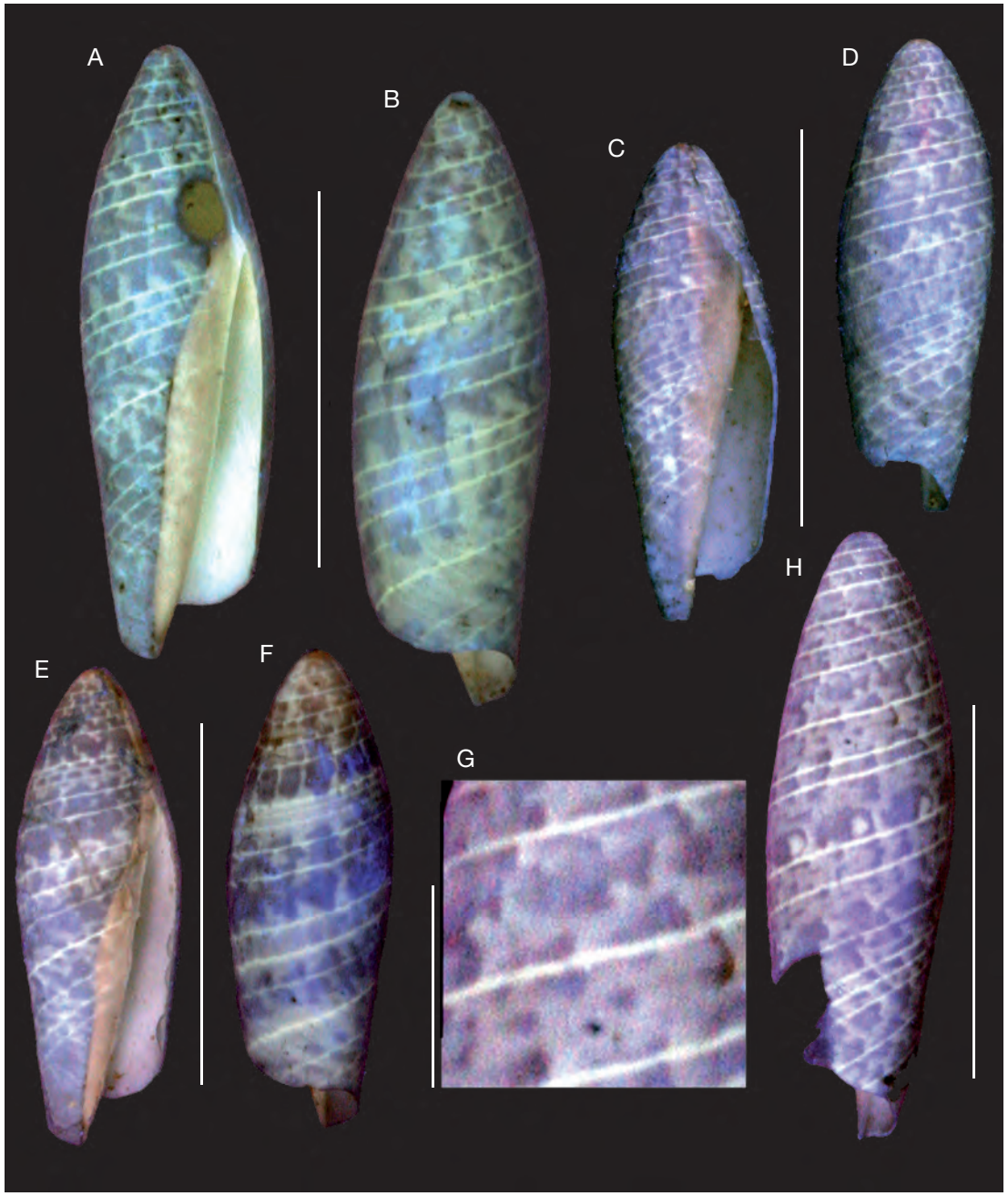

FIG. 19. — *Seraphs peterjungi* n. sp. under UV light: **A**, **B**, holotype MNHN A28578, Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, ventral view; **B**, dorsal view; **C**, **D**, paratype MNHN A28537 (Faullummel coll.), Chaussy (Les Garennes), Lutetian; **C**, ventral view; **D**, dorsal view; **E**, **F**, paratype MNHN A27273 (leg. Pacaud), Chaussy (Les Garennes), Lutetian; **E**, ventral view; **F**, dorsal view; **G**, **H**, paratype MNHN A28931 (leg. Pacaud), Chaussy (Les Garennes), Lutetian; **G**, detailed view of the dots; **H**, dorsal view. Scale bars: A-F, H, 10 mm; G, 2 mm. Photographs by C. Lemzaouda (MNHN).

TYPE LOCALITY. — Villiers-Saint-Frédéric (Yvelines, France), Lutetian (Middle Eocene).

TYPE MATERIAL. — *Ovula fragilis*: syntype(s) from Grignon (Yvelines, France), not found.
Ovula media: lectotype designated by Jung (1974) from the Deshayes collection and now deposited at the UCBL, not found; paralectotypes (UCBL, Deshayes coll.), not found.
A neotype designation is needed to clarify the taxonomic status of this species. A neotype from the locality Villiers-Saint-Frédéric (MNHN A28939, leg. Pacaud, Fig. 21A-F), near Grignon (Yvelines) is accordingly chosen here. This initiative conforms to the rules specified by the ICZN (1999: art. 75), as regards the designation of a neotype.

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Inflated shell up to 11 mm in height and 4 mm in diameter. Aperture long and narrow. Callus of inner lip clearly delineated, but weakly developed. Columella slightly bent backwards near the base. Outer lip thickened and extended above the apex. Outer lip forming an acute structure (Fig. 20B) hiding the actual apex (Jung 1974). Outer lip sinuous, prosocyrt on the abapical part and opisthocyrt on the adapical part of the shell (Fig. 20C). Siphonal notch moderately deep. Surface sculpture of narrow oblique grooves near the base (Fig. 20D).

Colour pattern

The residual pattern is composed of two levels of residual pigmentation: dark lines on a lighter background. These lines are axial and from wavy to zigzagging (Fig. 21A, G, H, L-N). They usually cover the outer lip and the extremities of the shell. On the median part, the shells show a gradual transition from wavy lines to a chessboard pattern (Meinhardt 1998) (Fig. 21A, B, D, E).

VARIABILITY

The lines can be more or less wavy. Some specimens have only axial straight lines on the whole shell surface (Fig. 21C, J, K), while other specimens have a chessboard pattern on the median part of the shell.

Subgenus *Miniseraphs* Jung, 1974

TYPE SPECIES. — *Terebellum* (*Seraphs*) *eratoides* Cossmann, 1889 by original designation. Lutetian, Paris Basin.

Diameza (*Miniseraphs*) *eratoides* (Cossmann, 1889) (Figs 20F-J; 22)

Terebellum (*Seraphs*) *eratoides* Cossmann, 1889: 98, 99, pl. 3, figs 7, 8;

Terebellum (*Seraphs*) *eratoides* – Cossmann 1904: 46. — Cossmann & Pissarro 1905: 97, pl. 16, fig. 36; 1911: pl. 32, fig. 158-7.

Seraphs (*Miniseraphs*) *eratoides* – Jung 1974: 30, pl. 9, figs 10-12, text-figs 19, 20. — Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162.

TYPE LOCALITY. — Chaussy, Les Garennes (Val d'Oise, France), Lutetian (Middle Eocene).

TYPE MATERIAL. — Lectotype designated by Jung (1974) from the Bernay collection; paralectotype (Boutillier coll.) from Vaudancourt (Oise), not found.
The type material of this species has not been found in the Bernay collection, now deposited at the UCBL. A neotype designation is needed to clarify the taxonomic status of this species. A neotype from the type locality (MNHN A28932, Faullummel coll., Fig. 22A-D) is accordingly chosen here. This initiative conforms to the rules specified by the ICZN (1999: art. 75), as regards the designation of a neotype.

OTHER MATERIAL EXAMINED. — See Appendix 1.

SHELL DESCRIPTION

Shell up to 8 mm in height and up to 5 mm in diameter, very stout with wide apical angle (Fig. 20F-H). Aperture long and narrow. Callus of the inner lip clearly delineated, but weakly developed. Columella slightly bent backwards near the base. Outer lip thickened and forming a small protuberance at the apex (Fig. 20J). Outer lip slightly sinuous for the whole height in labral view (Fig. 20G). Siphonal notch moderately deep on the dorsal side. Faint oblique to spiral grooves near the base (Fig. 20I).

COLOUR PATTERN DESCRIPTION

The residual pattern is only composed of 2 levels of residual pigmentation: dark lines on a lighter

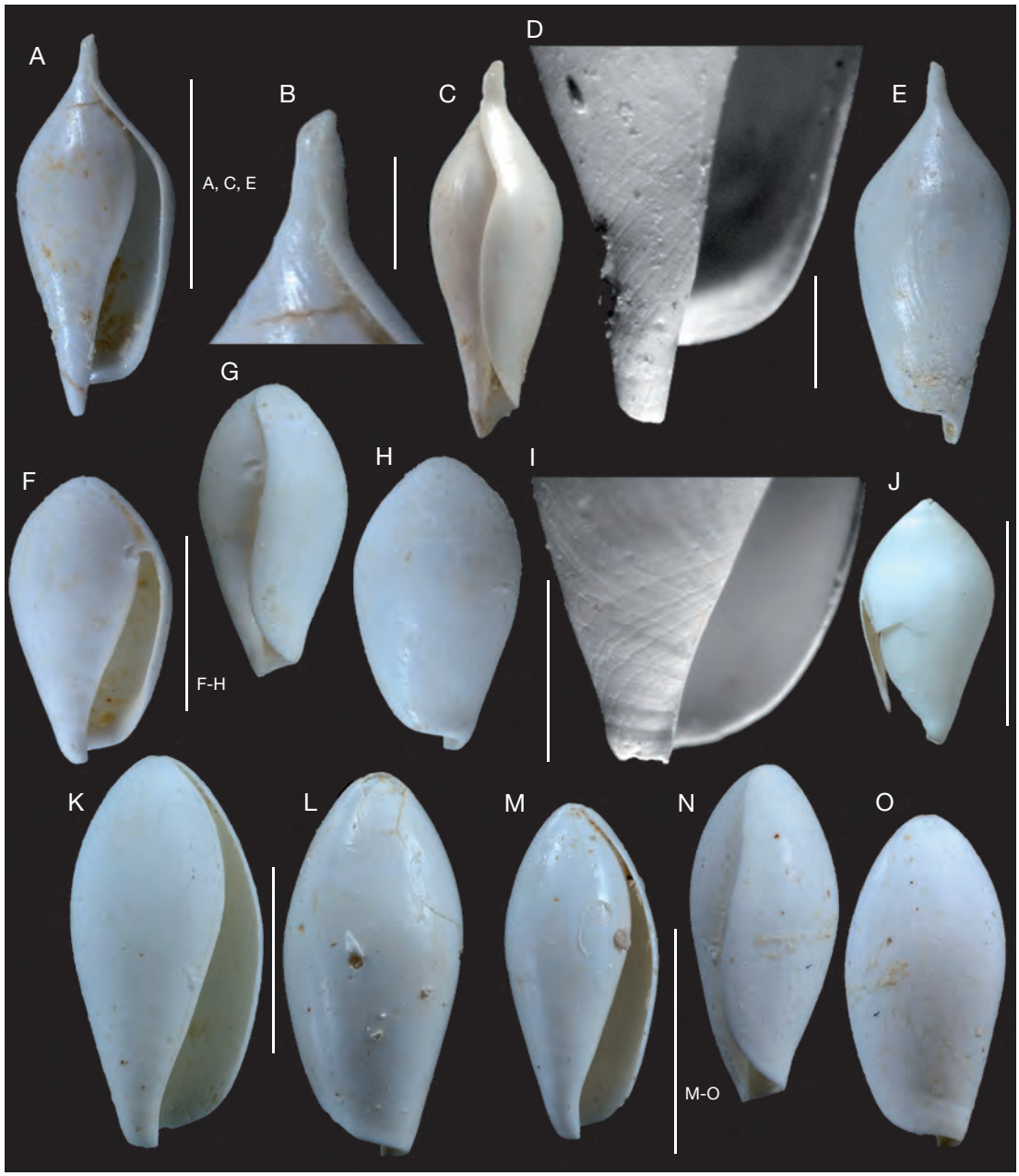

Fig. 20. — *Diameza* Deshayes, 1865 shells in normal light: **A**-**E**, *Diameza* (*s.s.*) *fragilis* (Defrance, 1825), MNHN A28784 (Faullummel coll.), Villiers-Saint-Frédéric, Yvelines, France, Lutetian; **A**, ventral view; **B**, detailed view of the apical part; **C**, labral view; **D**, detailed view of the oblique grooves; **E**, dorsal view; **F**-**J**, *Diameza* (*Miniseraphs*) *eratoides* (Cossmann, 1889); **F**-**H**, MNHN A28785 (Faullummel coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **F**, ventral view; **G**, labral view; **H**, dorsal view; **I**, MNHN A28934 (detailed view of the oblique grooves) (leg. Pacaud), Fontenay-en-Vexin (Beauregard), Eure, France, Lutetian; **J**, MNHN B63254 (dorsal view) (Lhomme coll.), Hervelon, Marne, France, Lutetian; **K**-**O**, *Diameza* (*Miniseraphs*) *Isabella* (Bernay *in* Deshayes, 1865); **K**, **L**, MNHN A28782 (leg.Pacaud), Parnes, Oise, France, Lutetian; **K**, ventral view; **L**, dorsal view; **M**-**O**, MNHN A28783 (leg. Pacaud), Cauvigny, Oise, France, Lutetian; **M**, ventral view; **N**, labral view; **O**, dorsal view. Scale bars: A, C, E-H, J-O, 5 mm; B, D, 1 mm; I, 2 mm. Photographs by C. Lemzaouda (MNHN).

background. These axial lines are wavy, but do not cover the whole shell surface. Most specimens show a combination of two morphologies: 1) dark wavy lines, sometimes forming zigzags (Fig. 22E), which are visible on the extremities of the shell and near the outer lip; 2) on the median part of the shell, a chessboard morphology (Fig. 22A, C, E, G, I, J), as defined by Meinhardt (1998: fig. 5.6). The chessboard pattern can appear as "light dots" on a darker background on poorly preserved shells (Fig. 22G, J).

VARIABILITY

The intraspecific variability is weak. Some specimens show numerous continuous wavy lines near the outer lip (Fig. 22E, F), while others show a chessboard pattern on the whole shell surface, except for the abapical and adapical extremities (Fig. 22G, H).

Diameza (*Miniseraphs*) *isabella*
(Bernay *in* Deshayes, 1865)
(Figs 20K-O; 23)

Terebellum isabella Bernay *in* Deshayes, 1865: 470, 471, pl. 92, figs 14-16.

Terebellum isabella – Bosatta *et al.* 1973: 189.

Terebellum (*Seraphs*) *isabellae* – Cossmann 1889: 98. — Oppenheim 1896: 195 *partim*. — Cossmann 1904: 46. — Cossmann & Pissarro 1911: pl. 32, fig. 158-6.

Diameza (*Miniseraphs*) *isabella* – Jung 1974: 30, 31, pl. 9, figs 13-18, text-figs 20, 21. — Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162.

TYPE LOCALITY. — Chaussy, Les Garennes (Val d'Oise, France), Lutetian (Middle Eocene).

TYPE MATERIAL. — Lectotype designated by Jung (1974) from the Bernay collection, and now deposited at UCBL, not found; paralectotype (UCBL, Deshayes coll.), not found. Accordingly, a neotype designation is needed to clarify the taxonomic status of this species. A neotype from the type locality (MNHN A28935, leg. Pacaud, Fig. 23A-D) is chosen here. This initiative conforms to the rules specified by the ICZN (1999: art. 75), as regards the designation of a neotype.

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Small shell up to 16 mm in height and up to 8 mm in diameter, inflated with wide apical angle. Aperture long and narrow. Callus of the inner lip clearly delineated, but weakly developed. Columella slightly bent backwards near the base. Outer lip thickened and extending to the apex (Fig. 20K). Outer lip prosocyrt on the abapical part and opisthocyrt on the adapical part in labral view (Fig. 20N). Siphonal notch moderately deep. Oblique grooves near the base of the shell.

Colour pattern

The colour pattern of the species is composed of 2 levels of pigmentation: dark axial wavy lines on a lighter background. The axial lines form some zigzags (Fig. 23). The zigzags cover mainly the median part of the shell. On the base and the apex, the lines remain straight or slightly sinuous, showing very weak curves (Fig. 23I-M, O, P). The width of the lines is almost homogenous. The space between them is equivalent to their width.

VARIABILITY

The specimens bear zigzags of greater (Fig. 23D) or lesser amplitude (Fig. 23I). Some specimens bear a gradual transition from wavy lines to a zigzag pattern (Fig. 23H, I), while others show an abrupt transition, probably due to a growth interruption (Fig. 23F, G). Wavy axial lines crossing and forming a localized grid, called meshwork (Fig. 23M, N) as defined by Meinhardt (1998: fig. 5.3c, d), have been observed too.

COMPARISONS OF THE THREE SPECIES OF *DIAMEZA*

Shell

Diameza (*s.s.*) *fragilis* displays a distinctive feature, the acute apical structure (Fig. 20B). According to Jung (1974), this feature is used to distinguish *Diameza* from *Miniseraphs*. *Diameza* (*s.s.*) *fragilis* is however closely related to *D.* (*Miniseraphs*) in sharing a small and inflated shell, a wide apical angle and a sinuous outer lip (Fig. 20). *Diameza* (*Miniseraphs*) *isabella* is very similar to *D.* (*M.*) *eratoides*. *Diameza* (*M.*) *isabella* is more slender (Fig. 20F, K) and the adult specimens are twice

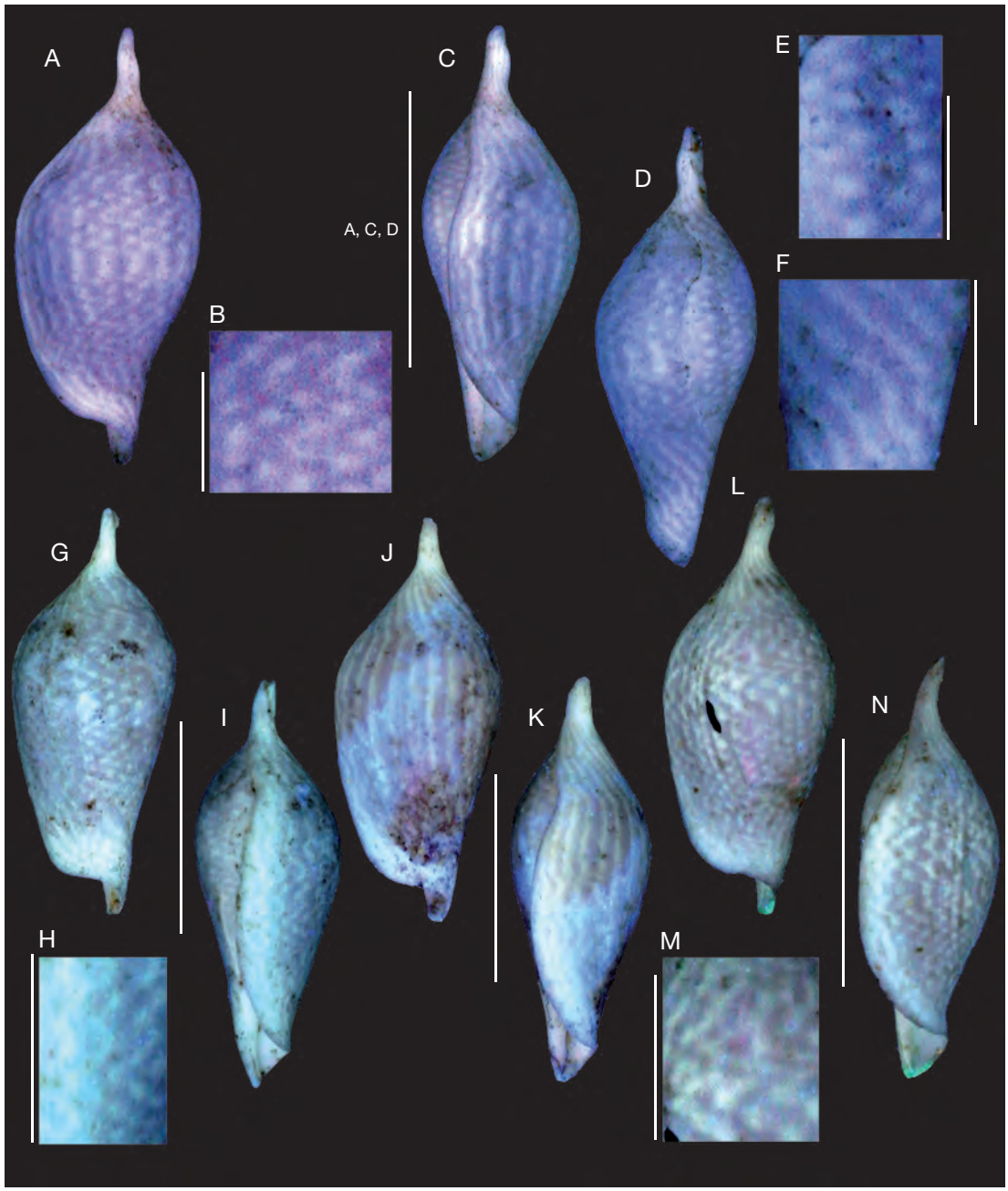

FIG. 21. — *Diameza* (*s.s.*) *fragilis* (Defrance, 1825) under UV light: **A**-**F**, neotype, MNHN A28939 (leg. Pacaud), Villiers-Saint-Frédéric, Yvelines, France, Lutetian; **A**, dorsal view; **B**, detailed view of the chessboard pattern; **C**, labral view; **D**, abapertural view; **E**, detailed view of the chessboard pattern; **F**, detailed view of the lines; **G**-**I**, MNHN A28940 (Faullummel coll.), Villiers-Saint-Frédéric, Lutetian; **G**, dorsal view; **H**, detailed view of the zigzagging lines; **I**, labral view; **J**, **K**, MNHN A28784 (Faullummel coll.), Villiers-Saint-Frédéric, Lutetian; **J**, dorsal view; **K**, labral view; **L**-**N**, MNHN A28942, Villiers-Saint-Frédéric, Lutetian; **L**, dorsal view; **M**, detailed view of the zigzagging lines; **N**, labral view. Scale bars: A, C-D, G, I-L, N, 5 mm; B, E, F, 1 mm; H, M, 2 mm. Photographs by C. Lemzaouda (MNHN).

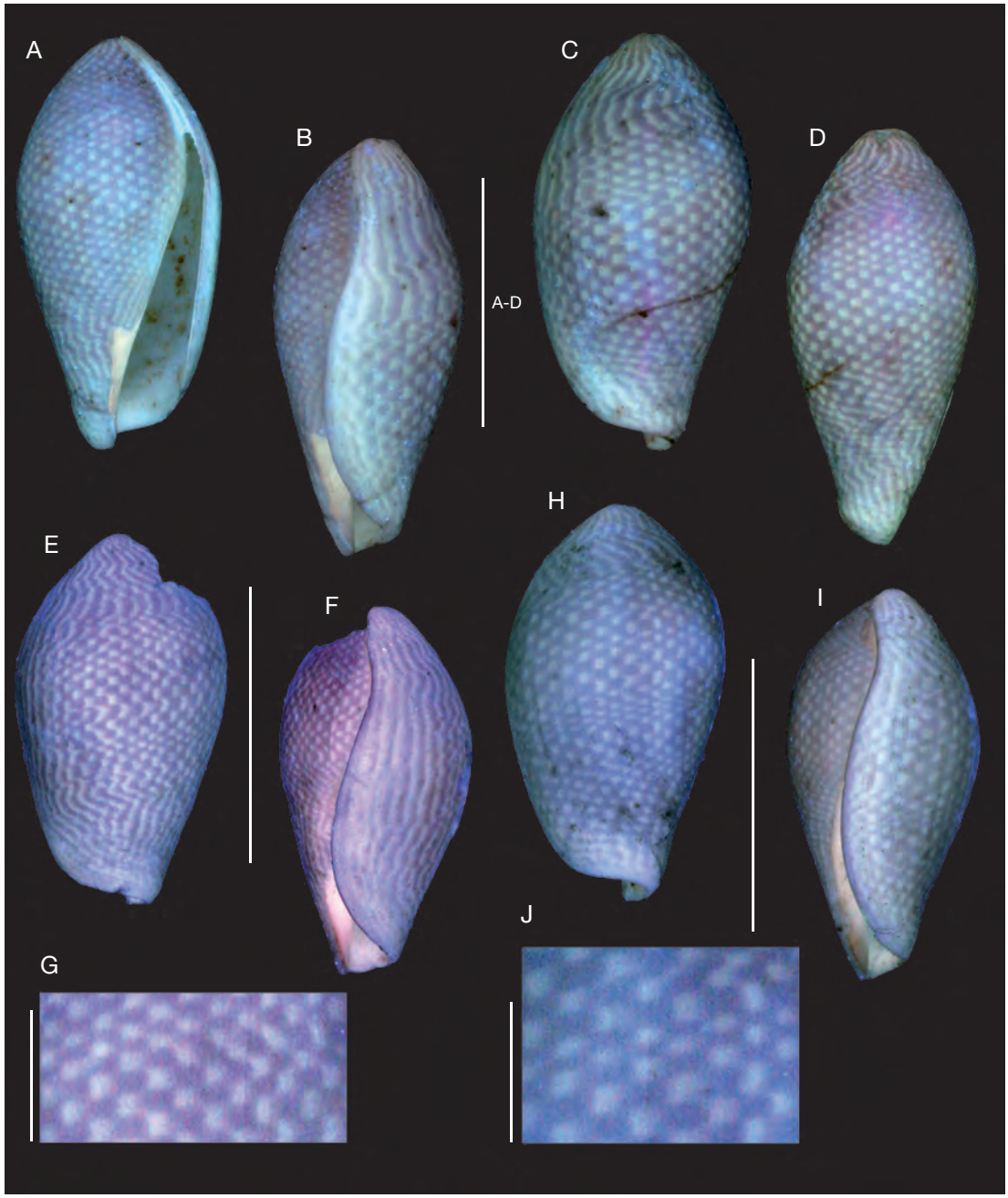

Fig. 22. — *Diameza* (*Miniseraphs*) *eratoides* (Cossmann, 1889) under UV light: **A**-**D**, neotype, MNHN A28932, Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, ventral view; **B**, labral view; **C**, dorsal view; **D**, abapertural view; **E**-**G**, MNHN A28934, Fontenay-en-Vexin, Eure, France, Lutetian; **E**, dorsal view; **F**, labral view; **G**, detailed view of the chessboard pattern; **H**-**J**, MNHN A28933, Fontenay-en-Vexin, Lutetian; **H**, dorsal view; **I**, labral view; **J**, detailed view of the chessboard pattern. Scale bars: A-F, H-I, 10 mm; G, J, 2 mm. Photographs by C. Lemzaouda (MNHN).

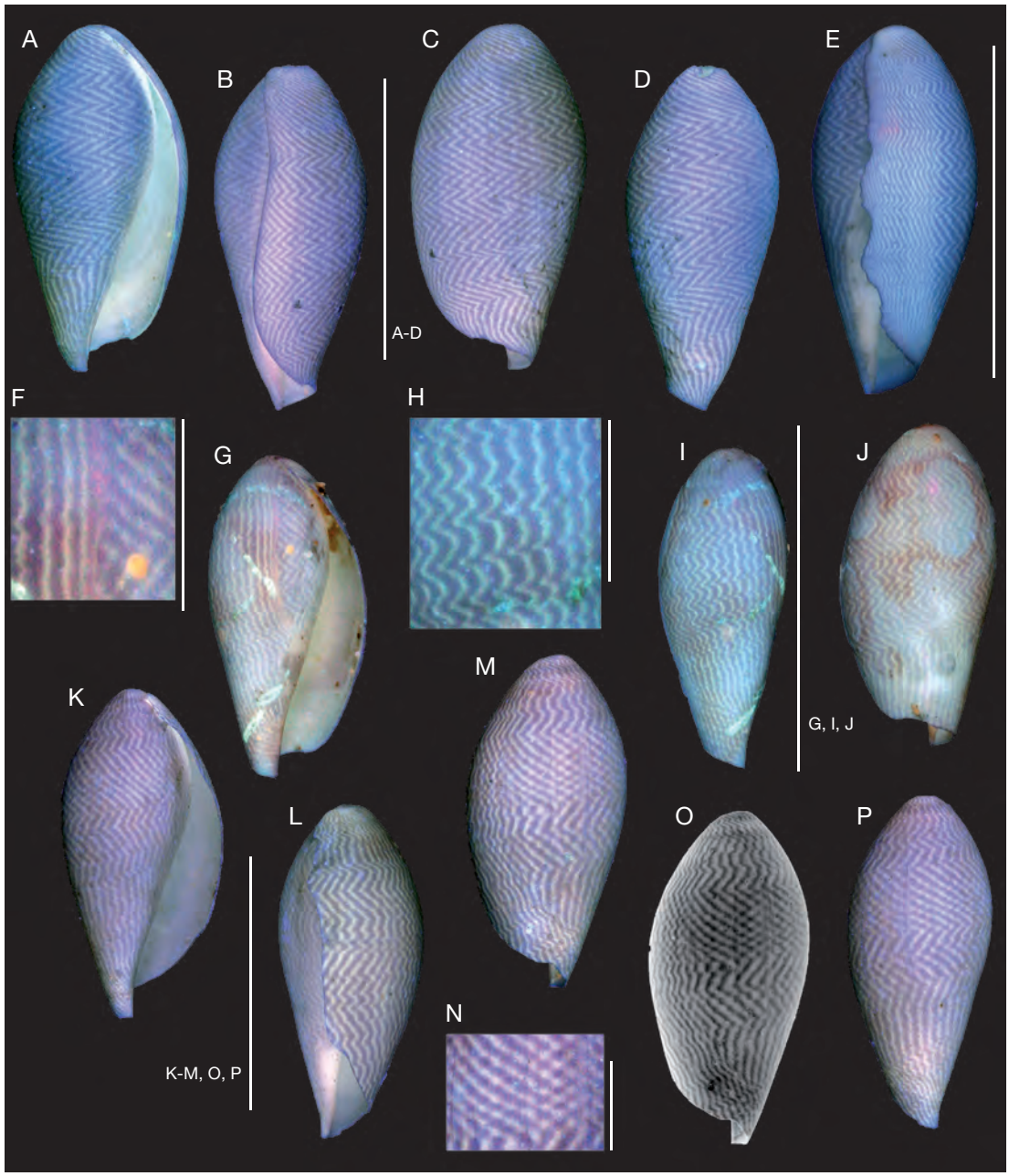

FIG. 23. — *Diameza* (*Miniseraphs*) *isabella* (Bernay, 1889) under UV light: **A**-**D**, neotype, MNHN A28935 (leg. Pacaud), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **A**, ventral view; **B**, labral view; **C**, dorsal view; **D**, abapertural view; **E**, MNHN A28938 (labral view) (leg. Pacaud), Chaussy (Les Garennes), Lutetian; **F**-**J**, MNHN A28937 (Faullummel coll.), Chaussy (Les Garennes), Lutetian; **F**, detailed view of the axial and zigzaging lines; **G**, ventral view; **H**, detailed view of the axial lines; **I**, abapertural view; **J**, dorsal view; **K**-**P**, MNHN A28936, Chaussy (Les Garennes), Lutetian; **K**, ventral view; **L**, labral view; **M**, dorsal view; **N**, detailed view of the zigzaging axial lines; **O**, dorsal view in negative; **P**, abapertural view. Scale bars: A-E, G, I-M, O-P, 10 mm; F, H, N, 2 mm. Photographs by C. Lemzaouda (MNHN).

as large as those of *D.* (*M.*) *eratoides* (Jung 1974). Furthermore, *D.* (*M.*) *eratoides* shows a small protuberance (Fig. 20J, rarely preserved) on the apex, missing in *D.* (*M.*) *isabella*.

Residual colour pattern

All species share a pattern composed of two levels of pigmentation. The colour pattern of *Diameza* (*s.s.*) *fragilis* (Fig. 21) is closely related to that of *D.* (*Miniseraphs*) *eratoides* (Fig. 22). It shares with *D.* (*M.*) *eratoides* a combination of two morphologies: 1) dark wavy lines visible on the extremities of the shell and near the outer lip; and 2) a chessboard pattern on the median part of the shell. Nevertheless, some shells of *Diameza* (*s.s.*) *fragilis* bear a residual pattern only composed of axial lines (Fig. 21J-K), lacking in *D.* (*Miniseraphs*) *eratoides*. *Diameza* (*M.*) *eratoides* differs from *D.* (*M.*) *isabella* by a chessboard pattern covering a large part of the shell. Moreover, the amplitude of the wave of each line is lower than that observed on *Diameza* (*Miniseraphs*) *isabella* (Fig. 23).

Genus *Paraseraphs* Jung, 1974

TYPE SPECIES. — *Paraseraphs tetanus* Jung, 1974 by original designation. Ypresian (Cuisian), Paris Basin.

Paraseraphs tetanus Jung, 1974
(Figs 24A-F; 25; 26)

Paraseraphs tetanus Jung, 1974: 34-36, pl. 9, fig. 26; pl. 10, figs 1-10, text-fig. 12, 26-28.

Terebellum fusiforme – d'Orbigny 1850: 314, no. 304. — Pictet 1855: pl. 64, fig. 2. — Deshayes, 1865: 470. — Mayer, 1866: 319, 332. — Newton, 1894: 97. — Cossmann, 1904: 43, 44, pl. 2, fig. 10; pl. 3, fig. 4. — Cossmann & Pissarro, 1911: pl. 31, fig. 158-1. Non Lamarck, 1802.

Terebellum (*s.s.*) *fusiforme* – Cossmann 1889: 96 *partim*. Non Lamarck, 1802.

Paraseraphs placitus Merle, 1986: 32. Non Jung 1974.

Paraseraphs tetanus – Savazzi 1991: 324, fig. 13G. — Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162. — Pacaud 2008: 724, fig. 2C, D.

TYPE LOCALITY. — Cuise-la-Motte (Oise, France), Ypresian (Cuisian, Lower Eocene).

TYPE MATERIAL. — Holotype (NMB H15409); 3 paratypes (NMB H15408, H15405, H16502).

OTHER MATERIAL EXAMINED. — See Appendix 1.

DESCRIPTION

Shell

Shell up to 38 mm in height and 8 mm in diameter, evolute with straight and almost parallel sides (Fig. 24A, C, D, F). Suture distinct on the adapical part (Fig. 24A, C, D, F). Aperture long and narrow. Callus of the inner lip well developed and well delineated. Columella bent backwards near the base of the shell (Fig. 24B, E). Outer lip slightly opisthocline and thickened on the adapical part. Outer lip not reaching directly to the apex, but bent towards the dorsal side of the shell (Fig. 24B, C, E, F). Callus of the inner lip, thin, extending on the spire towards the apex and forming a narrow band parallel to the outer lip. Siphonal notch moderately deep. No sculpture observed.

Colour pattern

The pattern is composed of 2 levels of colouration: dark elements on a lighter background (Fig. 25). The darker elements are usually very thin and form axial rows of dots (Fig. 25C, F, I) and segments (Fig. 25K). On the subsutural part of the last whorl and on the anal canal, a peculiar pattern can be distinguished. It corresponds to an oblique succession of darker and lighter "patches" (Fig. 25H, J, L, P, R). These "patches" are not true patches as defined in the part terminology, but are the result of the coalescence of axial segments.

VARIABILITY

Among 319 specimens from 5 localities (Cuisian), 304 (95.3%) show a residual pattern under UV light (Table 1). Thus, these observations provide a good general survey of intraspecific variability of the pattern of this species.

The residual pattern of *Paraseraphs tetanus* shows strong variability (Fig. 26). The dots are variable in size and shape from axially elongated to circular or triangular shape or indeed completely distorted (Fig. 26I, J). Their density on the shell, and the degree

FIG. 24. — *Paraseraphs* Jung, 1974 shells in normal light: **A**-**F**, *P. tetanus* Jung, 1974; **A**-**C**, MNHN A28579 (Faullummel coll.), Saint-Gobain, Aisne, France, Ypresian (Cuisian); **A**, ventral view; **B**, labral view; **C**, dorsal view; **D**-**F**, MNHN A28787 (Ferry coll.), Cuise-Lamotte (Butte-des-Usages), Oise, France, Ypresian (Cuisian); **D**, ventral view; **E**, labral view; **F**, dorsal view; **G**-**M**, *P. placitus* Jung, 1974; **G**-**J**, MNHN A28786 (Lhomme coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **G**, ventral view; **H**, labral view; **I**, detailed view of the apical part; **J**, dorsal view; **K**, MNHN A28962 (detailed view of the basal part) (leg. Pacaud), Fercourt, Oise, France, Lutetian; **L**, **M**, MNHN A28774 (Lhomme coll.), Chaussy (Les Garennes), Lutetian; **L**, dorsal view; **M**, labral view. Scale bars: A-H, J, L, M, 10 mm; I, 5 mm; K, 2 mm. Photographs by C. Lemzaouda (MNHN).

of coalescence, can be weak to very considerable. Some shells bear only a few dark dots disseminated on the surface (Fig. 26F, G, K). When the density of dots increases, they form some thin axial rows (Fig. 26D, E, H) or, by coalescence, compressed segments (Fig. 26A-C) or sinuous stripes (Fig. 26O-R). In spite of this variability, two representative morphological types can be distinguished (types 1 and 2, Fig. 27). Type 1 corresponds to the most abundant portion of the analysed specimens. The pattern of the type 1 is composed of axial rows of more or less coalescent dark dots (Fig. 26A-F). Type 2 bears some sinuous and more or less discontinuous axial stripes (Fig. 26O-R). Several shells show a morphology intermediate between both types (Figs 26G-K, L-N; 27). The relative abundance of these morphologies is given in Figure 27. The Figure 26 illustrates each type described above with several intermediate specimens, showing the impossibility of separating one type from another, as different species.

Paraseraphs placitus Jung, 1974
(Figs 24G-M; 28)

Paraseraphs placitus Jung, 1974: 38, pl. 10, figs 13-18, text-fig. 28.

Terebellum fusiforme – Sowerby 1821: 157, pl. 287. — De Blainville 1828: 276. — Deshayes 1835: 738, pl. 95, figs 30, 31. Non Lamarck, 1802.

Terebellum (*s.s.*) *fusiforme* – Glibert 1938: 65, 66, pl. 2, fig. 7. — Cossmann 1889: 96 *partim*. Non Lamarck, 1802.

Terebellum (*s.s.*) *fusiforme postconicum* Cossmann, 1904: 44. Non de Gregorio, 1880.

Paraseraphs placitus – Dolin *et al.* 1980: 28. — Le Renard 1992: 6. — Le Renard & Pacaud 1995: 112. — Pacaud & Le Renard 1995: 162.

Type locality. — Les Garennes, Chaussy (Val d'Oise, France), Lutetian (Middle Eocene).

Type material. — Holotype (NMB H14491); paratype (NMB H10539), Les Garennes, Chaussy (Val d'Oise, France); paratypes (UCBL coll. Deshayes), Mouchy-le-Châtel (Oise) and Parnes (Oise), not found.

Other material examined. — See Appendix 1.

Description

Shell

Shell up to 30 mm in height and 7 mm in diameter, moderately slender and evolute with distinct suture. Aperture long and narrow. Callus of the inner lip well developed, well delineated, extending to the apex and forming a narrow band parallel to the outer lip (Fig. 24I). Basal part of the columella bent backwards. Outer lip, almost straight and slightly opisthocline (Fig. 24H, M), not thickened on the basal part of the shell. Adapical part of the outer lip thickened and extending from the adapical end of the aperture, towards the apex (Fig. 24H), or bent towards the dorsal side (Fig. 24M). Siphonal notch moderately deep. Sculpture with a few oblique grooves near the base of the shell (Fig. 24K).

Colour pattern

Paraseraphs placitus has numerous and irregular dots with 2 levels of residual coloration on a lighter background (Fig. 28). The first level consists of triangular spots, darker than the background. These spots, more or less distorted, are orientated towards the growing edge (Fig. 28C, F, L). The second level consists of fluorescent spots with fuzzy borders, lighter than the background. These light spots, adjacent to the base of dark spots, are narrow and directed towards the inner lip in ventral view (Fig. 28C, F, L). They are variable in size. These two components form the dots. The density of dots is generally low. Also, a peculiar pattern can be distinguished on the adapical part of the outer lip: an oblique succession of darker and lighter "patches" (Fig. 28B, D, E, M, N). These "patches" are probably the result of the coalescence of the dark axial segments (Fig. 28D).

Variability

Sometimes the darker spots of the dots are larger near the edge of the outer lip (Fig. 28B, C, P) and are coalescent.

Paraseraphs armoricus (Vasseur, 1882)
(Figs 29A-C; 30)

Terebellum armoricum Vasseur, 1881: 174, no. 22 and p. 245, no. 43 (*nomen nudum*).

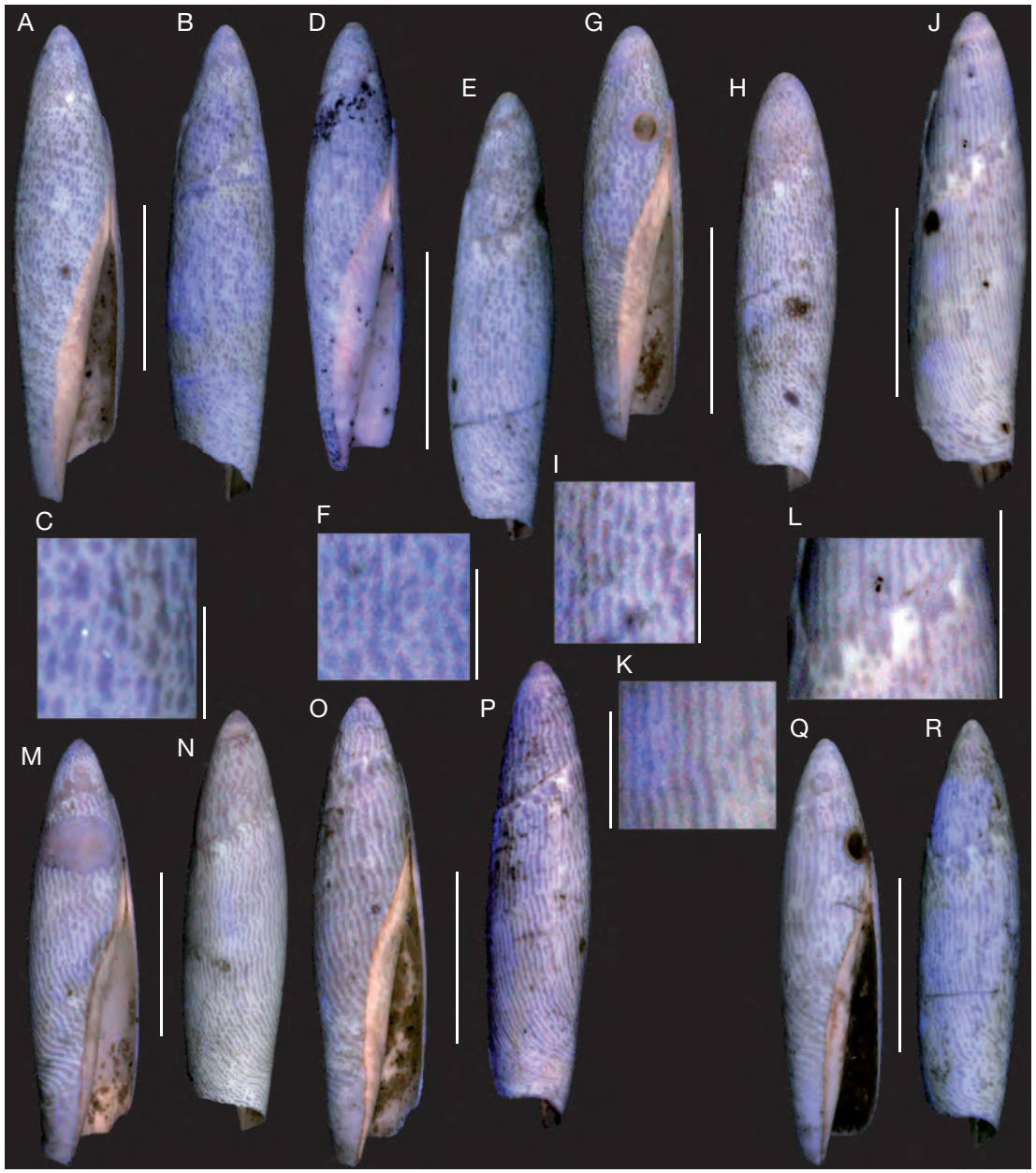

FIG. 25. — *Paraseraphs tetanus* Jung, 1974 under UV light: **A**-**C**, MNHN A28946, Cuise-Lamotte (Butte-des-Usages), Oise, France, Ypresian (Cuisian); **A**, ventral view; **B**, dorsal view; **C**, detailed view of the rows of dots; **D**-**F**, MNHN A28945, Saint-Gobain, Aisne, France, Ypresian (Cuisian); **D**, ventral view; **E**, dorsal view; **F**, detailed view of the the rows of dots; **G**-**I**, MNHN A28947, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **G**, ventral view; **H**, dorsal view; **I**, detailed view of the the rows of dots; **J**-**L**, MNHN A28948, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **J**, dorsal view; **K**, detailed view of the rows and lines; **L**, detailed view of the subsutural part; **M**, **N**, MNHN A28943, Cuise-Lamotte (Butte-de-Usages), Ypresian (Cuisian); **M**, ventral view; **N**, dorsal view; **O**, **P**, MNHN A28941, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **O**, ventral view; **P**, dorsal view; **Q**, **R**, MNHN A28944, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **Q**, ventral view; **R**, dorsal view. Scale bars: A, B, D, E, G, H, J, M-R, 10 mm; C, F, I, K, 2 mm; L, 5 mm. Photographs by C. Lemzaouda (MNHN).

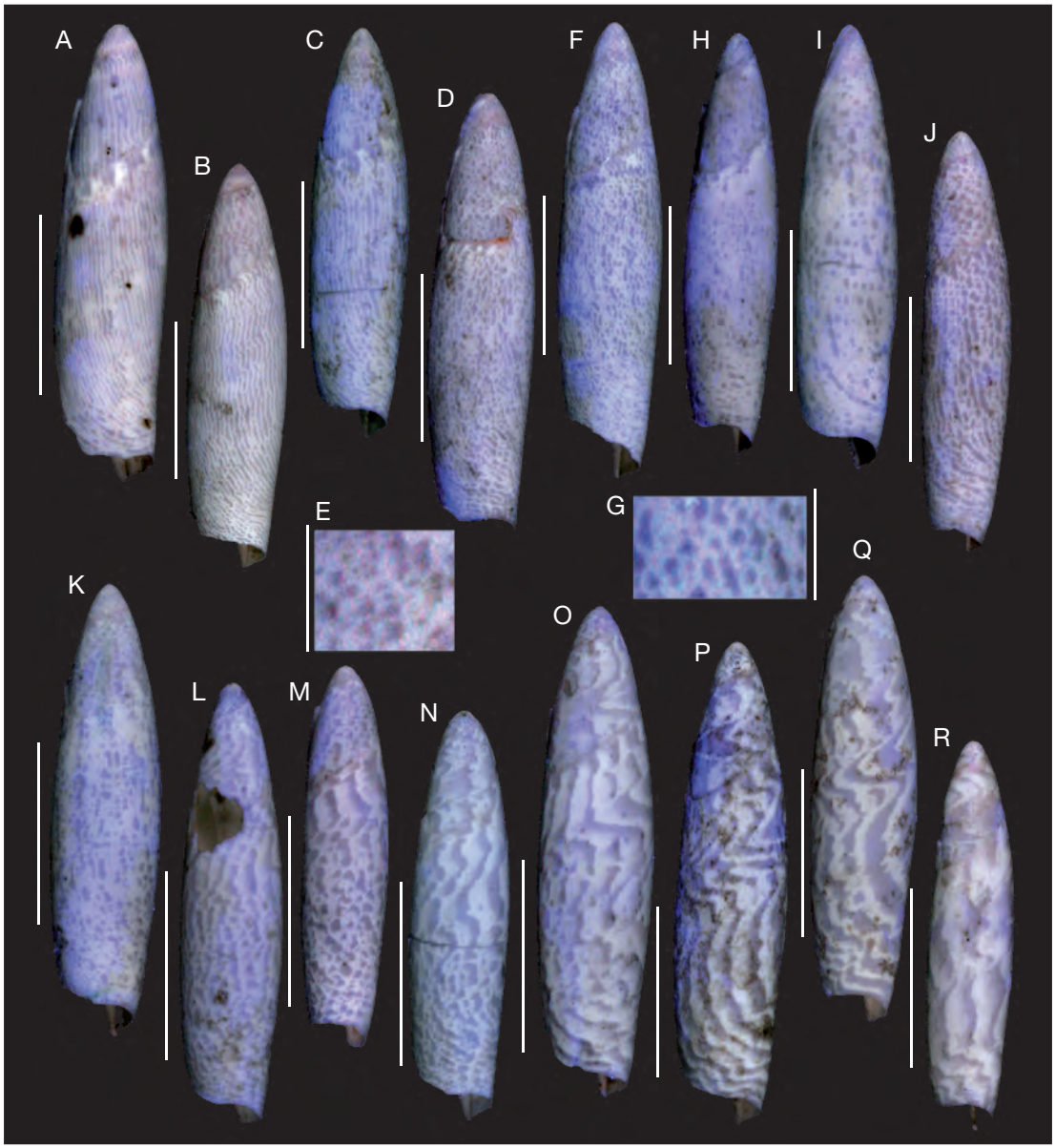

Fig. 26. — Variability of *Paraseraphs tetanus* Jung, 1974 in dorsal view and under UV light: **A**, MNHN A28948, Cuise-Lamotte (Butte-des-Usages), Oise, France, Ypresian (Cuisian); **B**, MNHN A28943, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **C**, MNHN A28944, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **D**, **E**, MNHN A28952, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **E**, detailed view of the dots; **F**, **G**, MNHN A28946, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **G**, detailed view of the dots; **H**, MNHN A28949, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **I**, MNHN A28579 (Faullummel coll.), Saint-Gobain, Aisne, France, Ypresian (Cuisian); **J**, MNHN A28953, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **K**, MNHN A28956 (Faullummel coll.), Saint-Gobain, Ypresian (Cuisian); **L**, MNHN A28954, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **M**, MNHN A28955, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **N**, MNHN A28958 (Faullummel coll.), Saint-Gobain, Ypresian (Cuisian); **O**, MNHN A28951, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **P**, MNHN A28950, Cuise-Lamotte (Butte-des-Usages), Ypresian (Cuisian); **Q**, MNHN A28957, Cuise-Lamotte (Butte-des-Usage), Ypresian (Cuisian); **R**, MNHN A28959 (Faullummel coll.), Saint-Gobain, Ypresian (Cuisian); **A**-**G**, Type 1; **H**-**N**, intermediaries 1-2; **O**-**R**, Type 2. Scale bars: A-D, F, H-R, 10 mm; E, G, 2 mm. Photographs by C. Lemzaouda (MNHN).

Terebellum armoricum Vasseur, 1882: pl. 2, fig. 20; pl. 3, fig. 55.

Terebellum cylindricum Cailliaud, 1856: 42 (*nomen nudum*). — Cailliaud *in* Vasseur 1881: 232 (*nomen nudum*).

Terebellum fusiforme – Cailliaud 1856: 42. — Vasseur 1881: 232. Non Lamarck, 1802.

Terebellum (*s.s.*) *armoricense* – Cossmann 1898: 340, pl. 8, fig. 10 and 15, unjustified emendation; 1904: 44.

Terebellum armoricensis – Cossmann 1917: pl. 2, fig. 20; pl. 3, fig. 55.

Paraseraphs armoricensis – Jung 1974: 36, 37, pl. 9, figs 19-25, text-fig. 28.

TYPE LOCALITY. — Saffré, Bois-Gouët (Loire-Atlantique, France), Bartonian (Middle Eocene).

TYPE MATERIAL. — The type material of Vasseur (1882) was lost (Cossmann 1898). Accordingly, Cossmann (1898: pl. 8, figs 10, 15) designated a neotype from the Dumas collection deposited in MNHN, but this specimen has not been found either. Later, Jung (1974: 36) wrongly considered the neotype of Cossmann to be the holotype of this species.

OTHER MATERIAL EXAMINED. — See Appendix 1.

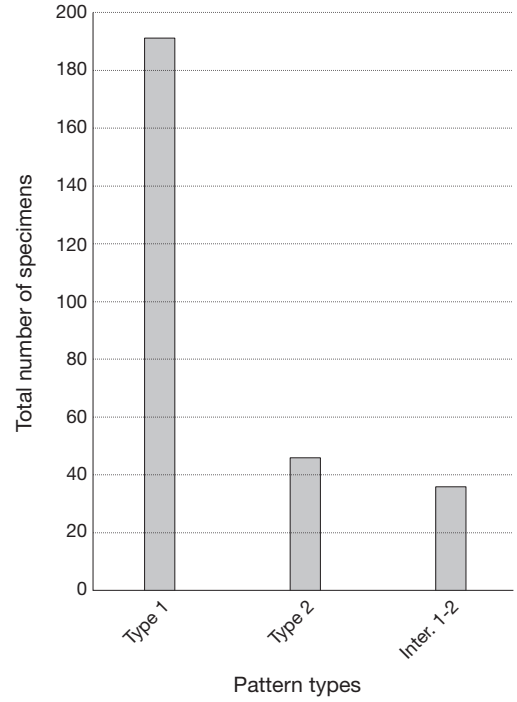

FIG. 27. — Distribution of the pattern types with their intermediaries (**Inter.**) in *Paraseraphs tetanus* Jung, 1974.

SHELL DESCRIPTION

Shell 73 mm in height and 13 mm in diameter, slender and elongated. Shell evolute with distinct suture. Aperture long and narrow. Callus of the inner lip well developed and clearly delineated (Fig. 29A, B). Abapical part of the columella bent backwards. Outer lip, almost straight (Fig. 29C), not thickened except near the adapical end of the aperture. Outer lip running towards the apex and slightly bent on the dorsal side of the shell (following Jung [1974], our material being broken). Siphonal notch moderately deep on the dorsal side. No sculpture on the surface of the shell.

COLOUR PATTERN DESCRIPTION

Paraseraphs armoricus bears numerous and variable-sized dots on a lighter background (Fig. 30). These dots, generally circular, spread over the whole surface of the shell. They show 2 levels of residual pigmentation (Fig. 30B, C, E): 1) round dark spots orientated toward the inner lip; and 2) white fluorescent, crescent-like spots orientated towards the growing edge. These 2 components form the dots. The density of dots is low, with little coalescence (Fig. 30B).

COMPARISONS OF THE THREE SPECIES OF *PARASERAPHS*: *P. TETANUS*, *P. PLACITUS* AND *P. ARMORICUS*

Shell

These species of *Paraseraphs* are easily distinguishable from the species of *Seraphs* by their evolute spire (Figs 24; 29). Moreover, the shells are usually more slender. According to our observations, several differential characters attributed by Jung (1974) to distinguish *Paraseraphs tetanus* and *P. placitus* seem to be erroneous. Jung (1974) believed that *P. tetanus* is more slender than *P. placitus*. In fact, the shape of *P. tetanus* is variable and some specimens can be as inflated as *P. placitus* (Fig. 24F, L). Furthermore,

Jung (1974) suggested that, on the posterior part of the shell, the outer lip of *P. tetanus* is bent towards the dorsal side, while that of *P. placitus* runs directly to the apex. For *P. tetanus*, his observations seem correct, but in *P. placitus*, the outer lip can continue directly to the apex or can be bent towards the dorsal side (Fig. 24H, M). Accordingly, this character is not consistent to distinguish the two species. On the other hand, contrary to Jung assumptions, the shell of *P. tetanus* does not show oblique grooves near the base. The Bartonian species *P. armoricus* is very similar to the other species, but much bigger (Fig. 29A-D).

Residual colour pattern

The dots constituting the pattern of *P. placitus* (Fig. 28) appear very similar to those of *S. volutatus*, *S. sopitus* and *S. olivaceus* (Figs 7-10). However, the dots are clearly ordered in these *Seraphs*, while no axial rows of dots have been observed in *P. placitus*. Regarding *P. armoricus* (Fig. 30), the orientation of the two components of the dots is inversed in comparison to *P. placitus* and even *Seraphs*. The darker spots are orientated towards the outer lip in *P. armoricus* and towards the inner lip in *P. placitus*. Furthermore, the shape of the dots is obviously different between *P. placitus* and *P. armoricus*. It is generally triangular for *P. placitus* (Fig. 28C, F, L), while it is circular for *P. armoricus* (Fig. 30B, E). The pattern of *P. tetanus* is quite variable, but differs sharply by the occurrence of axial rows and by lacking of white fluorescent spots (Fig. 25).

Using shell characters, it is difficult to separate these three species of *Paraseraphs*, while using residual colour pattern we can obviously observe differences justifying their distinction.

Paraseraphs praecedens n. sp.
(Fig. 29E, F)

TYPE LOCALITY. — Abbecourt (Oise), France, Thanetian (Upper Paleocene), biozone NP9.

TYPE MATERIAL. — Holotype (MNHN A05707, leg. Pacaud)

ETYMOLOGY. — As the precursor of the Eocene *Paraseraphs*.

DESCRIPTION OF THE HOLOTYPE (FIG. 29E, F)

Shell 19 mm in height and 7 mm in diameter, inflated and evolute with distinct suture. Spire short and blunt. Aperture long and narrow. Callus of the inner lip not preserved. Basal part of the columella and outer lip not preserved. No sculpture on the surface of the shell. No residual pattern observed under UV light (shell too poorly preserved).

COMPARISONS OF THE SHELLS

This species is easily distinguishable from the members of *Seraphs* by its evolute spire. Within *Paraseraphs*, although the shell of *Paraseraphs praecedens* n. sp. is incompletely preserved, it seems clearly stouter than the other species (Fig. 29D-F). Also, it is the smallest species of the genus.

DISCUSSION

From the Thanetian, *Paraseraphs praecedens* n. sp. is the oldest record of *Paraseraphs* for the world and the oldest record for the Seraphsidae in Europe. Previously, the oldest European occurrence of the Seraphsidae was *Paraseraphs tetanus* from the Ypresian (Cuisian, biozone NP 12) of the Paris Basin. Another species in this family is recorded in the ?Late Paleocene-Early Eocene, *Seraphs minus* (Vincent, 1913) from Angola (Landana beds, Cabinda, West Africa). Jung (1974) regarded it as a *nomen dubium*, because the two syntypes "represent the immature stage of some species of *Seraphs*". However, although this species is only based on young specimens, it should be considered as one of the oldest records of the Seraphsidae, along with *P. praecedens* n. sp.

GENERAL DISCUSSION

So far, the colour patterns of the Seraphsidae have never been recorded; except in the single reference (concerning *Seraphs volutatus*) by Jung (1974): "Most of the perfectly preserved shells from the middle Eocene of Villiers-Saint-Frédéric near Paris show remnants of the color pattern which consists of many small, somewhat irregular dots". Accordingly, the present study provides new information on the evolution of the pattern of the Seraphsidae, on the intraspecific variability of the studied spe-

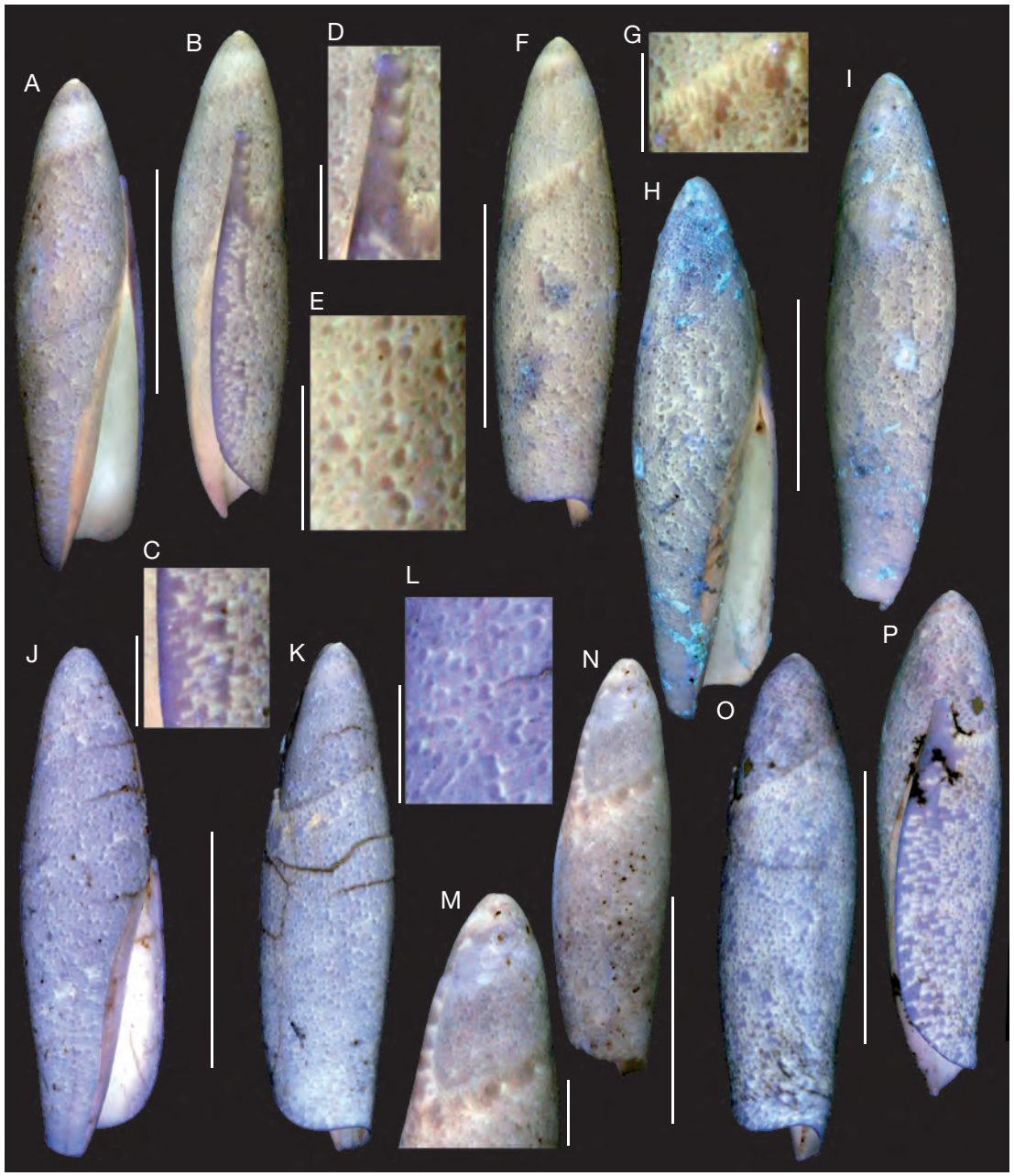

FIG. 28. — *Paraseraphs placitus* Jung, 1974 under UV light: **A**-**G**, MNHN A28961 (leg. Pacaud), Fercourt, Oise, France, Lutetian; **A**, ventral view; **B**, labral view; **C**, detailed view of the outer lip; **D**, detailed view of the adapical part of the outer lip; **E**, detailed view of the dots; **F**, dorsal view; **G**, detailed view of the subsutural part; **H**, **I**, MNHN A28960 (leg. Pacaud), Parnes, Oise, France, Lutetian; **H**, dorsal view; **I**, abapertural view; **J**-**L**, MNHN A28963 (Ballot coll.), Grignon, Yvelines, France, Lutetian; **J**, ventral view; **K**, dorsal view; **L**, detailed view of the dots; **M**, **N**, MNHN A28966 (Boule coll.), Chaussy (Les Garennes), Val d'Oise, France, Lutetian; **M**, detailed view of the apical part; **N**, dorsal view; **O**, **P**, MNHN A28964 (Ballot coll.), Grignon, Lutetian; **O**, dorsal view; **P**, labral view. Scale bars: A, B, F, H-K, N-P, 10 mm; C-E, G, L, M, 2 mm. Photographs by C. Lemzaouda (MNHN).

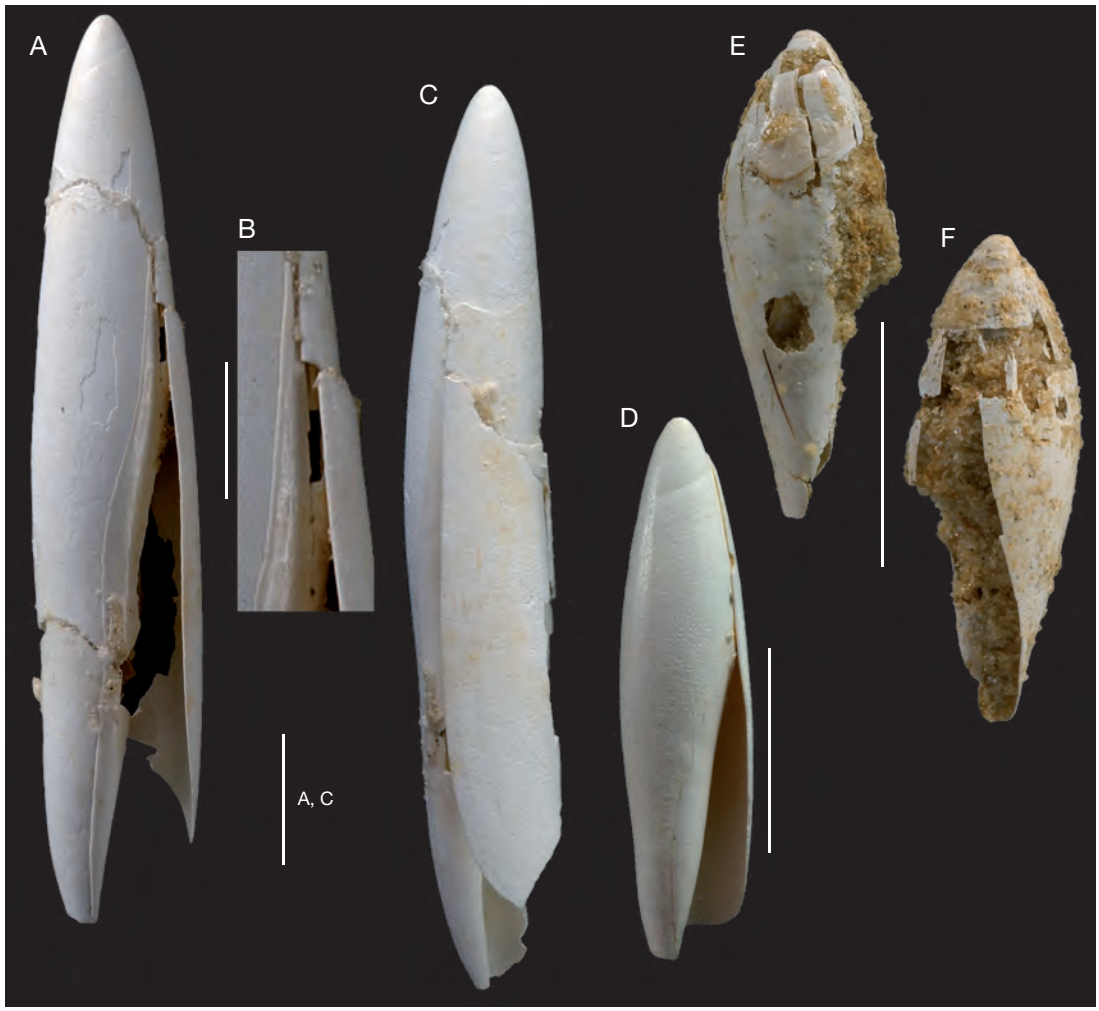

Fig. 29. — *Paraseraphs* Jung, 1974 shells in normal light: **A**-**C**, *P. armoricus* (Vasseur, 1882), MNHN A28788 (leg. Pacaud), Saffré (Bois-Gouët), Loire-Atlantique, France, Bartonian; **A**, ventral view; **B**, detailed view of the adapical part of the aperture; **C**, labral view; **D**, *P. tetanus* Jung, 1974, MNHN A29224 (ventral view) (Ferry coll.), Cuise-Lamotte, Oise, France, Ypresian (Cuisian), in comparison to *P. armoricus* and *P. praecedens* n. sp.; **E**, **F**, *P. praecedens* n. sp., holotype MNHN A05707 (leg. Pacaud), Abbecourt, Oise, France, Thanetian; **E**, ventral view; **F**, dorsal view. Scale bars: A, C, D-F, 10 mm; B, 5 mm. Photographs by C. Lemzaouda (MNHN).

cies, on their stratigraphic range (Fig. 31) and on the systematics on the family.

Evolution of the colour pattern of the Seraphsidae through time

Most of the morphologies constituting the colour pattern of the Recent species *Terebellum terebellum* (Figs 1; 2) were already present in Palaeogene species (dots with 2 levels of residual pigmentation, rows of dots, spiral lines). There is no significant difference, except for the occurrence of zigzags and chessboard pattern only recorded in the genus *Diameza* (Figs 21; 22). Dockery (1980) assumed that Eocene molluscs of the Moodys Branch Formation exhibit colour patterns that still persist in living representatives of the same family or genus. The same can be said for the Palaeogene Seraphsidae, and from the Early Eocene to the Recent few changes in pattern are recorded.

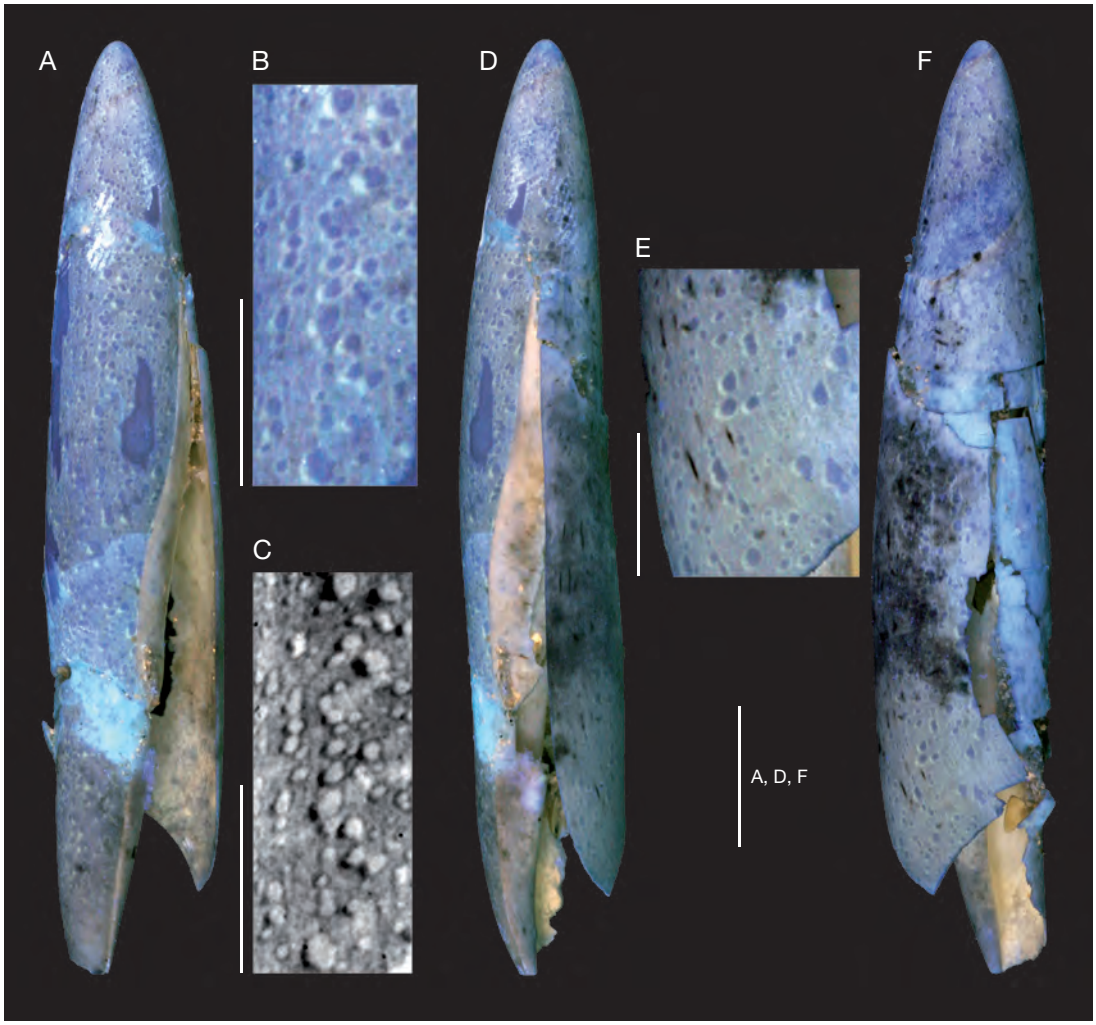

FIG. 30. — *Paraseraphs armoricus* (Vasseur, 1882) under UV light: **A**-**F**, MNHN A28788, Saffré (Bois Gouët), Loire-Atlantique, France, Lutetian; **A**, ventral view; **B**, **C**, detailed views of the dots (**C** in negative view); **D**, labral view; **E**, detailed view of the dots; **F**, dorsal view). Scale bars: A, D, F, 10 mm; B, C, E, 5 mm. Photographs by C. Lemzaouda (MNHN).

INTRASPECIFIC VARIABILITY:

Among the species, from examining very numerous samples, a very considerable intraspecific variability observed in *Paraseraphs tetanus* (304 ex.) and *Seraphs chilophorus* (160 ex.) is also apparent within the Recent species *Terebellum terebellum* (Figs 1; 2). However, lower variability is recorded in *S. volutatus* (494 ex.), *D.* (*M.*) *isabella* (117 ex.) and *P. placitus* (66 ex.). Our study allows an overall view of variability and the distinction of new species, when the sample is sufficient. As a result, a new species *S. peterjungi* n. sp. (24 ex.), has been described and two species are in open nomenclature, because of insufficient specimens (*Seraphs* sp. 1 and *Seraphs* sp. 2). The pattern variability appears low for the following species: *Seraphs sopitus*, *S. olivaceus*, *S. leukoleptus*, *S. peterjungi* n. sp., *Diameza* (*s.s.*) *fragilis*, *D.* (*M.*) *eratoides* and *Paraseraphs armoricus*, but the number of studied specimens does not exceed 30 (Table 1).

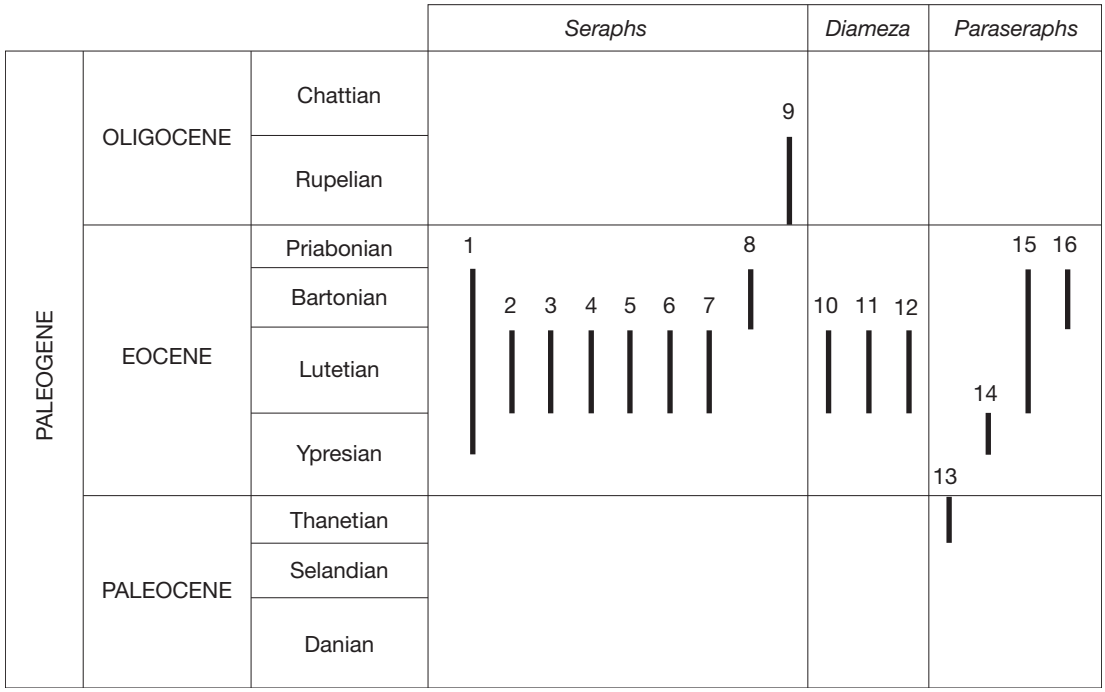

FIG. 31. — New stratigraphic ranges of the Paleogene Seraphsidae Jung, 1974: **1**, *Seraphs volutatus* (Solander *in* Brander, 1766); **2**, *Seraphs olivaceus* (Cossmann, 1889); **3**, *Seraphs chilophorus* (Cossmann, 1889); **4**, *Seraphs peterjungi* n. sp.; **5**, *Seraphs leukoleptus* Jung, 1974; **6**, *Seraphs* sp. 1; **7**, *Seraphs* sp. 2; **8**, *Seraphs sopitus* (Solander *in* Brander, 1766); **9**, *Seraphs subconvolutus* (d'Orbigny, 1852); **10**, *Diameza* (*s.s.*) *fragilis* (Defrance, 1825); **11**, *Diameza* (*Miniseraphs*) *eratoides* (Cossmann, 1889); **12**, *Diameza* (*Miniseraphs*) *isabella* (Bernay *in* Deshayes, 1865); **13**, *Paraseraphs praecedens* n. sp.; **14**, *Paraseraphs tetanus* Jung, 1974; **15**, *Paraseraphs placitus* Jung, 1974; **16**, *Paraseraphs armoricus* (Vasseur, 1882).

SYSTEMATIC RESULTS

1) *Seraphs peterjungi* n. sp. is defined on the base of the residual pattern, but it resembles the shell shape of *S. chilophorus*. Accordingly, both species cannot be distinghished without a study under UV light; 2) in previous works, *Diameza* and *Miniseraphs* were regarded as two subgenera of *Seraphs*. The morphologies of the residual pattern, only slightly variable, are very close but strongly differ from those of the members of *Seraphs*. Considering also the shell morphology, *Diameza fragilis*, *Miniseraphs eratoides* and *M. isabella* are excluded from *Seraphs*. These three species are, here, regarded as belonging to a distinct genus *Diameza* including two subgenera: *Diameza* and *Miniseraphs*. *Seraphs* no longer includes any subgenera; 3) the use of the residual colour pattern as a taxonomic tool provides a new complex of characters enabling us to validate or to invalidate some previous results. For example, in the genus *Paraseraphs*, several shell shape characteristics have been proposed by Jung (1974) to differentiate *P. tetanus* from *P. placitus*. Although observation of the residual patterns under UV light justifies the definition of two species, Jung's differential characteristics make their distinction more difficult and are probably erroneous.

CONCLUSION

Dommergues *et al.* (2006) use a palaeontological approach (shell shape and sculpture) in a study of two Recent and closely related species of the genus *Trivia* Gray, 1837. They show that the only way to distinguish them without the soft

parts is by the colour pattern: *Trivia monacha* (Da Costa, 1778) can be easily recognised by three dark coloured dots, while *T. arctica* (Pultenay, 1799) lacks them. In their work, in spite of strong analysis of the shell shape variability, they state that the palaeontological approach does not "unmask" the real biodiversity. This work shows how observation under UV light provides a contribution to the identification of different species with morphologically similar forms. Thus, the residual colour pattern should be regarded as an additional feature to consider in the concept of palaeontological species.

In the case of the two European *Trivia*, the occurrence of the dots in *T. monacha* is a sufficiently constant pattern to distinguish the species from *T. arctica*. Nevertheless, as seen in the single extant Seraphsidae, *Terebellum terebellum*, huge intraspecific pattern variability is reported. Thus, in the case of the Seraphsidae, it is not possible to consider differences in remnants of the pigmentation from a small sample as the results of speciation and too small sample does not allow for the avoidance of such pitfalls as the overestimation of the fossil biodiversity. This is precisely the case with *S. chilophorus* and *Paraseraphs tetanus*, which display a strong intraspecific variability. In conclusion, we fully agree with Dommergues *et al.* (2006), that colour pattern should be regarded as an additional feature to consider in the concept of palaeontological species, but, as with other characters, it is necessary to take account of the intraspecific variability.

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APPENDIX 1

List of the fossil material. Abbreviations: **no**, no collection number; **x**, inadequate preservation, UV test useless. All the numbered specimens are deposited at the MNHN except the specimen EM 33124.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
Seraphs volutatus (Solander *in* Brander, 1766)					
Ypresian, Paris Basin					
A30419	Leroy	1	Sapicourt, Marne, France	Ypresian	1
A30420	Leroy	1	Sapicourt, Marne, France	Ypresian	1
Lutetian, Paris Basin					
B71552	Museum	4	Beynes, Yvelines, France	Lutetian	4
A11189	d'Orbigny	4	Blaye, Gironde, France	Lutetian	x
A27554	Galerie de Zoologie	4	Boursault, Marne, France	Lutetian	3
B63228	Museum	4	Chambors, Oise, France	Lutetian	4
B63234	Museum	1	Chamery, Marne, France	Lutetian	1
A28878	Museum	3	Chaussy, Val-d'Oise, France	Lutetian	3
A27560	Morlet	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27577	Faullummel	12	Chaussy, Val-d'Oise, France	Lutetian	11
A28516	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	0
A28539	Faullummel	2	Chaussy, Val-d'Oise, France	Lutetian	2
A28541	Schtrock	1	Chaussy, Val-d'Oise, France	Lutetian	0
A25577	Museum	12	Chaussy, Val-d'Oise, France	Lutetian	12
B70329	Morlet	2	Chaussy, Val-d'Oise, France	Lutetian	2
A28548	Lhomme	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28549	Pacaud	6	Chaussy, Val-d'Oise, France	Lutetian	4
A28555	Pacaud	3	Chaussy, Val-d'Oise, France	Lutetian	3
A27681	Mouchart	26	Cressay, Yvelines, France	Lutetian	24
A27567	Pacaud	1	Cressay, Yvelines, France	Lutetian	1
B63233	Lhomme	1	Damery, Marne, France	Lutetian	1
A27540	Galerie de Zoologie	19	Ferme de l'Orme, Yvelines, France	Lutetian	16
B70327	Morlet	6	Ferme de l'Orme, Yvelines, France	Lutetian	6
B63223	Museum	10	Ferme de l'Orme, Yvelines, France	Lutetian	10
B63249	Museum	16	Ferme de l'Orme, Yvelines, France	Lutetian	14
A27589	Pacaud	2	Ferme de l'Orme, Yvelines, France	Lutetian	2
B63222	Museum	3	Ferme de l'Orme, Yvelines, France	Lutetian	3
B63224	Lhomme	3	Ferme de l'Orme, Yvelines, France	Lutetian	2
A27562	Museum	15	Ferme de l'Orme, Yvelines, France	Lutetian	13
A28886	Valenciennes	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
A27609	Valenciennes	21	Fontenay-en-Vexin, Eure, France	Lutetian	21
A27614	Pacaud	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
A28875	Valenciennes	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
B63238	de Morgan	35	Fresville, Manche, France	Lutetian	23
A28794	Museum	9	Gentilly, Val-de-Marne, France	Lutetian	x
B63218	Lhomme	3	Grignon, Yvelines, France	Lutetian	3
A27548	Watelet	4	Grignon, Yvelines, France	Lutetian	3
B63220	Museum	21	Grignon, Yvelines, France	Lutetian	19
A27682	Schtrock	1	Grignon, Yvelines, France	Lutetian	x
A28568	Museum	1	Grignon, Yvelines, France	Lutetian	1
A28573	Museum	3	Grignon, Yvelines, France	Lutetian	3
A28574	Museum	2	Grignon, Yvelines, France	Lutetian	2
A28575	Museum	3	Grignon, Yvelines, France	Lutetian	3
A28576	Museum	26	Grignon, Yvelines, France	Lutetian	26
A28776	Galerie de Zoologie	1	Grignon, Yvelines, France	Lutetian	1
B70325	Lamarck	1	Grignon, Yvelines, France	Lutetian	1
A28775	Lamarck	2	Grignon, Yvelines, France	Lutetian	2
A28873	Museum	1	Grignon, Yvelines, France	Lutetian	1

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
A28874	Museum	1	Grignon, Yvelines, France	Lutetian	1
A28569	Museum	1	Grignon, Yvelines, France	Lutetian	1
B63219	Morlet	1	Grignon, Yvelines, France	Lutetian	1
A28514	Museum	21	Grignon, Yvelines, France	Lutetian	21
A28524	Pacaud	3	Grignon, Yvelines, France	Lutetian	3
A28528	Ballot	6	Grignon, Yvelines, France	Lutetian	6
A28535	Schtrock	1	Grignon, Yvelines, France	Lutetian	1
A27633	Galerie de Zoologie	26	Grignon, Yvelines, France	Lutetian	23
A28542	Museum	6	Grignon, Yvelines, France	Lutetian	6
B63221	Museum	5	Grignon, Yvelines, France	Lutetian	5
A27520	Hoffstetter	1	Grignon, Yvelines, France	Lutetian	1
A27679	Brongniart	8	Grignon, Yvelines, France	Lutetian	8
A27556	Museum	13	Grignon, Yvelines, France	Lutetian	13
A27516	Margerie	3	Grignon, Yvelines, France	Lutetian	3
A27557	Saint-Marceau	4	Hermonville, Marne, France	Lutetian	x
A11188	d'Orbigny	2	Hermonville, Marne, France	Lutetian	x
A27592	Galerie de Zoologie	4	Hermonville, Marne, France	Lutetian	4
B63230	Morlet	1	Latainville, Oise, France	Lutetian	1
B63232	Lhomme	1	Montainville, Yvelines, France	Lutetian	1
B63246	Lhomme	2	Montchauvet, Yvelines, France	Lutetian	2
B63246	Museum	2	Montchauvet, Yvelines, France	Lutetian	2
A27630	Galerie de Zoologie	8	Mouchy-le-Châtel, Oise, France	Lutetian	8
A27598	Roissy	12	Parnes, Oise, France	Lutetian	10
B63210	Museum	1	Parnes, Oise, France	Lutetian	1
A28515	Roissy	1	Parnes, Oise, France	Lutetian	1
A28532	Museum	2	Parnes, Oise, France	Lutetian	2
B63217	Museum	1	Parnes, Oise, France	Lutetian	1
B70328	d'Orbigny	7	Parnes, Oise, France	Lutetian	7
A27545	Bernay	2	Parnes, Oise, France	Lutetian	2
B71553	Museum	2	Parnes, Oise, France	Lutetian	2
B63214	de Morgan	1	Parnes, Oise, France	Lutetian	1
A27565	Pacaud	1	Parnes, Oise, France	Lutetian	1
B63216	Museum	3	Parnes, Oise, France	Lutetian	x
B70328	d'Orbigny	7	Parnes, Oise, France	Lutetian	7
A28793	Roissy	2	Parnes, Oise, France	Lutetian	x
A27588	Pacaud	5	St-Lubin-de-la-Haye, Eure-et-Loir, France	Lutetian	4
A27586	Pacaud	1	St-Lubin-de-la-Haye, Eure-et-Loir, France	Lutetian	1
A27586	Museum	1	St-Lubin-de-la-Haye, Eure-et-Loir, France	Lutetian	0
A11187	Galerie de Zoologie	3	St-Thomas, Aisne, France	Lutetian	x
A27680	Brongniart	1	Septeuil, Yvelines, France	Lutetian	1
A28518	Bertrant	19	Thiverval, Yvelines, France	Lutetian	17
B70326	Morlet	3	Thury-en-Valois, Oise, France	Lutetian	3
B63226	Museum	1	Ully-Saint-Georges, Oise, France	Lutetian	1
A27546	Galerie de Zoologie	2	Vaudancourt, Oise, France	Lutetian	x
A27578	Faullummel	6	Venteuil-Arty, Marne, France	Lutetian	6
A27517	Margerie	9	Villiers-St-Frédéric, Yvelines, France	Lutetian	9
A27515	Braillon	7	Villiers-St-Frédéric, Yvelines, France	Lutetian	7
J09265	Cossmann	11	Villiers-St-Frédéric, Yvelines, France	Lutetian	11
B63225	Museum	3	Villiers-St-Frédéric, Yvelines, France	Lutetian	3
A05708	Pacaud	9	Villiers-St-Frédéric, Yvelines, France	Lutetian	9
IM 665	Houdas	6	Villiers-St-Frédéric, Yvelines, France	Lutetian	6
Lutetian, Cotentin					
A28877	Pacaud	7	Hauteville-Bocage, Manche, France	Lutetian	x
A27584	Pacaud	6	Hauteville-Bocage, Manche, France	Lutetian	4

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
Lutetian, Italy					
A27538	Galerie de Zoologie	1	Val Ciupio, Italy	Lutetian	x
Bartonian, Paris Basin					
A28791	Galerie de Zoologie	4	Acy-en-Multien, Oise, France	Bartonian	x
A28570	Museum	1	Caumont, Seine-et-Marne, France	Bartonian	1
A28879	Faullummel	3	Luzancy, Seine-et-Marne, France	Bartonian	2
A28583	Faullummel	2	Mary-sur-Marne, Seine-et-Marne, France	Bartonian	2
A27523	Pacaud	1	Ronquerolles, Val-d'Oise, France	Bartonian	x
B63235	1965-11	2	Verneuil, Marne, France	Bartonian	1
Bartonian, Loire-Atlantique					
A27529	Pacaud	10	Bois-Gouët, Loire-Atlantique, France	Bartonian	3
Seraphs sopitus (Solander *in* Brander, 1766)					
Bartonian, Paris Basin					
A28881	Faullummel	2	Baron, Oise, France	Bartonian	1
A28883	Faullummel	1	Le Guépelle, Val-d'Oise, France	Bartonian	0
A27526	Pacaud	1	Le Guépelle, Val-d'Oise, France	Bartonian	1
A28884	Pacaud	1	Le Guépelle, Val-d'Oise, France	Bartonian	1
A28880	Faullummel	1	Le Limon, Seine-et-Marne, France	Bartonian	1
A28778	Faullummel	1	Le Limon, Seine-et-Marne, France	Bartonian	1
A27524	Pacaud	6	Le Quoniam, Val-d'Oise, France	Bartonian	5
A28882	Faullummel	1	Vendrest, Seine-et-Marne, France	Bartonian	0
Bartonian, England					
B45405		1	Barton-on-sea, Hampshire, UK	Bartonian	1
no	Morton	12	Barton-on-sea, Hampshire, UK	Bartonian	0
Seraphs olivaceus (Cossmann, 1889)					
Lutetian, Paris Basin					
A28526	Ledon	3	Chaussy, Val-d'Oise, France	Lutetian	3
A27582	Faullummel	2	Chaussy, Val-d'Oise, France	Lutetian	2
A27552	Schtrock	1	Chaussy, Val-d'Oise, France	Lutetian	0
A27591	Houdas	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28577	Ledon	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28885	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A29225	Ledon	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28560	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A29057	Houdas	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27593	Pacaud	4	Fercourt, Oise, France	Lutetian	4
A27608	Valenciennes	3	Fontenay-en-Vexin, Eure, France	Lutetian	2
A27631	Galerie de Zoologie	1	Mouchy-le-Châtel, Oise, France	Lutetian	1
A28546	Pacaud	1	Parnes, Oise, France	Lutetian	1
B63839	Morlet	1	Parnes, Oise, France	Lutetian	1
Seraphs sp. 1					
Lutetian, Paris Basin					
A25011	Faullummel	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28547	Museum	1	Parnes, Oise, France	Lutetian	1
Seraphs sp. 2					
Lutetian, Cotentin					
A28887	de Morgan	1	Fresville, Manche, France	Lutetian	1
Seraphs leukoleptus Jung, 1974					
Lutetian, Paris Basin					
IM 923	Houdas	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27551	Schtrock	1	Chaussy, Val-d'Oise, France	Lutetian	0
A28527	Ledon	1	Chaussy, Val-d'Oise, France	Lutetian	1

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
A28781	Ledon	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28968	Houdas	1	Chaussy, Val-d'Oise, France	Lutetian	1
Seraphs subconvolutus (d'Orbigny, 1852)					
Rupelian, Aquitan Basin					
no	Cluzaud	1	Gaas (Lagouarde), Landes, France	Rupelian	0
no	Aucoin	2	Gaas (Lagouarde), Landes, France	Rupelian	0
no	Cluzaud	8	Gaas (Espibos), Landes, France	Rupelian	0
no	Aucoin	2	Gaas (Espibos), Landes, France	Rupelian	0
A28967	Aucoin	1	Gaas (Espibos), Landes, France	Rupelian	0
Seraphs chilophorus (Cossmann, 1889)					
Lutetian, Paris Basin					
B63229	Morlet	1	Châteaurouge, Oise, France	Lutetian	1
A28505	Morlet	4	Chaussy, Val-d'Oise, France	Lutetian	4
A28510	Museum	5	Chaussy, Val-d'Oise, France	Lutetian	5
A28536	Faullummel	2	Chaussy, Val-d'Oise, France	Lutetian	2
A28540	Faullummel	3	Chaussy, Val-d'Oise, France	Lutetian	3
A27558	Morlet	3	Chaussy, Val-d'Oise, France	Lutetian	3
A27585	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
B63242	Lhomme	2	Chaussy, Val-d'Oise, France	Lutetian	2
A28551	Pacaud	17	Chaussy, Val-d'Oise, France	Lutetian	17
A28557	Pacaud	12	Chaussy, Val-d'Oise, France	Lutetian	12
A28558	Ledon	8	Chaussy, Val-d'Oise, France	Lutetian	8
A27595	Faullummel	4	Chaussy, Val-d'Oise, France	Lutetian	4
A28779	Ledon	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28509	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A27612	Pacaud	16	Fercourt, Oise, France	Lutetian	15
A28922	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A28923	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A28924	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A28925	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A28926	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A27610	Pacaud	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
A25009	Museum	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
A27596	Galerie de Zoologie	1	Grignon, Yvelines, France	Lutetian	1
A28513	Caze	1	Grignon, Yvelines, France	Lutetian	1
A28529	Ballot	1	Grignon, Yvelines, France	Lutetian	1
A28534	Museum	1	Grignon, Yvelines, France	Lutetian	1
A28543	Museum	1	Grignon, Yvelines, France	Lutetian	1
B63213	Museum	1	Parnes, Oise, France	Lutetian	1
A27600	Roissy	3	Parnes, Oise, France	Lutetian	3
A27583	Pacaud	32	Parnes, Oise, France	Lutetian	32
A27601	Galerie de Zoologie	1	Parnes, Oise, France	Lutetian	0
A28565	Morlet	1	Parnes, Oise, France	Lutetian	1
A28581	d'Orbigny	1	Parnes, Oise, France	Lutetian	1
A28790	d'Orbigny	1	Parnes, Oise, France	Lutetian	1
A28927	Roissy	1	Parnes, Oise, France	Lutetian	1
A28928	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28889	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28888	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28890	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28891	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28919	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28920	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28929	Pacaud	1	Parnes, Oise, France	Lutetian	1

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
B63227	Museum	1	Saint-Félix, Oise, France	Lutetian	1
B63211	Morlet	2	Saint-Félix, Oise, France	Lutetian	2
A27587	Pacaud	1	St-Lubin-de-la-Haye, Eure-et-Loir, France	Lutetian	1
A27783	Pacaud	1	St-Lubin-de-la-Haye, Eure-et-Loir, France	Lutetian	1
B63243	1965-11	6	Saulxmarchais, Yvelines, France	Lutetian	6
A28921	1965-11	1	Saulxmarchais, Yvelines, France	Lutetian	1
A28517	Bertrant	1	Tiverval, Yvelines, France	Lutetian	1
B63241	Lhomme	1	Vaudancourt, Oise, France	Lutetian	1
Bartonian, Paris Basin					
A28561	Pacaud	7	Caumont, Seine-et-Marne, France	Bartonian	6
A28571	Museum	2	Caumont, Seine-et-Marne, France	Bartonian	2
A28572	Museum	2	Caumont, Seine-et-Marne, France	Bartonian	2
Seraphs peterjungi n. sp.					
Lutetian, Paris Basin					
A28580	Museum	1	Beynes, Yvelines, France	Lutetian	1
A28789	Museum	1	Beynes, Yvelines, France	Lutetian	1
A28506	Morlet	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28538	Faullummel	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27613	1965-11	2	Chaussy, Val-d'Oise, France	Lutetian	2
A27550	Schtrock	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28550	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28559	Ledon	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28578	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27273	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28931	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28537	Faullummel	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27634	Pacaud	5	Fercourt, Oise, France	Lutetian	5
A28512	Caze	1	Grignon, Yvelines, France	Lutetian	1
A28530	Ballot ?	1	Grignon, Yvelines, France	Lutetian	1
A27632	Galerie de Zoologie	1	Grignon, Yvelines, France	Lutetian	1
A11186	d'Orbigny	1	Parnes, Oise, France	Lutetian	1
A28511	Roissy	1	Parnes, Oise, France	Lutetian	1
A28521	Pacaud	1	Parnes, Oise, France	Lutetian	1
A28520	1965-11	1	Saulxmarchais, Yvelines, France	Lutetian	1
Diameza (*s.s.*) *fragilis* (Defrance, 1825)					
Lutetian, Paris Basin					
A27563	Morlet	1	Ferme de l'Orme, Yvelines, France	Lutetian	0
B63255	1965-11	1	Grignon, Yvelines, France	Lutetian	1
A27519	Pacaud	10	Villiers-St-Frédéric, Yvelines, France	Lutetian	7
A27535	Schtrock	2	Villiers-St-Frédéric, Yvelines, France	Lutetian	2
A27541	Faullummel	23	Villiers-St-Frédéric, Yvelines, France	Lutetian	17
A28784	Faullummel	1	Villiers-St-Frédéric, Yvelines, France	Lutetian	1
A28940	Faullummel	1	Villiers-St-Frédéric, Yvelines, France	Lutetian	1
A28942	Faullummel	1	Villiers-St-Frédéric, Yvelines, France	Lutetian	1
A28939	Pacaud	1	Villiers-St-Frédéric, Yvelines, France	Lutetian	1
EM 33124 (Univ. Claude Bernard Lyon 1)	Caillat	1	Grignon	Lutetian	1
Diameza (*Miniseraphs*) *eratoides* (Cossmann, 1889)					
Lutetian, Paris Basin					
A28523	Pacaud	2	Chaussy, Val-d'Oise, France	Lutetian	2
A27534	Faullummel	9	Chaussy, Val-d'Oise, France	Lutetian	6
A27581	Pacaud	7	Chaussy, Val-d'Oise, France	Lutetian	6

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
A28785	Faullummel	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28932	Faullummel	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27527	Pacaud	13	Fontenay-en-Vexin, Eure, France	Lutetian	10
A28933	Pacaud	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
A28934	Pacaud	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
B63254	Lhomme	1	Hervelon, Marne, France	Lutetian	0
Diameza (*Miniseraphs*) *isabella* (Bernay *in* Deshayes, 1865)					
Lutetian, Paris Basin					
A27561	Pacaud	1	Cauvigny, Oise, France	Lutetian	1
A28783	Pacaud	1	Cauvigny, Oise, France	Lutetian	1
A28507	Morlet	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27542	Pacaud	7	Chaussy, Val-d'Oise, France	Lutetian	7
B63245	1965-11	3	Chaussy, Val-d'Oise, France	Lutetian	2
A27543	Galerie de Zoologie	2	Chaussy, Val-d'Oise, France	Lutetian	2
B72974	Dolleans	1	Chaussy, Val-d'Oise, France	Lutetian	1
B63244	Lhomme	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27579	Faullummel	41	Chaussy, Val-d'Oise, France	Lutetian	34
A28552	Pacaud	27	Chaussy, Val-d'Oise, France	Lutetian	25
A28556	Pacaud	3	Chaussy, Val-d'Oise, France	Lutetian	2
A28562	Faullummel	4	Chaussy, Val-d'Oise, France	Lutetian	3
A27599	Schtrock	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28564	Pacaud	3	Chaussy, Val-d'Oise, France	Lutetian	3
A28553	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28937	Faullummel	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28935	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28936	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28938	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	1
B63248	1965-11	1	Fercourt, Oise, France	Lutetian	1
B63231	Morlet	1	Liancourt-Saint-Pierre, Oise, France	Lutetian	1
B63252	1965-11	1	Liancourt-Saint-Pierre, Oise, France	Lutetian	1
B63247	Lhomme	1	Mouchy-le-Châtel, Oise, France	Lutetian	1
A27580	Pacaud	6	Parnes, Oise, France	Lutetian	6
B63251	Sarrazin	3	Parnes, Oise, France	Lutetian	3
A28782	Pacaud	1	Parnes, Oise, France	Lutetian	1
B63250	1965-11	2	Ponchon, Oise, France	Lutetian	0
B63253	1965-11	2	Vaudancourt, Oise, France	Lutetian	1
A27683	Pacaud	1	Vaudancourt, Oise, France	Lutetian	1
A28582	Museum	4	Villiers-St-Frédéric, Yvelines, France	Lutetian	4
A28563	Pacaud	8	Bois-Gouët, Loire-Atlantique, France	Bartonian	8
Paraseraphs tetanus Jung, 1974					
Ypresian, Paris Basin					
B63205	Lhomme	2	Aizy-Jouy, Aisne, France	Ypresian	2
A28508	Ferry	20	Cuise-Lamotte, Oise, France	Ypresian	20
A27518	Pacaud	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28519	Museum	126	Cuise-Lamotte, Oise, France	Ypresian	117
A27590	Roissy	9	Cuise-Lamotte, Oise, France	Ypresian	9
A27597	Ferry	8	Cuise-Lamotte, Oise, France	Ypresian	8
A27559	Morlet	10	Cuise-Lamotte, Oise, France	Ypresian	10
A10425	d'Orbigny	7	Cuise-Lamotte, Oise, France	Ypresian	7
A27555	Léveque	2	Cuise-Lamotte, Oise, France	Ypresian	2
B63198	Calas	3	Cuise-Lamotte, Oise, France	Ypresian	3
A28581	Ferry	20	Cuise-Lamotte, Oise, France	Ypresian	19
A28946	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28949	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28950	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
A28951	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28943	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28944	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28948	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28952	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28953	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28954	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28955	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28957	Museum	1	Cuise-Lamotte, Oise, France	Ypresian	1
A28787	Ferry	1	Cuise-Lamotte, Oise, France	Ypresian	1
A29224	Ferry	1	Cuise-Lamotte, Oise, France	Ypresian	1
A27528	Pacaud	5	Monampteuil, Aisne, France	Ypresian	5
A27602	Faullummel	47	Saint-Gobain, Aisne, France	Ypresian	43
A28545	Museum	2	Saint-Gobain, Aisne, France	Ypresian	2
A27547	Galerie de Zoologie	7	Saint-Gobain, Aisne, France	Ypresian	7
A27549	Schtrock	1	Saint-Gobain, Aisne, France	Ypresian	0
A27539	Pacaud	30	Saint-Gobain, Aisne, France	Ypresian	30
A28579	Faullummel	1	Saint-Gobain, Aisne, France	Ypresian	1
A28956	Faullummel	1	Saint-Gobain, Aisne, France	Ypresian	1
A28958	Faullummel	1	Saint-Gobain, Aisne, France	Ypresian	1
A28959	Faullummel	1	Saint-Gobain, Aisne, France	Ypresian	1
A27531	Pacaud	1	Gan, Pyrénées-Atlantiques, France	Ypresian	1
Paraseraphs placitus Jung, 1974					
Lutetian, Paris Basin					
A27521	Pacaud	1	Châteaurouge, Oise, France	Lutetian	1
A27532	Pacaud	8	Chaussy, Val-d'Oise, France	Lutetian	8
B63212	Boule	2	Chaussy, Val-d'Oise, France	Lutetian	2
B70331	Morlet	6	Chaussy, Val-d'Oise, France	Lutetian	6
B63240	Lhomme	4	Chaussy, Val-d'Oise, France	Lutetian	3
A27611	Galerie de Zoologie	1	Chaussy, Val-d'Oise, France	Lutetian	1
A28554	Pacaud	1	Chaussy, Val-d'Oise, France	Lutetian	0
IM 544	Houdas	8	Chaussy, Val-d'Oise, France	Lutetian	8
A28966	Boule	1	Chaussy, Val-d'Oise, France	Lutetian	1
A27594	Pacaud	2	Fercourt, Oise, France	Lutetian	1
A28961	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A28962	Pacaud	1	Fercourt, Oise, France	Lutetian	1
A27533	Pacaud	2	Fontenay-en-Vexin, Eure, France	Lutetian	2
A27566	Pacaud	1	Fontenay-en-Vexin, Eure, France	Lutetian	1
A28525	Museum	9	Grignon, Yvelines, France	Lutetian	5
A28531	Ballot	3	Grignon, Yvelines, France	Lutetian	3
A28963	Ballot	1	Grignon, Yvelines, France	Lutetian	1
A28964	Ballot	1	Grignon, Yvelines, France	Lutetian	1
A28533	Museum	1	Parnes, Oise, France	Lutetian	1
A27536	Pacaud	5	Parnes, Oise, France	Lutetian	5
A27537	Galerie de Zoologie	4	Parnes, Oise, France	Lutetian	3
B63209	Sarazin	3	Parnes, Oise, France	Lutetian	3
B63208	Morlet	1	Parnes, Oise, France	Lutetian	1
A28960	Pacaud	1	Parnes, Oise, France	Lutetian	1
B63206		1	Ponchon, Oise, France	Lutetian	1
Bartonian, Paris Basin					
A27522	Pacaud	3	Baron, Oise, France	Bartonian	1
A28965	Faullummel	1	Baron, Oise, France	Bartonian	1
A27553	Galerie de Zoologie	2	Caumont, Seine-et-Marne, France	Bartonian	2
A27525	Pacaud	1	Le Guépelle, Val-d'Oise, France	Bartonian	0

APPENDIX 1 – Continuation.

Registration number	Collection	Num. of spec.	Locality	Stage	Positive under UV light
Paraseraphs armoricus (Vasseur, 1882)					
Bartonian, Loire-Atlantique					
J09267	Hébert	1	Arthon, Loire-Atlantique, France	Bartonian	x
A27530	Pacaud	2	Bois-Gouët, Loire-Atlantique, France	Bartonian	2
A28788	Pacaud	1	Bois-Gouët, Loire-Atlantique, France	Bartonian	1
no	Morlet	1	?	Bartonian?	1
Bartonian, Aquitan Basin					
A28397	Ledon	4	Blaye, Gironde, France	Bartonian	x
Paraseraphs praecedens n. sp.					
Thanetian, Paris Basin					
A05707	Pacaud	1	Abbecourt, Oise, France	Thanetian	0

APPENDIX 2

List of the Recent material: *Terebellum terebellum* (Linnaeus, 1758) from South East Pacific.

Coll. Malacologie, MNHN	Num. of spec.	Locality
24 (nebulosum, punctulorum)	4	New Caledonia
27 (nebulosum, punctulorum)	5	New Caledonia
19 (punctulorum)	4	Atoll de Surprise (New Caledonia)
37	1	Atoll de Surprise (New Caledonia)
39 (nebulosum)	1	Atoll de Surprise (New Caledonia)
37	1	Atoll de Surprise (New Caledonia)
10 (punctulorum)	2	Baie de St Vincent (New Caledonia)
12 (punctulorum)	1	Baie de St Vincent (New Caledonia)
11	2	Grand Récif Sud (New Caledonia)
15 (puntulorum, nebulosum)	2	Grand Récif Sud (New Caledonia)
21 (punctulorum)	9	Grand Récif Sud (New Caledonia)
36 (punctulorum)	3	Grand Récif Sud (New Caledonia)
38 (punctulorum)	2	Grand Récif Sud (New Caledonia)
53 (delicatum)	1	Grand Récif Sud (New Caledonia)
11 (punctulorum)	1	Grand Récif Sud (New Caledonia)
16 (punctulorum)	1	Grand Récif Sud (New Caledonia)
21	1	Grand Récif Sud (New Caledonia)
34	1	Grand Récif Sud (New Caledonia)
18 (punctulorum)	5	Île des Pins (New Caledonia)
17 (punctulorum)	4	Île Ouen-Baie du Prony (New Caledonia)
9 (punctulorum)	3	Lagon Nord (New Caledonia)
13	1	Lagon Nord (New Caledonia)
35 (lineatum)	2	Lagon Nord (New Caledonia)
35 (punctulorum)	1	Lagon Nord (New Caledonia)
52 (punctulorum, nebulosum)	5	New Caledonia
32 (nebulosum)	2	Balabio (New Caledonia)
1 (punctulorum)	1	Balabio (New Caledonia)
6 (nebulosum)	2	Canala (New Caledonia)
14 (punctulorum)	3	Nouméa (New Caledonia)
40 (lineatum)	6	Nouméa (New Caledonia)
23	1	Nouméa (Baie des Citrons) (New Caledonia)
31 (nebulosum, punctulorum)	6	Nouméa (Quatre bancs de l'Ouest) (New Caledonia)
31 (nebulosum)	1	Nouméa (Quatre bancs de l'Ouest) (New Caledonia)

APPENDIX 2 – Continuation.

Coll. Malacologie, MNHN	Num. of spec.	Locality
28 (punctulorum)	3	Poindimié (New Caledonia)
59 (nebulosum)	4	Poindimié (New Caledonia)
22 (punctulorum)	1	Poum (New Caledonia)
25 (lineatum, nebulosum, punctulorum)	3	Poum (New Caledonia)
26 (lineatum, nebulosum)	6	Poum (New Caledonia)
29 (punctulorum)	1	Poum (New Caledonia)
41 (punctulorum, nebulosum)	3	Poum (New Caledonia)
58 (delicatum, lineatum)	6	Poum (New Caledonia)
8 (nebulosum, punctulorum?)	2	Thio (New Caledonia)
5 (nebulosum, lineatum)	21	Yaté (New Caledonia)
30 (delicatum)	2	Belep (New Caledonia)
54 (punctulorum, nebulosum)	4	New Caledonia
56 (punctulorum, nebulosum)	4	New Caledonia
2 (lineatum)	1	New Caledonia
55 (punctulorum, nebulosum)	3	Andaman? (Inde)
20 (nebulosum)	1	Seychelles
49 (punctulorum)	1	Aoré Island (Aimbuei Bay) (Vanuatu)
51 (nebulosum)	1	Baldwin Bay (Vanuatu)
42 (nebulosum)	1	Belmoul Lagoon (Vanuatu)
44 (nebulosum)	1	Palikulo Bay (Vanuatu)
45 (nebulosum)	2	SE corner of Santo (Vanuatu)
46 (delicatum)	1	Segond Channel (Vanuatu)
43 (punctulorum)	1	Tangoa Island (Vanuatu)
48 (nebulosum)	2	Tutuba Island (Vanuatu)
47 (nebulosum)	1	W Aésé Island (Vanuatu)
47 (nebulosum)	1	W Aésé Island (Vanuatu)
50 (delicatum)	2	W Tangoa Island (Vanuatu)
57 (nebulosum, lineatum)	15	Plateau des Chesterfield
3 (nebulosum)	1	Plateau des Chesterfield
3 (nebulosum)	1	Plateau des Chesterfield
3	1	Plateau des Chesterfield
3 (nebulosum)	11	Plateau des Chesterfield
4 (nebulosum)	7	Plateau des Chesterfield
7 (nebulosum)	3	Plateau des Chesterfield
33 (lineatum)	1	?