The smooth-shelled Neritidae Rafinesque, 1815 (Mollusca, Gastropoda) from the Ypresian of the Paris Basin, with the introduction of three new species.

Xavier Vrinat

79 rue de Parmain, F-95430 Butry-sur-Oise, France; e-mail: xavier.vrinat@sfr.fr

Received: 13 November, 2017, revised version accepted 25 April, 2019

Abstract: This paper discusses the smooth-shelled species of Neritidae present (or supposedly present) in the Ypresian of the Paris Basin. These species have been previously assigned to the genera *Neritina* Lamarck, 1816, *Clithon (Pictoneritina)* Iredale 1936, *Theodoxus (Vittoclithon)* H. B. Baker, 1923, *Neritodryas* Von Martens 1869 and *Neritoplica* Oppenheim, 1892. This study is based on a simplified and homogeneous approach to the identification of the various species of this family of gastropods, based on a limited number of distinguishing criteria. Examination of more than 250 specimens from public institutions and private collections, including the types of most of the taxa considered, allowed the compilation of a clear reference iconography and the introduction of three new taxa: *Clithon (Pictoneritina) coeuvrensis* nov. sp., *Clithon (Pictoneritina) tigrinus* nov. sp. and *Clithon (Pictoneritina) occultatus* nov. sp. A key based on shell characters is given to facilitate the identification of the species.

Key words: Neritidae, Ypresian, Paris Basin, *Clithon, Neritodryas, Neritoplica, Theodoxus.*

Neritidae Rafinesque, 1815 (Mollusca, Gastropoda) à coquille lisse, de l'Yprésien du Bassin de Paris, introduction de trois nouveaux taxons.

Résumé:
Cet article propose une revue des Neritidae dotés d'une coquille lisse, présents (ou supposés présents) à l'Yprésien du Bassin Parisien. Ces taxons ont été précédemment distribués entre les genres *Neritina* Lamarck, 1816, *Clithon (Pictoneritina)* Iredale 1936, *Theodoxus (Vittoclithon)* H. B. Baker, 1923, *Neritodryas* von Martens 1869, et *Neritoplica* Oppenheim, 1892. Cette étude est basée sur une approche simplifiée et homogène de l'identification des différentes espèces de cette famille de gastéropodes, basée sur un nombre limité de critères physiques de discrimination. L'examen de plus de 250 spécimens provenant d'institutions publiques et de collections privées, y compris les types de la plupart des taxons considérés, nous permet de proposer une iconographie de référence claire, et nous conduit à introduire trois nouveaux taxons, *Clithon (Pictoneritina) coeuvrensis* nov. sp*,, Clithon (Pictoneritina) tigrinus* nov. sp. et *Clithon (Pictoneritina) occultatus* nov. sp. Une clé d'identification basée sur les caractéristiques des coquilles est proposée pour faciliter l'identification des espèces..

Mots clés: Neritidae, Yprésien, Bassin de Paris, *Clithon, Neritodryas, Neritoplica, Theodoxus.*

Introduction

The molluscan fauna of the Ypresian (subdivided into Sparnacian and Cuisian) of the Paris basin comprises many specimens and taxa of the Neritidae Rafinesque, 1815. In the literature the descriptions of these taxa are sometimes very lengthy (obscuring essential characteristics by details), or too succinct (omitting essential characteristics), or papers contradict each other. The confusion is further increased by the poor quality figures of some key papers. The "*Iconographie*" of Cossmann & Pissaro (1907, pls V & VI) is of limited help: the figures are not always clear, the numbering is sometimes faulty, and some interpretations by Cossmann (1888) of taxa previously described are debatable.

This work proposes a simplified and homogeneous approach to the identification of the smooth-shelled Neritidae from the Ypresian of the Paris basin. Some Thanetian and Lutetian taxa have been reviewed as they have also been reported from the Ypresian or for verification of possible synonymy. The existing taxa have been reviewed and are redescribed, whereas good quality figures are provided including the available type specimens.

Abbreviations:

IRScNB: Institut royal des Sciences naturelles de Belgique, Collections paléontologiques, Bruxelles (Belgique)
MNHN: Muséum national d'Histoire naturelle, Collection de Paléontologie, Paris (France)
MHNN: Muséum d'Histoire Naturelle, Collection paléontologique, Nantes (France)
NHM: National History Museum, Palaeontology collections of the Department of Earth Sciences, London (Great Britain)
UCBL-EM: Université Claude Bernard, Collections de l'Ecole Nationale Supérieure des Mines de Paris, en dépôt dans les Collections de Géologie, Lyon (France)

Material

More than 250 specimens have been studied, from the Université Claude Bernard in Lyon (France), the Muséum national d'Histoire naturelle in Paris (France), the Institut Royal des Sciences Naturelles de Belgique of Brussels (Belgium), the Natural History Museum of London (United Kingdom) and the Muséum d'Histoire Naturelle of Nantes (France), including types from the Cossmann, Deshayes, Sowerby and Pacaud collections, besides specimens from private collections:

- coll. De Boury, UCBL, France
- coll. Cossmann, MNHN, France
- coll. Deshayes, UCBL, France
- coll. Faullummel, MNHN, France
- coll. Hessel, Naturalis Biodiversity Center, Leiden, and private, The Netherlands.
- coll. Laporte, now owned by Lenaerts, private, Belgium
- coll. Leroy, MNHN & private, France
- coll. Lhomme, MNHN, France
- coll. Marcomini, MNHN & private, France
- coll. Marquet, IRScNB, Belgium
- coll. J. de C. Sowerby, NHM, UK
- coll. Vrinat, MNHN & private, France

Method of characterisation of Neritidae species (Pl. 1)

In order to simplify identification, this review focuses on four characteristics: the shape of the spire, the development of columellar teeth, the extent of the columellar callus, and the colour pattern. This arbitrary choice is an easy option, since it uses the most obvious criteria for differentiation. In present-day specimens the radula and operculum are also used for identification, but except for very few opercula these are not available for fossils.

For each of these characteristics, the following classification criteria have been established:

Development of columellar teeth
- Absent, although a vague pleat may be present on the adapical side.
- Little developed, generally bordering a concavity of the columella.
- One single tooth, on the adapical side.
- Several teeth, of variable strength, generally with a stronger one on adapical side.

Shape of the spire
- Involute or almost involute. The protoconch, and sometimes the entire spire, is hidden inside the last whorl.
- Flush or slightly protruding.
- Conoidal. In contrast to the overal globular shape of most Neritidae, spires with a rounded sub-conical shape are referred to as "conoidal".
- Shouldered.
- Elliptical. A prominent spire (protruding out of the last whorl) in the shape of an elliptical cone.

Extent of the columellar callus
- Thick and widely spread.
- Widespread.
- Moderately wide.
- Narrow.

Ornamental pattern
- Random pale marks, more or less organised in spirals.
- Axial lines (rather narrow), more or less zig-zag.
- Axial bands (rather broad).
- Spiral bands.
- Other regular (sub-geometrical) pattern.
- No pattern.

Plate 1 illustrates a large number of the features listed above and used in the body of this work.

There is not always a sharp boundary between these criteria, besides which the variability of the species and the age of the observed individual should be considered. For example, Bandel (2001), Symonds (2008), Lozouet & Plaziat (2008) and many other authors have illustrated the variability of the ornamental pattern of nerites within the same taxon, particularly as a function of the salinity of the living environment. Other characteristics tend to change with age, for example the strength of the columellar teeth and the development of a shoulder on the last whorl. In addition, wear can make a protruding spire appear flush, uncover an involute spire, or abrade the columellar callus. To really understand a species, it is therefore important to have a sufficient number of specimens, at different stages of development and in a proper state of conservation. This was not available for all species.

Systematics

Species historically placed in the genus *Neritina* Lamarck, 1816 have been since assigned to several genera (Pacaud & Le Renard (1995, p. 154), Symonds & Pa-

caud (2010, p. 62), Pacaud (2017, p. 194 & 195)): *Clithon (Pictoneritina)* Iredale, 1936, *Theodoxus (Vittoclithon)* or *Clithon (Vittoclithon)* H.B. Baker, 1923, *Neritodryas* Von Martens, 1869 and *Neritoplica* Oppenheim, 1892.

Although protoconch type is not always a sufficient criterion for defining genera, for species previously assigned to the genera *Clithon* and *Theodoxus,* Bandel (2001, p. 69-70) is followed: species with a planktrotrophic protoconch are assigned to *Clithon* and species with a lecitotrophic protoconch to *Theodoxus*. As a matter of fact, all the species studied have a planktrotrophic protoconch (when visible). Two species with hidden protoconch are doubtfully assigned to *Clithon* as well.

The validity of the subgenus *Pictoneritina* Iredale, 1936 is not accepted by all, as stated by Eichhorst (2016, p.154). Nevertheless, based on the analysis by Symonds (2015, p. 147-148), it is herein retained, though use of a specific genus or subgenus, dedicated to fossil representatives of the *Clithon* group would probably be more appropriate.

Although fequently shown as dated 1825 in many previous works (e.g. Le Renard, 1995, p. 136), the pages of Deshayes' "*Description des coquilles fossiles des environs de Paris*" (Tome 2, p. 81-146) covering the Neritinas were published in 1832, as demonstrated by Newton (1891, p. 308-309) and reminded by Glibert (1962, p. 104).

Two *Neritodryas* taxa recently described from the Ypresien of the Paris Basin *(Neritodryas guillioui* Symonds & Pacaud, 2010 and *Neritodryas marqueti* Symonds, 2016) have been excluded from this review, as they typically have spiral ribs and are only known from their type specimens.

Note that the synonomy is restricted to the most important papers.

Family Neritidae Rafinesque, 1815
Genus *Clithon* Montfort,
Subgenus *Pictoneritina* Iredale, 1936

Clithon (Pictoneritina) barbei Symonds & Pacaud, 2010
Pl. 2, fig. 5

Type material – Holotype NHM PI TG 26448 (Symonds collection). Paratype NHM PI TG 26449 (M. Symonds). Paratype MNHN.F.A33473 (Ledon collection).

Type locality – Pourcy (Marne). Lower Cuisian, Ypresian (Lower Eocene).

Other studied material – Pourcy (Marne): 1 specimen (Laporte collection), 1 specimen (Vrinat collection).

Description – Shell with a hardly visible spire, a moderately developed columellar callus, and three to four weak teeth on the columella. The ornamentation, very characteristic when present, is composed of three rather large spiral bands (based on Symonds & Pacaud, 2010).

Discussion – This species, uncommon and apparently endemic to Pourcy, seems well characterised and easily identifiable. Its regular bands, very pale, and the shape of its spire differentiate it from *Clithon (Pictoneritina) zonarius* (Deshayes, 1832).

Clithon (Pictoneritina) bouryi (Cossmann, 1888)
Pl. 3, figs 2-6

Type material – Syntypes UCBL-EM31892 (de Boury collection, figured) and MNHN.F.J05785 (Cossmann collection).

Type locality – Cuise-la-Motte (Oise). Cuisian, Ypresian (Lower Eocene)

Other studied material – **Saint-Gobain** (Aisne): 2 specimens (Vrinat collection), 1 specimen (Leroy collection), 3 specimens (Laporte collection). **Coeuvres-et-Valsery** (Aisne): 2 specimens (Leroy collection). **Pourcy** (Marne): 1 specimen (Leroy collection).

Description – A barely protruding spire, a wide callus, a large number of columellar denticles (or folds according to Cossmann (1888, p. 91)) of variable strength, and, when preserved, an ornamentation of fine motives of variable form, organised in spirals.

Discussion – Cossmann (1888: p. 92) reports this species from Cuise-la-Motte and Sapicourt. Herein it is reported from Saint-Gobain, Coeuvres-et-Valsery and Pourcy. It seems to be rare. Thanks to its unique columellar teeth arrangement this taxon is very remarkable and easily separable from others. Starting on the adapical end of the columella, a sub-rectilinear portion (about a quarter of the length of the columella) can bear up to four very small teeth, bordered abapically by a rather strong tooth, then the second part of the columella in the shape of a scythe, carries up to seven very small teeth. In some ways this tooth arrangement is closer to that of some modern species of *Clithon* (for example specimens figured by Bandel (2001, figs 118, 167, 172 & 178), than to any of the other species studied here. Its protoconch is also particularly close to that of *Clithon oualaniense* (Lesson, 1831) as figured by Bandel (2001, fig. 247).

Clithon (Pictoneritina) coeuvrensis nov. sp.
Pl. 3, fig. 1

Type material – Holotype MNHN.F.A71151 (Leroy collection).

Type locality – Coeuvres-et-Valsery (Aisne). Cuisian, Ypresian (Lower Eocene).

Etymology – Named after the type locality.

Description – Medium size (height 7 mm) semiglobose shell, consisting of about 2 whorls, with a slightly protruding spire and a visible protoconch of planktotrophic type. Large oblique semicircular aperture. Columellar callus broad, but not bulging. The columella has a faint tooth located at about a quarter from the adapical side, followed by a weak depression, in the form of a scythe, with slight undulations (prefiguring weak teeth). Ornamentation of cream-coloured spots of variable shape (from small disk to pseudo-chevron) on a brown background, amalgamating progressively on the last whorl to form rather wide, zigzag axial lines.

Discussion – Normally one would not describe a new species on the basis of a single specimen, but an exception is made for this unique specimen (Pl. 3, fig. 1). At first, it was identified as *N. dutemplei* (Deshayes, 1864), because of the ornamental resemblance with one specimen (Pl. 15, fig. 5). However, the extent of the columellar callus did not correspond and closer examination of the columella demonstrates this species belongs to *Clithon (Pictoneritina)* Iredale, 1936. It is close to *C. sainceny-ensis,* based on the extent of the columellar callus (albeit more limited) and the poorly-defined columellar teeth but differs radically in ornamentation and by its less elongated, more globular shape.

Clithon (Pictoneritina) inequidentata (Récluz, 1850)
Pl. 2, figs 2 & 3

1832 *Neritina lineolata* Deshayes [non Lamarck 1816], p. 152; pl. XIX, figs 7 and 8
1850 *Nerita sublineolata* d'Orbigny, 346

Type material – Syntypes UCBL-EM32171a and b (Deshayes collection)

Type locality – Houdan (Yvelines), middle Lutetian (Middle Eocene)

Description – This taxon has a slightly protruding spire, a moderately developed columellar callus, three obsolete teeth on the columella (the median being the strongest), as well as an abapical obtuse protrusion ("saillie obtuse"), and an ornamentation of small axial lines (Deshayes, 1832).

Discussion – This taxon was described by Deshayes (1832) from the Lutetian of the Houdan area. It was renamed by Récluz (1850) and by d'Orbigny (1850), because of primary homonymy with a species of Lamarck figured in 1816 (pl. 455, fig. 4) (not 1822 as mentioned by Pacaud (2007, p. 30), see Petit (2011, p. 1)). It is normally known from this level only. Nevertheless, the MNHN collections (Lhomme collection, MNHN.F.B57240) include a specimen from the Cuisian identified as this species.

Examination of the syntypes (UCBL-EM32171) confirms the above description, except for the columella which does not have three teeth (as mentioned by Deshayes, 1832) but two rounded teeth, the first and stronger one, adapical, marks the beginning of a rather strong depression ending with an indistinct tooth.

A syntype of *Clithon (Pictoneritina) elegans* (Deshayes, 1832) (UCBL-EM32169) was also examined (Pl. 2, fig. 1). It has a tooth-free columella, a moderately developed columellar callus, a protruding spire and a slight shoulder. Its unique ornamentation is formed of lines starting axially from the adapical suture (on the subshouldered area of the last whorl), becoming spiral on the last whorl.

Comparison of these types with the specimen from the Cuisian mentioned above (MNHN.F.B57240) shows that the latter is neither a *Clithon (Pictoneritina) inequidentata* (Récluz, 1850), nor a *Clithon (Pictoneritina) elegans* (Deshayes, 1832). It represents a form of *Clithon (Pictoneritina) zonarius* (Deshayes, 1832) and is discussed below.

Clithon (Pictoneritina) nucleus (Deshayes, 1832)
Pl. 4, figs 1-6 & Pl. 5, figs 1-6; Table 2

Type material – Six syntypes, UCBL-EM32198 (Deshayes collection). The figured specimen (Deshayes, 1832, pl. XXV, figs 3-5) is not labelled as such and was not recognised amongst these syntypes.

Type locality – Cuise-la-Motte (Oise). Cuisian, Middle Ypresian (Lower Eocene)

Other studied material – **Cuise-la-Motte** (Oise): 2 specimens (Deshayes collection, UCBL-EM30639a and b), 1 specimen (Cossmann collection, MNHN.F.J09794), 1 specimen (Leroy collection), 7 specimens (Vrinat collection), 3 specimens (Laporte collection), 1 specimen (MNHN.F.A71152). **Gland** (Aisne): 1 specimen (Cossmann collection, MNHN.F.J09795). **Saint-Gobain** (Aisne): 1 specimen (Marcomini collection).

Description – Flush spire, a rather thick columellar callus, four teeth on the columella (sometimes only three), the tooth on the apical side being stronger (Deshayes, 1832, p. 156). The figured specimen (Deshayes, 1832, pl. XXV, figs 3-5), however, has a rather prominent spire. Deshayes (1864) describes the ornamentation of the only intact specimen he could examine. It is composed of broad axial lines interrupted by two narrow bands with lanceolate brown spots.

Discussion – The syntypes comprise six shells, all slightly worn, with very variable spires, sometimes flush, sometimes slightly protruding. The main common characteristic seems to be the columellar teeth and the columellar callus, rather widely spread abapically.

A second batch in the Deshayes collection was examined, amongst which the well-preserved specimen (UCBL-EM30639a) reported in Deshayes (1864, p. 23) was recognised. It is accompanied by a smaller specimen (UCBL-EM30639b). Their examination partially confirms the diagnosis by Deshayes, except for the rather protruding spire and the sub-shoulder, especially on specimen a. Specimen a is covered with fairly close axial lines, broken by two or even three spiral bands, while specimen b has beige, axial or sub-axial, segments, sometimes in the form of chevrons, and three beige spiral lines on a brown background.

Cossmann (1888, 87, pl. III, fig. 39) and the "*Iconographie*" are rather confusing, since a taxon almost devoid of teeth was described and figured in these papers. The specimen figured by Cossmann (UCBL-EM31894, de Boury collection) was examined and was found with certainty to belong to another, new taxon, described below. The review of the Cossmann collection at the MNHN is confusing as well. Three batches from Mercin-et-Vaux, Cuise-la-Motte and Gland were examined, which mostly contain poorly preserved shells representing several species. Only one specimen from Gland and another from Cuise-la-Motte are considered to belong to *C. nucleus*.

Finally, according to Symonds & Pacaud (2010, p. 60), *C. nucleus* presents an almost involute spire, and an ornamentation composed of undulating axial lines, sometimes interrupted by two or three pale spiral bands. This indication on the spire is not consistent with my observations, except on a specimen in the Cossmann collection (MNHN.F.J09794) (Pl. 5, fig. 2). This one has also a non-typical arrangement of the teeth and might represent another taxon, possibly new.

In addition to the type series, 18 well-preserved specimens have been identified as representing this taxon. There is a large variation in ornamentation, which can nevertheless be characterised by the presence of alternating pale and dark, more or less regularly spaced, zigzag or undulating axial lines, sometimes interrupted by brown or whitish spirals. The adapical tooth, stronger than the others, appears generally wider, rather rounded, compared to the other taxa of the same genus.

Clithon (Pictoneritina) occultatus nov. sp.
Pl. 6, figs 1-6 & Pl. 7, figs 1-6

1902 *Neritina consobrina*[sic] sensu Cossmann [non *Nerita sobrina* de Férussac, 1823], p. 31; pl. VI, fig. 26.

Type material – Holotype MNHN.F.A71143 (Vrinat collection). Paratypes MNHN.F.J03781 (Cossmann collection), MNHN.F.A71144 and MNHN.F.A71145 (Vrinat collection), MNHN.F.A71146 and MNHN.F.A71147 (Leroy collection).

Type locality – Pourcy (Marne). Lower Cuisian, Ypresian (Lower Eocene).

Etymology – From the Latin *occultatus* (hidden), in reference to the fact that it was long mistaken for another taxon and remained ignored despite its frequent presence in old and recent collections.

Other studied material – **Pourcy** (Marne): 2 specimens (Laporte collection), 12 specimens (Vrinat collection), 4 specimens (Leroy collection). **Cuise-la-Motte** (Oise): 4 specimens (Vrinat collection), 2 specimens (Romanek collection). **Brasles** (Aisne): 1 specimen (Hessel collection). **Saint-Gobain** (Aisne): 1 specimen (Vrinat collection), 1 specimen (Leroy collection).

Description – Medium size **(**maximum height does not exceed 10-11 mm), semiglobose shell, consisting of about 2.5 whorls. Oblique, semicircular aperture. In its typical form, this taxon has three well-defined teeth, regularly spaced, in the central third of the columella. The first, stronger, adapical, is at the end of a fairly pronounced concavity in which the other two teeth are located. The concavity ends rather abruptly abapically, forming a notch on the columella. The spire is conoid, quite high. The columellar callus is moderately wide.

Other shells show significant variations, notably in the disposition of the teeth: a first fairly strong, adapical tooth, and, after a fairly large gap, a group of three to five smaller teeth, decreasing in size abapically, arranged in a columellar depression. The 'secondary' teeth are quite small and pointed. The spire, also variable, is pronounced, sometimes quite high and shouldered. However, the columellar callus remains moderately wide.

When well preserved, the ornamentation consists of beige spots organised in spirals, on a brown background, sometimes aggregating to discontinuous spiral bands that are not sharply defined.

Discussion – Cossmann twice (1888, p. 86-87; 1902, p. 31, pl. VI, fig. 26) reviews the taxon *Nerita sobrina* of de Férussac (which he wrongly spells as *Neritina consobrina*, as did Deshayes before him). Probably influenced by material from Pourcy that he was studying at the time, he describes and figures a shell from this locality with a clearly conoidal spire, a moderately wide columellar callus, ornamented with pale spots on a dark background.

Examination of the figured material (MNHN.F.J03781) confirms the description by Cossmann (to which one can add the presence of three teeth on the columella, the strongest on the apical side) and shows clearly that he made a mistake, as the specimens he reviewed are very different from the figures in de Férussac (1823) and the material of *Clithon (Pictoneritina) sobrinus* (de Férussac, 1823) in the Deshayes collection. It belongs to another species, described here.

This species is abundant at Pourcy. Examination of a good number of specimens shows a great variety of forms that differ noticeably from the type described above. This is particularly the case with the disposition of the teeth, their number (up to five) and the concavity on the columella, which may be more or less clearly marked. The shape of the spire may be just flush, sub-shouldered or sometimes clearly shouldered.

This taxon is close to *Clithon (Pictoneritina) zonarius* (Deshayes, 1832), which can be distinguished by a spire that remains lower and an ornamentation with well-marked spiral bands. *Clithon (Pictoneritina) occultatus* sometimes shows undefined partial spiral bands, mostly on the last whorl, just in contact with the columellar callus. These faint bands are thus quite different from the clear and continuous spiral bands observed on *Clithon (Pictoneritina) zonarius* (Deshayes, 1832). They seem to result from the accidental agglomeration of pale patches and may have been created, or at least accentuated (particularly near the aperture) by a degree of wear.

In terms of ornamentation *Clithon (Pictoneritina) occultatus* also bears a resemblance to the Bartonian species *Clithon (Pictoneritina) passyanus* (Deshayes, 1864), but differs in particular by its spire (which is not or hardly protruding in *C. passyanus*) and the extent of its columellar callus (smaller for *C. passyanus*). It also resembles some younger (late Eocene and early Oligocene) species, *Clithon (Pictoneritina) planulatus* (Edwards, 1866) (figured by Symonds (2006, p. 14-15), which has a broader aperture and weaker columellar teeth), *Clithon (Pictoneritina) cranmorensis* Symonds, 2006 and *Clithon (Pictoneritina) pococki* Symonds, 2015 (which both differ notably by their even weaker teeth).

Clithon (Pictoneritina) pisiformis (de Férussac, 1823)
Pl. 8, figs 1-7

Type material – Syntypes not found.

Type locality – Epernay (Marne) or Soissons (Aisne), "dans les lignites" (lignite deposits are diachronous: Sparnacian (lower Ypresian) in the Soisson area and Cuisian (upper Ypresian) in Champagne (Arnaud Leroy, pers. com.)), Ypresian (Lower Eocene).

Other studied material – **Aÿ Mont-Bernon** (Marne): 4 specimens (Deshayes collection, UCBL-EM32161). **Pourcy** (Marne): 2 specimens (Faullummel collection, MNHN.F.A29402), 3 specimens (Vrinat collection).

Description – Flush spire. The columella displays small teeth (typically three to four) within a depression. The columellar callus is widespread. The ornamentation consists of rather thin wavy axial lines (de Férussac (1823, fig. 11) and descriptions by Deshayes (1832, p. 155; 1864, p. 23)).

Discussion – The material in the Deshayes collection (UCBL-EM32161) includes four specimens of Aÿ - Mont Bernon, which match these characteristics, apart from the callus which might be slightly worn on some specimen. The axial lines covering the best preserved specimens, slightly sinuous rather than zigzag, are fairly wide and spaced apart.

Symonds (2008, figs 11 and 12) illustrates a slightly different form, from Abbey Wood (UK), that Spijkerman *et al*. (2015, figs 32a and 32b) also report from Pourcy. All figured specimens have a prominent spire, and the specimens figured in the latter paper have a strong tooth on the columella, followed by two weaker ones, grouped in a depression, and a moderately spread columellar callus. They are covered with zigzag axial lines, rather thin, rather closely spaced. Following the opinion of these authors, three specimens are figured herein (see Pl. 8, figs 5 to 7) that have a very similar ornamentation, from the same deposit at Pourcy. The specimen from the Faullummel collection at MNHN was wrongly identified as *Clithon (?Vittoclithon) saincenyensis* (Deshayes, 1864). One of these specimens (Pl. 8, fig. 7), however, has very strong teeth on the columella, perhaps a gerontic character, which separates it from the other illustrated specimens.

Specimens with the typical ornamental pattern were also found at Pourcy (see Pl. 8, fig. 4).

Clithon (Pictoneritina) saincenyensis (Deshayes, 1864)
Pl. 9, figs 1-6 & Pl. 15, fig. 6

Type material – Five syntypes, UCBL-EM32672 (Deshayes collection)

Type locality – Sinceny (Aisne). Sparnacian, Ypresian (Lower Eocene)

Other studied material – **Sinceny** (Aisne): 4 specimens (Leroy collection), 11 specimens (Lhomme collection, MNHN.F.B57207), 1 specimen (Hasse collection, KBIN/IRScNB I.G. 8444). **Rilly** (Marne): 1 specimen (Deshayes collection, UCBL-EM32170c). **Sarron** (Oise): 1 specimen (Dautzenberg collection, IRScNB I.G. 10591), 19 specimens (MNHN.F.B57208). **Pourcy** (Marne): 2 specimens (Vrinat collection), 1 specimen (Marquet collection, IRScNB).

Description – Deshayes (1864) characterises this species by a hardly or not protruding spire and a wide columellar callus. The columella has a concavity in which sometimes some very weak teeth are present. Deshayes does not give any indication of the ornamentation.

Discussion – The syntypes are of rather poor quality, but at least one specimen shows the remains of the outer layer, adorned with thin zigzag axial lines. Specimens in good condition are easily available in other collections, the best preserved of which clearly show an ornamentation of thin, dark, zigzagging axial lines on a pale

background, especially the specimen in the Deshayes collection (UCBL-EM32170c) mentioned below in the discussion on *Clithon sobrinus*.

Columellar teeth are sometimes almost invisible. When they are more developed they consist, starting from the adapical side, of a first rounded bump at the first third of the columella marking the beginning of the concavity mentioned by Deshayes (1864). This generally takes the form of a scythe, but sometimes abruptly ends abapically, to form a small notch along the columella. Two bulges can appear in this concavity, and even develop to form real, rather square, teeth (Pl. 9, figs 4 & 6).

As indicated by Deshayes (1864), the spire is fairly constantly flush or barely protruding, and the widely spread (especially abapically) columellar callus remains flat.

Clithon (Pictoneritina) sobrinus (de Férussac, 1823)
Pl. 10, figs 1-6 & Pl. 11, figs 1-6; Table 1

1832 *Neritina consobrina* Deshayes, p. 153 (incorrect subsequent spelling)
1907 *Neritina consobrina* var. *perlonga* Cossmann & Pissarro, pl. V, fig. 39-7"

Type material – Syntypes not found.

Type locality – Epernay (Marne), Ypresian (Lower Eocene).

Other studied material – **Rilly** (Marne): 3 specimens (Deshayes collection, UCBL-EM32170). **Pourcy** (Marne): 6 specimens (Vrinat collection), 5 specimens (Laporte collection), 1 specimen (Leroy collection). **Mont-Bernon** (Marne): 2 specimens (Deshayes collection, UCBL-EM30642). **Soissons** (Aisne): 4 specimens (Leroy collection).

Description – Shell with a protuberant, elliptical spire, a thick columellar callus, a columella marked by a slight depression bordered by weak teeth. The shell is uniformly brown, without visible ornamental pattern (de Férussac, 1823, fig. 12).

Discussion – Deshayes (1832, 153, pl. XIX, figs 5 & 6) describes and represents under the name *Neritina consobrina* (incorrect subsequent spelling, as recently pointed out by Pacaud (2017, p. 195)) a taxon he clearly relates to *Nerita sobrina* of de Férussac (he refers precisely to figure 12 of plate 2 published by the latter). Nevertheless, the description and the associated figure in Deshayes (1832) do not agree with the species of de Férussac, as it mentions for example 3-4 small serrations towards the centre of the columella. Deshayes (1864, p. 22) revised his description to one that corresponds better to the figure of de Férussac: an elongated conoidal spire, a large and thick columellar callus and an ornamentation presenting a multitude of lines so thin and close ("une multitude de linéoles tellement fines et serrées") that the shell appears to be uniformly brown coloured.

The material in the Deshayes collection (UCBL-EM32170) includes three specimens from Rilly (Marne), as well as an operculum. The best preserved specimen, reported as being the illustrated specimen (UCBL-EM32170c), bears a multitude of very thin, barely zigzag axial lines, as indicated by Deshayes (1864). A second specimen (UCBL-EM32170b) appears at first sight to be of a uniform light brown colour, but it is possible to see with a magnifying glass the same axial lines partially erased by wear. The spire is not protuberant, except on one specimen (UCBL-EM32170a), again as a consequence of wear. The examination of the callus and columellar teeth give, at least in part, an explaination for the confusing descriptions and figures of Deshayes: this material includes two different taxa.
On specimens UCBL-EM32170a and b, the columellar callus is widely spread, and also rather thick. The columella is marked in its centre by a depression with two very weak teeth. Apart from the spire, which is not protuberant, these two specimens correspond quite well to the figure of de Férussac.
On the other hand, the specimen UCBL-EM32170c (Pl. 9, fig. 2) from the same lot shows a wide, rather flat, columellar callus. The columella is decorated with three teeth, the adapical one more pronounced, is at the beginning of a depression of the columella, which contains the other two very weak teeth. This depression ends forming an abapical notch on the columella. Based on these characters this last specimen is assigned to *Clithon (Pictoneritina) saincenyensis* (Deshayes, 1864).

Cossmann, (1888, p. 86-87), reviewing the taxon *Nerita sobrina* of de Férussac, remains quite close to the diagnosis above, albeit mentioning a conoid spire and an ornamentation of very thin wavy axial lines. In the same work (1988, p. 90-91, he also considers *C. pisiformis* and *C. sobrinus* to be two forms of the same species. As discussed above, his second review of sobrinus (1902, p. 31, pl. VI, fig. 26) demonstrates that his interpretation of this taxon is erroneous. As a result of this error, Cossmann & Pissarro (1907, pl. V, fig. 39-7) introduced a new taxon from Pourcy: *Neritina consobrina perlonga*, through a figure of the "*Iconographie*", which shows the dorsum. On the next plate (pl. VI), the figure at the top left (on the left of number 39-8) appears to shows the same shell, now in apertural view. The opinion of Pacaud (2017, p. 19) is confirmed by the examination of the figured specimen (MNHN.F.J02078). It shows a highly developed callus, a strongly protruding, elliptical spire, a columella with a concavity, at each end of which there is a small tooth-like projection. The shell is worn externally and does not show any ornamentation. These elements clearly allow this taxon to be considered a junior synonym of *Neritina sobrina* de Férussac, 1823.

This taxon is very common in Pourcy. The best preserved

specimens have an ornamentation of thin axial lines. Generally, the lines are wider spaced and larger than on Deshayes' specimens, but never come close to the ornamentation encountered for example in *Clithon pisiformis*. On some specimens there is an obsolete fold in the columellar depression. This well-defined depression occupies about a third of the columella. The columellar callus is often very convex and always very broad. The spire is protruding on adult specimens.

A few specimens with an ornamentation of spiral bands (Pl. 11, figs 3 to 5) are included in this taxon, as well as four specimens from the Sparnacian clays of Soissons (Pl. 11, fig. 6).

The disposition of the columellar teeth is very different from that of the other taxa assigned to *Clithon (Pictoneritina)*. It is closer to the disposition observed on *Theodoxus fluviatilis* (Linnaeus, 1758), type species of *Theodoxus* de Montfort, 1810 which shows a slight depression of the columella (which can form very weak points at its extremities). Therefore the taxon *sobrinus* could be assigned to this genus but its protoconch seems to be planktotrophic. As it is hardly visible on the studied specimen, the generic assignment of this taxon could change after further studies.

Clithon (Pictoneritina) tigrinus nov. sp.
Pl. 12, figs 1-6; Table 1

Type material – Holotype MNHN.F.A71148 (Vrinat collection). Paratypes: UCBL-EM30644a/b/c/d/e (Deshayes collection), UCBL-EM31894 (de Boury collection), MNHN.F.A71153 (unknown collection). MNHN.F.A71149 and MNHN.F.A71150 (Vrinat collection)

Type locality – Butte des Usages, Cuise-la-Motte (Oise). Cuisian, Ypresian (Lower Eocene).

Etymology – From the Latin *tigrinus* (striped), a reference to its ornamentation.

Other studied material – **Cuise-la-Motte** (Oise): 4 specimens (collection Deshayes, UCBL-EM30644b to e), 9 specimens (Vrinat collection), 1 specimen (Laporte collection).

Description – Small semiglobose shell (height of the largest specimen: 5 mm) with fairly protruding spire, although involute at its apex (the protoconch is hidden by the last whorl, except on a worn specimen (Pl. 12, fig. 5), possibly planktotrophic). Aperture oblique, semicircular, with a depression framed by pseudo-teeth on the columella. This depression is quite wide (approximately half the columellar width), but not very accentuated. The smooth, moderately developed columellar callus is larger abapically. The very distinctive ornamentation, with its very geometrical aspect, consists of rather thick zigzag axial lines, red brown on a cream background, interrupted by one to three rather broad whitish spiral bands.

For the reasons given above for *Clithon (Pictoneritina) sobrinus* (de Férussac, 1823), after verification of the type of protoconch the generic assignation of this taxon might change.

Discussion – Several specimens of this new species were collected at Cuise-la-Motte, and it appears to be endemic to this location. Deshayes already isolated a series of five specimens (UCBL-EM30644) of the same origin, leaving this taxon in open nomenclature. It was also found it in the MNHN collections (MNHN.F.A71153), wrongly identified as "*Neritina nucleus* Desh.", and in the de Boury Collection (UCBL-EM31894), mis-identifed by Cossmann (1888, p. 87; pl. III, fig. 39) as *Neritina nucleus* Deshayes, 1832. Thus, in total, 18 specimens with very constant characteristics were available for examination, supporting the validity of this taxon.

This species has similarities with *Clithon (Pictoneritina) sobrinus* (de Férussac 1823) in terms of arrangement of the teeth, bordering a depression on the columella, and the protuberant spire. In addition to the very different ornamentation, they can be distinguished by the characteristics presented in Table 1.

Its ornamentation is somewhat similar to that of *Neritoplica subornata*, but that species has a single columellar tooth, quite characteristic for the genus. Based on columellar teeth disposition, *C. tigrinus* can easily be differentiated from *C. nucleus* (which sometimes has a very similar ornamentation : e.g. Pl. 4, fig. 6) and *C. pisiformis*.

	Clithon (Pictoneritina) sobrinus	***Clithon (Pictoneritina) tigrinus***
Protoconch	Visible	Hidden
Columellar concavity	Fairly accentuated, albeit narrow, occasionally bearing faint folds	Larger and shallower
Callus	Well developed columellar callus	Moderately developed columellar callus, abapically wider
Size	Medium (height up to 8 or 9 mm)	Small (maximum height 5 mm)

Table 1. comparison of taxa *Clithon (Pictoneritina) sobrinus* (de Férussac, 1823) and *Clithon (Pictoneritina) tigrinus* nov. sp.

Clithon (Pictoneritina) zonarius (Deshayes, 1832)
Pl. 13, figs 1-6 & Pl. 14, figs 1-3; Table 2

Type material – Five syntypes, UCBL-EM32197 (Deshayes collection). Not designated on the label in the Deshayes collection, the figured specimen is nevertheless easily recognisable.

Type locality – Cuise-la-Motte (Oise). Cuisian, Middle Ypresian (Lower Eocene)

Other studied material – **Cuise-la-Motte** (Oise): 1 specimen (Deshayes collection, UCBL-EM30643), 1 specimen (Vrinat collection). **Brasles** (Aisne): 3 specimens (Leroy collection). **Mons-en-Laonnois** (Aisne): 1 specimen (Lhomme collection, MNHN.F.B57240). **Trosly-Breuil** (Oise): 1 specimen (Faullummel collection, MNHN.F. A29399).

Description – A fairly prominent spire, a moderately developed columellar callus, four to six weak and uneven teeth in the middle of the columella, and an ornamentation consisting of three dark brown spiral bands, usually punctuated with whitish dots (Deshayes, 1832, p. 136, pl. XXV, figs 1 & 2).

Discussion – The description above correctly represents the figured specimen UCBL-EM32197a, which is easily recognised. On others, such as specimen UCBL-EM32197b, there are only three teeth on the columella, (four if the abapical end of the columellar depression is counted). The first, adapical, tooth is quite strong, followed, after a marked space, by two to four weak teeth in a depression of the columella.

Cossmann (1888, p. 87) confirms this description but the "*Iconographie*", under number 39-8, shows only the back of a specimen with an ornamentation very close to that of specimen UCBL-EM30639a assigned by Deshayes to *Clithon (Pictoneritina) nucleus* (Deshayes, 1832). Coss-

	Clithon (Pictoneritina) nucleus	***Clithon (Pictoneritina) zonarius***
Spire	**Deshayes, 1832:** Short, non-protruding spire. **Cossmann, 1888:** Subulated, rounded spire. **Syntypes: a:** Slightly protruding and conoidal spire, visible protoconch; **b:** Flush spire, hardly visible protoconch (very abraded). **Other specimens from the Deshayes collection:** Protruding, sub-shouldered spire. Visible protoconch.	**Deshayes, 1832:** Protruding spire, obtuse at the top. **Cossmann, 1888:** Slightly prominent spire, marginated at the suture. **Syntypes: a:** Shouldered, very protruding spire, apparent protoconch; **b:** Slightly salient, sub-shoulder spire. Apparent protoconch.
Callus	**Deshayes, 1832:** Fairly thick callus, more widely spread abapically (according to fig. 3). **Syntypes:** Moderately spread callus, more widely spread abapically (slightly abraded).	**Deshayes, 1832:** Barely spread. **Cossmann, 1888:** Widely spread. **Syntypes: a:** Moderately developed; **b:** Moderately developed, more spread abapically (slightly abraded).
Teeth	**Deshayes, 1832:** Three or four unequal teeth in the middle of the columella. **Cossmann, 1888:** Almost always devoid of teeth. **Syntypes: a:** Three strong teeth, **b:** Three weaker teeth. **Other specimens from the Deshayes collection: a:** Very strong and square adapical tooth, followed by two weaker teeth; **b:** same disposition, but weaker teeth.	**Deshayes, 1832:** Four to six uneven serrations on the slightly arched columella. **Cossmann, 1888:** Four to six, 1st and 2nd abapical teeth stronger. **Syntypes: a:** Six teeth, 1st and 2nd adabical teeth stronger; **b:** Three rounded teeth, adapical tooth stronger.
Ornamentation	**Deshayes, 1864:** Large dark axial lines on a whitish background, interrupted by two spiral bands forming brown chevrons. **Cossmann, 1888:** Ornamentation close to that of zonarius, but more even. **Other specimens from the Deshayes collection: a:** Ornamentation of axial lines broken by two or even three spiral bands; **b:** Ornamentation of beige axial or sub-axial segments, sometimes in chevrons, and two beige spirals, on a brown background.	**Deshayes, 1832:** Brown spiral bands (punctuated with whitish spots) on a white background. **Deshayes, 1864:** Brownish colour, irregularly white spotted, divided by two pale transverse areas (= spiral bands). **Cossmann, 1888:** Wide brown areas separated by narrower whitish spaces cut by uneven patterns. **Syntypes: a:** Three clear spiral stripes on brown background (one band is hardly visible); **b:** Three neat white spiral stripes on brown background, stained with white spots.

Table 2. Comparison of *Clithon (Pictoneritina) nucleus* (Deshayes, 1832) and *Clithon (Pictoneritina) zonarius* (Deshayes, 1832)

mann (1888, p. 87) also notes that *zonarius* and *nucleus* are difficult to distinguish from one another based on the publications of Deshayes (1832, 1864). As distinguishing characters, he mentions the shape of the spire and the strength of the four to six teeth, the adapical and second abapical ones being stronger on *C. zonarius*, whereas the columella is almost always devoid of teeth in *nucleus* (but, as mentioned above the specimens he identified as *nucleus* belong to another species).

Table 2 compares *C. nucleus* and *C. zonarius*. It is based on the examination of more than thirty specimens assigned to these two taxa. The most obvious distinguishing morphological criterion is the strength of the adapical tooth, which is much wider in *C. nucleus*. The variation in strength could, however, be environmentally related as illustrated by Symonds (2008) and others. In that case both taxa could represent a single species. Further work incorporating other criteria is required to conclude.

The well-preserved shells that are herein included in this taxon, uncommon in collections, show alternating pale spirals and large brown areas with whitish rounded spots. Besides at Cuise-la-Motte, it was found at Brasles. Additionally, three specimens (including the specimen in the Lhomme collection kept in the MNHN, incorrectly identified as *Clithon (Pictoneritina) inequidentata* (Récluz, 1850)) are also included, that have a very similar morphology, with a slightly protruding spire, four to five moderately marked columellar teeth, moderately developed callus. They have, however, a unique ornamentation, with three cream spiral bands separating brown zones (as in the syntypes of *Clithon (Pictoneritina) zonarius* (Deshayes, 1832)), axially striped with cream (Pl. 14, figs 1-3) instead of white spots.

Genus *Neritina* Lamarck, 1816

?Neritina levesquei Récluz, 1850 and ***?Neritina nouleti*** Récluz, 1850

Type material – not found.

Type locality – Soissons (Aisne). Sparnacian, Ypresian (Lower Eocene)

Description – Short spire, three columellar teeth (*N. levesquei*); conical spire and three columellar teeth (*N. nouleti*).

Discussion – The descriptions, which are not very detailed, did not allow a comparison with any taxa previously or subsequently described, or with available specimens. The Récluz collection could not be located. As far as known, these taxa have not been considered by any later author, except Pacaud (2017, p. 195), who considers *N. nouleti* a synonym of *C. (Pictoneritina) sobrinus*. This doesn't seem likely, since *N.nouleti* is supposed to have three teeths on the columella, whereas *C. (Pictoneritina) sobrinus* shows only two.

Herein both species are considered to be nomina dubia.

Genus *Neritodryas* Martens, 1869

Neritodryas dutemplei (Deshayes, 1864)
Pl. 15, figs 1-5

Type material – Two figured syntypes UCBL-EM32670a and b (Deshayes collection)

Type locality – Aÿ (Marne). Ypresian (Lower Eocene)

Other studied material – **Pourcy** (Marne): 2 specimens (Cossmann collection, MNHN.F.J09775), 5 specimens (Vrinat collection), 3 specimens (Leroy collection). **Sinceny** (Aisne): 1 specimen (Hessel collection), 3 specimens (Lhomme collection, MNHN.F.B57205).

Description – According to Deshayes (1864 : p. 21; pl. 66 fig. 21-22 and 24). This species has a conoid spire, shouldered on the last whorl. The figure of Deshayes shows an edentate columella, and a moderately developed columellar callus. The ornamentation of this species is variable, according to the author, from uniformly pale brown shells, to others (such as the one figured) with alternating light and dark spiral bands, the darker being decorated with pale spots forming chevrons.

Discussion – The study of the syntypes confirms these characteristics. A central depression on the solumella can be mentioned as well The figure of the "*Iconographie*" (MNHN.F.J09775, Cossmann collection) also corresponds well to this description. This taxon seems well characterised, in spite of the variability in ornamentation (a sub-adult specimen (Pl. 15, fig. 5) illustrates its ontogeny). The species might be confused with *Neritodryas guillioui* Symonds & Pacaud, 2010, which is very close, but differs by 14-18 low spiral ribs on the last whorl (and therefore is excluded from this study), albeit these ribs are not clearly visible on the paratypes (MNHN.F. A31492, MNHN.F.A32900) examined.

Neritodryas laubrierei (Cossmann, 1888)
Pl. 14, figs 4-6

Type material – Syntype MHNN.P.003139 (de Laubrière collection)

Type locality – Chenay (Marne). Chalons sur Vesles sands, Thanetian (Upper Palaeocene).

Other studied material – **Chalons-sur-Vesle** (Marne): 3 specimens (Cossmann collection, MNHN.F.J02075 and MNHN.F.J09786). **Prouilly** (Marne): 15 specimens

(Leroy collection). **Cauroy-les-Hermonville** (Marne): 2 specimens (Leroy collection).

Description – This taxon has a short, slightly prominent spire, no tooth on the columella, a moderately developed callus. Cossmann (1888) gives no indication of ornamentation.

Discussion – This second species of Neritidae described by Cossmann (1888) comes from the Thanetian of Chenay (Marne). It is incorporated within this study for comparison with *Neritodryas dutemplei* (Deshayes, 1864) from the Ypresian as the original figure suggests it being closely related.

Examination of the specimen figured in the "*Iconographie*" (MNHN.F.J02075), from Chalons-sur-Vesle, confirms these diagnostic elements. The surface of this specimen is however poorly preserved. Another specimen in the Cossmann collection (MNHN.F.J09786) that was examined appears to be adorned with beige axial bands on a lighter background, but is also in fairly poor condition. Fortunately, several other specimens (Leroy collection) in excellent condition (Pl. 14, figs 5 & 6) could be examined, which display the ornamentation of this taxon, consisting of dark axial bands, more or less zigzag, on a pale background.

Based on the limited development of the callus, the absence of teeth on the columella and the planktotrophic protoconch this taxon is placed in the genus *Neritodryas* Martens, 1869, instead of *Theodoxus* de Montfort, 1810 (as proposed by Cossmann (1925, p. 222)), or *Theodoxus (?Vittoclithon)* H.B. Baker 1923 (as proposed by Wenz (1929, p. 2912-2913)). It differs from *Neritodryas dutemplei* (Deshayes, 1864) by the neater shoulder on the last whorl. The last whorl and the penultimate whorl thus form a sharp angle, close to 100 °, clearly enhancing the spire. In *N. dutemplei*, on the other hand, the last whorl overlaps the penultimate and forms an inclined ramp. This is also evident in the shape of the aperture, the labrum and columella forming a closed angle at the adapical end. The ornamentation of *N. laubrierei* is also very different from that of *N. dutemplei*.

Genus *Neritoplica* Oppenheim, 1892

Neritoplica subornata (d'Orbigny, 1850)
Pl. 2, fig. 5

1843 *Neritina ornata* Melleville [non *Nerita ornata* J. de C. Sowerby, 1835], p. 50; pl. 6, figs 9 and 10
1864 *Neritina graciosa* Deshayes, p. 19; pl. 66, figs 27 to 29

Type material – not found.

Type locality – Chalons-sur-Vesles (Marne). Thanetian (Upper Palaeocene)

Other studied material – **Prouilly** (Marne): 1 specimen (Leroy collection). **Saint-Gobain** (Aisne)?: 1 specimen (collection IRScNB I.G. 9694)

Description – This species is clearly described and illustrated (d'Orbigny, 1850) as having a single strong posterior columellar tooth, a poorly visible spire, a moderately developed callus, an ornamentation of thin zigzag axial lines, often interrupted by white spiral lines (typically two).

Discussion – Apart from some questions of homonymy and etymology (*ornata* corrected to *subornata* by d'Orbigny in 1850, then renamed again as *gratiosa* or *graciosa* by Deshayes in 1864), this taxon is well defined and widely accepted.

This species is common in the Thanetian. It is included in this study solely on the basis of a very characteristic specimen, catalogued as coming from the Cuisian of Saint-Gobain, in an old collection of the IRScNB (John Laporte, pers. comm.). However, the geographical and stratigraphic origin of this specimen is questionable, as the species is confined to environments with reduced salinity and is unknown from the Ypresian elsewhere.

Neritoplica uniplicata (J. de C. Sowerby, 1823)
Pl. 16, figs 1-8

1823 *Nerita globosa* an *globulus* de Férussac, pl. 2, fig. 14.

Type material – Syntype NHMUK PI TG 26818.

Type locality – Charlton and Woolwich, Greater London (England), Blackheath Formation (Todd & Symonds, pers. com.), Ypresian (Lower Eocene).

Other studied material – **Mont-Bernon, Epernay** (Marne): 1 specimen (collection Douvillé, UCBL-EM30641). **Epernay** (Marne): 1 specimen (Cossmann collection, MNHN.F.J02077). **Disy-Cumières** (Marne): 3 specimens (Deshayes collection, UCBL-EM32160b/c/d). **Pourcy** (Marne): 15 specimens (Vrinat collection).

Description – This taxon is characterised by an involute ("concealed") spire, a "plait" on the slightly convex columella ("rather convex columellar lip"), and an olive green colour for the freshest specimens. The spire is marked by the presence of a curved suture ("single curve") starting from a slight hollow. The figure from Sowerby (1823, pl. 385, fig. 9-10) shows a fairly strong tooth and a widespread columellar callus.

Discussion – The legend of figure 14 of plate 2 of de Férussac (1823) is missing (Pacaud (2017, p. 194)). It represents a taxon named *Nerita globulus*, as indicated by

Defrance (1825, p. 481), Deshayes (1832, p. 151), and Récluz (1850, p. 154), who consider *Neritina uniplicata* J. de C. Sowerby, 1823 to be a junior synonym. The order of priority of the works of de Férussac and J. de C. Sowerby. has been extensively discussed, recently by Symonds (2002, p. 2) and Pacaud (2017, p. 194), and the case has been decided in favour of J. de C. Sowerby.

Neither the figure of de Férussac (1823, pl. 2, fig. 14) nor that of Deshayes (1832, p. 151, pl. XVII, fig. 19 and 20) clearly shows the characteristics of this taxon (involute spire, strong adapical tooth, large callus), contrary to the work of J. de C. Sowerby. They show instead a shell with a flush spire, a broad and slightly convex columellar callus, a columella displaying a weak tooth on the apex side. The drawing of de Férussac does not show any ornamentation, only thin growth marks. Deshayes states that the spire is not very apparent (frequently abraded), that the columellar callus is convex and thick, and that the tooth is rather prominent (not reflected in the figures).

The specimens in the Deshayes collection (UCBL-EM30641) are nevertheless well preserved, and the characteristics of this taxon are obvious. On some large specimens, the spire tends to become prominent, even if the first whorls remain hidden.

Cossmann (1888, p. 86) and Cossmann & Pissarro (1907, pl. V, fig. 39-6) indicate that this species has an ornamentation composed of rather thin spiral lines. The specimen figured by Cossmann & Pissarro (Cossmann collection, MNHN.F.J02077) is indeed a particular variety of *Neritoplica uniplicata*, with an ornamental pattern which is not typical of the species (which is generally not ornamented). Spijkerman *et al*. (2015) also report and illustrate this variety from Pourcy, and it was also found at Mont-Bernon, Epernay (Douvillé collection, UCBL-EM30641).

Dichotomous identification key

Given the large variability in some species and the limited number of criteria selected for this review, the characterisation of the species retained as valid is not always straightforward. Nevertheless, a dichotomous key is presented as practical tool. The first characteristic used is the disposition of columellar teeth, allowing identification of generic position. Additional criteria, such as the shape of the aperture, could complete the criteria for separating the species.

0 (1) Edentate; a vague fold may be present on the apex side [***Neritodryas***] 8 (9)
1 (0) 0ne or more teeth or folds, columella with a concavity..... 2 (3)

2 (3) Single tooth, adapical [***Neritoplica***] 10 (11)
3 (2) Several teeth of variable strength 4 (5)

4 (5) Two weak teeth, bordering a weak, central, concavity [***Clithon (Pictoneritina)***] 6 (7)
5 (4) Several teeth on the columella, with a stronger one, adapical [***Clithon (Pictoneritina)***]..... 12 (13)

6 (7) Protoconch visible. Columellar depression clearly visible, narrow, sometimes with small folds. Columellar callus strongly developed, may be thick and bulging. Ornamentation of wavy axial lines, thin or very thin, or of spiral bands..... ***Clithon (Pictoneritina) sobrinus*** (de Férussac, 1823) - Ypresian
7 (6) Protoconch hidden. Wider and shallower columellar depression. Columellar callus moderately developed, ornamentation consisting of rather thick, zigzag, redish brown axial lines on a beige background, ususally interrupted by one or two beige spiral bands..... ***Clithon (Pictoneritina) tigrinus*** nov. sp. - Ypresian

8 (9) Spire shouldered. Ramp connecting last whorl to previous whorl. Columellar callus poorly developed. Ornamentation of thin brown and beige spiral bands, sometimes marked with chevrons ....***Neritodryas dutemplei*** (Deshayes. 1864) - Ypresian
[Similar shells from the Ypresian, but with spiral ridges, correspond to ***Neritodryas guillioui*** Symonds & Pacaud, 2010 or ***Neritodryas marqueti*** Symonds, 2016.]
9 (8) Spire shouldered. Last whorl connected to the previous whorl with a sharp angle. Columellar callus poorly developed. Ornamentation of more or less zigzag axial bands..... .....***Neritodryas laubrierei*** (Cossmann, 1888) - Thanetian

10 (11) Spire involute. Callus moderately developed. Ornamentation absent or with spiral bands .... ***Neritoplica uniplicata*** (J. de C. Sowerby, 1823) - Ypresian
11 (10) Spire flush. Callus moderately developed. Ornamentation of undulating axial lines..... ..... ***Neritoplica subornata*** (d'Orbigny, 1850) - Thanetian, Ypresian (?)

12 (13) Teeth weak 14 (15)
13 (12) Teeth strong or moderately strong 22 (23)

14 (15) Spire flush. Columellar callus moderately developed. Ornamentation of sharp spiral bands ..... ***Clithon (Pictoneritina) barbei*** Symonds & Pacaud, 2010 -Ypresian

15 (14) Columellar callus more developed 16 (17)

16 (17) Columellar callus broadly spread, not bulging. Columellar concavity in the shape of a scythe, sometimes abruptly ending abapically. Spire just flush or barely protuberant. Ornamentation of very thin and close axial lines ..... ***Clithon (Pictoneritina) saincenyensis*** (Deshayes, 1864) - Ypresian

17 (16) Columellar callus less spread, shape more globular. Ornamentation of variably shaped cream-coloured spots on a brown background, sometimes forming rather wide zigzag axial lines ..... ***Clithon (Pictoneritina) coeuvrensis*** **nov sp.** - Ypresian

22 (23) Columella with sub-rectilinear adapical portion (about a quarter of the length of the columella), which can bear up to four very small teeth, bordered abapically by a rather strong tooth, then a second part of the columella, in the shape of a scythe, carrying up to 7 very small teeth. Spire weakly to moderately protruding, last whorl shouldered. Ornamentation of very fine motifs (typical form, from Saint Gobain or Pourcy) or portions of lines (Coeuvres), arranged in spirals ..... ***Clithon (Pictoneritina) bouryi*** (Cossmann, 1888) - Ypresian

23 (22) Columella with rather strong tooth at a quarter of the distance from the adapical end. Two to five weaker teeth, often decreasing in size, equally spaced, follow after a marked space 24 (25)

24 (25) Teeth moderately strong in adult specimens, rather weak in young specimens. Spire flush, columellar callus broadly spread, ornamentation of wavy axial lines of small to medium thickness ..... ***Clithon (Pictoneritina) pisiformis*** (de Férussac, 1823) - Ypresian

25 (24) Other characteristics 26 (27)

26 (27) Secondary teeth quite sharp, small when they are numerous. Spire quite variable, conoidal (type specimen from Pourcy), quite often low, sometimes sub-shouldered. Ornamentation of pale spots on a dark background, more or less arranged in spirals ..... ***Clithon (Pictoneritina) occultatus*** nov. sp. - Ypresian

27 (26) Other characteristics 28 (29)

28 (29) Teeth well-marked (three), the adapical one usually very wide, rounded at the end. Spire variable, columellar callus moderately developed, abapically wider. Ornamentation of alternating brown and whitish axial lines, having a certain regularity, sometimes locally formed into a spiral of chevrons or crossed by a white spiral line ..... ***Clithon (Pictoneritina) nucleus*** (Deshayes, 1832) - Ypresian

29 (28) Teeth less pronounced, often five. Spire fairly low, sub-shouldered. Columellar callus, moderately developed. Ornamentation of pale spiral bands separating brown bands, often marked with round whitish spots or axial stripes ..... ***Clithon (Pictoneritina) zonarius*** (Deshayes, 1832) - Ypresian

Conclusions

Although this study may not be definitive, the illustration of type specimens, the homogenous morphological approach adopted and the dichotomous key, should significantly progress the identification of Neritidae from the Ypresian of the Paris Basin. The illustration of several specimens of *Clithon (Pictoneritina) occulatus* nov. sp. from the type locality Pourcy documents the typical intraspecific variability in species of *Clithon (Pictoneritina).*

Among the criteria selected, some appear to be more reliable and useful than others. The number and arrangement of columellar teeth allow easy identification of the genus and of sub-groups within *Clithon,* but are not always helpful to differentiate the various species in *Clithon (Pictoneritina).* The same applies to the shape of the spire, which is generally very variable in species of *Clithon (Pictoneritina).*

The extent of the columellar callus is fairly stable, but again less useful within *Clithon (Pictoneritina),* except for the separation of *Clithon (Pictoneritina) saincenyensis* and *sobrinus* which at first glance can be very similar.

The ornamentation pattern can vary significantly, but generally for each taxon a specific ornamentation style can be defined, allowing their separation. It thus remains a useful criterion, even though it may be influenced by the paleo-environment. Caution with the presence or development of spiral bands or lines: it may characterize some taxa (e.g. *Clithon (Pictoneritina) zonarius* and *C. barbei*), but in other taxa, specimens with spiral bands and lines are part of normal variation (*Neritoplica uniplicata* and *Clithon (Pictoneritina) sobrinus*). Finally, in *Clithon (Pictoneritina) nucleus* and *C. occultatus* stripes or portions of stripes may appear, closely interwoven with the usual ornamentation. This might be caused by wear. It would be interesting to study the ontogenesis of these spiral bands and lines in greater detail to determine where they provide evidence to separate taxa.

Other authors use additional criteria, which could com-

plement this study or lead to revisions. An interesting example (Arnaud Leroy, pers. comm.) is the palatal apophysis, a tooth (or fold) located on the adapical side of the aperture that guides the operculum. Its shape appears variable and could help to characterise the different species. According to the author's observations it is present in *Clithon (Pictoneritina) occultatus* and *Neritodryas dutemplei*, reduced to a vague fold in *Clithon (Pictoneritina) sobrinus*, and absent in *Neritoplica uniplicata*.

Within the genera *Neritodryas* and *Neritoplica* intraspecific variability is low or moderate. Therefore, the characterisation of species is quite straightforward. It is not clear whether this is helped by a lower frequency of these species.

Clithon (Pictoneritina) comprises several stable taxa: *saincenyensis, bouryi* and *tigrinus*. *Clithon sobrinus*, although fairly variable, remains fairly distinctive, thanks to its columella, always with a concavity devoid of real teeth. *Clithon pisiformis*, as defined in this paper, presents two quite distinct forms, which might represent separate taxa. Separation of *C. nucleus*, *C. zonarius* and *C. occultatus* can be difficult, therefore other authors might group them differently. The occurrence of numerous species, some difficult to segregate, has also been noted for extant species of *Clithon* and *Theodoxus* by Bandel (2001: 66; 97; 153) who suggests this was caused by hybridisation between closely related sympatric species (sometimes between species belonging to different subgenera or even genera).

The taxa currently classified in *Clithon (Pictoneritina)* can be separated into four groups which might be separate subgenera (or genera):

- *C. sobrinus* and *C. tigrinus*, with a distinctive depression on the columella.
- *C. bouryi* with its unique arrangement of columellar teeth.
- *C. saincenyensis* and *C. coeuvrensis*, with a broad and flat columellar callus and poorly-developed columellar teeth.
- *C. pisiformis, C. nucleus, C. zonarius* and *C. occultatus*, with moderately-spread callus and a noticeably strong adapical tooth, followed by several weaker teeth.

Acknowledgements

I am particularly grateful to Jean-Michel Pacaud (MNHN) for his review of this paper, as well as our informal exchanges notably about taxonomic or nomenclatural issues. Without these, this work would not have been possible.

I also thank Jean-Michel Pacaud (MNHN), as well as Emmanuel Robert (UCBL), Denis Demarque (MHNN) and Jon Todd (NHM) for information and access to the public collection they curate.

I'm grateful as well to Arnaud Leroy, Jean-Luc Marcomini, Fabrice Moreau and Christian Romanek for the access granted to relevant material of their private collections, and, when I presented them the draft of this work, their friendly and encouraging support; John Laporte, for the picture of Pl. 10, fig. 6, informations about Dutch and Belgian collections and advice on macrophotography; Bruno Casanova (NHM), for the picture of Pl. 16, fig. 3; to the anonymous reviewers for their helpful comments; and, last but not least, my wife Rachel, Malcolm Symonds and Han Raven for the painstaking work of improving the English version of this paper.

References

Bandel, K. 2001. The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of related Neritimorpha (Gastropoda). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 85: 65-164, fig. 1-315.

Cossmann, M. 1888. Catalogue Illustré des coquilles fossiles de l'Éocène des Environs de Paris. (3ème fascicule). *Annales de la Société Royale Malacologique de Belgique* 23: 3-328, pl. I-XII.

Cossmann, M. 1902. Catalogue Illustré des coquilles fossiles de l'Éocène des Environs de Paris. (Appendice nº 3). *Annales de la Société Royale Malacologique de Belgique* 36: 9-110 (sep. 5-106), pl. I-VI, 4 text-figs.

Cossmann M. 1925. *Essais de paléoconchologie comparée*, 13. Paris. Presses Universitaires de France. 345 pp., 11 plates.

Cossmann M. & Pissarro G. 1907. *Iconographie complètedes coquilles fossiles de l'Éocène des environs de Paris*. *Tome 2*. Hermann, Paris: pl. 1-9.

Defrance, J.L.M. 1825. *Dictionnaire des Sciences Naturelles*, 34 (Myd-Nik), Levrault, Strasbourg : 480-482 (Néritine, *Neritina* fossiles).

Deshayes, G.-P. 1832. *Description des coquilles fossiles des environs de Paris*. *Tome 2. Livraisons 8, 10 et 12*, l'auteur, Béchet Jeune, Baudouin frères, Treuttel & Wurtz, Paris: 81-146. *Atlas 2*, Levrault, Paris, pl. 9-17.

Deshayes, G.-P. 1864. *Description des Animaux sans vertèbres découverts dans le bassin de Paris. Tome III. Livraisons 41-44*. Paris (Baillière): 1-200, Atlas II, pl. 63-85.

Eichhorst, T.E. 2016. *Neritidae of the world*. *Volume 1*. Harxheim: Conchbooks. 695 pp.

de Férussac, A.E.J.P.J.F. d'Audebard 1823. *Histoire Naturelle Générale et particulière des Mollusques Terrestres et Fluviatiles, tant des espèces que l'on trouve aujourd'hui, que des dépouilles fossiles de celles qui n'existent plus, classées d'après les caractères essentiels que présentent ces animaux et leurs coquilles*, Baillière, Paris, livraison 20, pl. 77, 125, 127, 128, 131, Nérites fossiles, pl. 2.

Glibert, M. 1962. Les Archaeogastropoda fossiles du Cénozoïque étranger des collections de l'Institut royal des Sciences naturelles de Belgique. *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique*, 2ème série 68: 1-131 (sans fig.).

Iredale, T. 1936. Australian Molluscan Notes No. 2. *Records of the Australian Museum* 19(5): 267-340.

Lamarck, J.B.P.A. 1816. Mollusques et polypes divers. In: J.

G. Bruguière, et al., 1791-1827, *Tableau encyclopédique et méthodique de trois règnes de la nature. Vers, coquilles, mollusques et polypiers*. Agasse, Paris. Part 23, 1-16, pls. 391-488, 431bis, 431bis*.

Le Renard, J. 1995. Révision des Mollusques paléogènes du bassin de Paris III. Chronologie des créateurs de références primaies. *Cosmanniana* 3(4): 133-150.

Lozouet, P. & Plaziat, J.C. 2008. *Mangrove environments and molluscs: Abatan River, Bohol and Panglao Islands, Central Philippines*. Hackenheim, Conchbooks - 1 vol. 160 pp.

Melleville, M. 1843. Mémoire sur les sables tertiaires inférieurs du bassin de Paris, avec la description de 78 espèces de coquilles fossiles inédites de ce terrain. *Annales des Sciences Géologiques* 2: 1-29 & 77-120, pl. 1-9.

Newton, R.B. 1891. *Systematic list of the F.E. Edwards collection of British Oligocene and Eocene mollusca in the British Museum (Natural History), with references to the type-specimens from similar horizons contained in other collections belonging to the Geological Department of the Museum*. London, British Museum, XXVIII + 365 pp.

Orbigny, A. Dessalines d' 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*. T. II. Paris, 428 p.

Pacaud, J.-M. 2007. Nouveautés nomenclaturales et taxonomiques introduites par Alcide d'Orbigny dans le *Prodrome* (1850, 1852) pour les espèces du Paléocène et de l'Éocène. *Geodiversitas* 29(1):17-85.

Pacaud, J.-M. 2017. Remarques taxonomiques et nomenclaturales sur les mollusques gastropodes du Paléogène de France et description d'espèces nouvelles. 1ère partie: Vetigastropoda et Neritimorpha. *Cossmanniana* 19: 181-205.

Pacaud, J.-M. & Le Renard J. 1995. Révision des Mollusques Paléogènes du Bassin de Paris. IV - Liste systématique actualisée. *Cossmanniana* 3(4): 151-187.

Petit, R. E. 2011 - Reprint of Lamarck's 1816 "Liste des objets". *Conchologia Ingrata* 3: 1-18

Récluz, C.A. 1850. Notice sur le genus *Nerita* et sur le sous-genus *Neritina*, avec le Catalogue synonymique des Néritines. *Journal de Conchyliologie* 1(2): 131-164, pl. III &VII.

Sowerby, J de C. 1823. *The Mineral Conchology of Great Britain or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth.* London, vol. 4 (fin) et vol. 5 (début), livraisons 67-76, pl. 384-443.

Spijkerman, E., van Nieulande, F.A.D., Wesselingh, F.P., Reich, S. & Tracey S. 2015. Pourcy (Paris Basin, France): Preliminary assessment of an early NW Eocene tropical coastal environment from molluscs and vertebrate fossils. *Cainozoic Research* 15 (1-2): 155-189.

Symonds, M. F. 2002. The Neritidae of the Barton Group (Middle Eocene) of the Hampshire Basin. *Tertiary Research* 21(4): 1-10, pl. 1-3, text-fig. 1.

Symonds, M.F. 2008. Changes in colour patterns in fossil Neritidae. *Mollusc World* 16, 5-7. The Conchological Society of Great Britain & Ireland.

Symonds, M.F. 2015. New species of Neritidae (Gastropoda, Neritimorpha) from the Solent Group (late Eocene and early Oligocene) of the Hampshire Basin. *Cainozoic Research* 15(1-2): 147-153.

Symonds, M.F. & Pacaud J.-M. 2010. New species of Neritidae (Neritimorpha) from the Ypresian and Bartonian of the Paris and Basse-Loire Basins, France. *Zootaxa* 2606: 55-68.

Wenz, W. 1929. *Fossilium Catalogus. I: Animalia. Pars 43: Gastropoda extramarina tertiaria X*. Berlin (Junk): 2887-3014.

Key to the plates

Plate 1

Some particular distinguishing characteristics.

1 Columella with a depression in the shape of a scythe (on *C. bouryi*).
2 Columella with teeth, showing a sub-quadrangular depression, bordered by a clear abapical notch (*C. occultatus*).
3 Columella without teeth, showing a sub-elliptic depression, smoothly ending adapically and abapically (*C. tigrinus*).
4 Involute spire (*N. uniplicata*).
5 Flush spire (*C. barbei*).
6 Weakly protruding spire (*C. tigrinus*).
7 Conoidal spire (*C. occultatus*).
8 Shouldered spire (*N. dutemplei*).
9 Sub-shouldered or "sub-elliptical" spire (*T. tigrinus*).
10 Elliptical spire (*C. sobrinus*).
11 Wide columellar callus (*C. saincenyensis*).
12 Moderately wide columellar callus (*C. occultatus*).
13 Moderately wide columellar callus, wider abapically (*T. tigrinus*).
14 Narrow columellar callus (*N. dutemplei*).

Plate 2

Various Neritidae.

1a ***Neritina elegans*** Deshayes, 1832. **Syntype**. Height 4.0 mm. Middle Lutetian (Middle Eocene); Houdan (Yvelines). Deshayes collection, UCBL-EM32169

1b Label from the Deshayes collection.

2a ***Neritina lineolata*** Deshayes, 1832 [non Lamarck, 1822]. **Syntype (figured)**. Height 5.5 mm. Middle Lutetian (Middle Eocene); Houdan (Yvelines). Deshayes collection, UCBL-EM32171a

2b Label from the Deshayes collection.

3 ***Neritina lineolata*** Deshayes, 1832 [non Lamarck, 1822]. **Syntype**. Height 5.5 mm. Middle Lutetian (Middle Eocene); Houdan (Yvelines). Deshayes collection, UCBL-EM32171b.

4 ***Neritoplica subornata*** (d'Orbigny, 1850). Height 5.5 mm. Thanetian (Upper Palaeocene); Prouilly (Marne). Leroy collection.

5 ***Clithon (Pictoneritina) barbei*** Symonds & Pacaud, 2010. Height 5.0 mm. Cuisian, Ypresian (Lower Eocene); Pourcy (Marne). Vrinat collection.

6 ***Clithon (Pictoneritina)*** sp. Height 7.5 mm. Cuisian, Ypresian (Lower Eocene); Courcelles-Sapicourt (Marne). Leroy collection. Unique specimen possibly belonging to a new taxon. It is morphologically quite close to a specimen (Pl. 13, fig. 4) assiged to the taxon *C. zonarius,* left unnamed because of its uniqueness and the low visibility of the columellar teeth.

Plate 3

Clithon (Pictoneritina) coeuvrensis nov. sp.

1 **Holotype**. Height 7.0 mm. Cuisian, Ypresian (Lower Eocene); Coeuvres-et-Valsery (Aisne). Leroy collection, MNHN.F.A71151.

Clithon (Pictoneritina) bouryi (Cossmann, 1888). Ypresian (Lower Eocene).

2 Height 3.5 mm. Cuisian; Saint-Gobain (Aisne). Vrinat collection.

3 Height 5.0 mm. Cuisian; Saint-Gobain (Aisne). Leroy collection.

4 Height 5.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection.

5 Height 2.5 mm. Cuisian; Coeuvres-et-Valsery (Aisne). Leroy collection.

6 Height 3.0 mm. Cuisian; Coeuvres-et-Valsery (Aisne). Leroy collection.

Plate 4

Clithon (Pictoneritina) nucleus (Deshayes, 1832). Cuisian, Ypresian (Lower Eocene); Cuise-la-Motte (Oise).

1a **Syntype**. Height 7.4 mm. Deshayes collection, UCBL-EM32198a

1b Label from the Deshayes collection

2 **Syntype**. Height 7.8 mm. Deshayes collection, UCBL-EM32198b.

3a Height 7.8 mm. Deshayes collection, UCBL-EM 30639a.

3b Label from the Deshayes collection.

4 Height 3.0 mm. Deshayes collection, UCBL-EM30639b.

5 Height 3.0 mm. Vrinat collection.

6 Height 5.5 mm. Vrinat collection.

Plate 5

Clithon (Pictoneritina) nucleus (Deshayes, 1832). Cuisian, Ypresian (Lower Eocene).

1 Height 6.0 mm. Cuise-la-Motte (Oise). Vrinat collection.

2 Height 3.0 mm. Cuise-la-Motte (Oise). Cossmann collection, MNHN.F.J09794.

3 Height 6.0 mm. Cuise-la-Motte (Oise). Leroy collection. Doubtfull specimen with involute spire and non-typical teeth arrangement.

4 Height 7.5 mm. Saint-Gobain (Aisne). Marcomini collection. Doubtful specimen with ornementation close to that of some specimens identified as *C. (P.) zonarius* (Deshayes, 1832) (Pl. 15, figs 1-3), but with strong teeth, as observed on typical *C. (P.) nucleus*.

5 Height 4.0 mm. Gland (Aisne). Cossmann collection, MNHN.F.J09795.

6 Height 5.0 mm. Cuise-la-Motte (Oise). Unknown collection, MNHN.F.B57236. Specimen with a quite typical ornamentation, but an uncommon arrangement of the teeth.

Plate 6

Clithon (Pictoneritina) occultatus nov. sp. Lower Cuisian, Ypresian (Lower Eocene); Pourcy (Marne).

1 **Holotype**. Height 7.0 mm. Vrinat collection, MNHN.F.A71143.

2a **Paratype**. Height 9.0 mm. Cossmann collection, MNHN.F.J03781.

2b Label of the Cossmann collection.

3 **Paratype**. Height 6.0 mm. Vrinat collection, MNHN.F.A71144. Specimen with a flush spire and a paler ornamentation than the typical form.

4 **Paratype**. Height 4.5 mm. Vrinat collection, MNHN.F.A71145.

5 **Paratype**. Height 4.5 mm. Leroy collection, MNHN.F.A71146. Rare specimen with the operculum in position.

6 **Paratype**. Height 8.0 mm. Leroy collection, MNHN.F.A71147. Specimen with a shouldered spire.

Plate 7

Clithon (Pictoneritina) occultatus nov. sp. Ypresian (Lower Eocene).

1 Height 8.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection.
2 Height 7.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection. Specimens with an ornamentation made of zigzag axial lines. The last specimen illustrates how the ornamentation evolves to the more typical pattern of pseudo-chevrons, more or less organized into spirals.
3 Height 8.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection. Specimen having a particularly high number of teeth (6), as well as folds on the columellar callus. It may be of a gerontic nature, the extent of its callus and ornamentation being otherwise typical.
4 Height 5.0 mm. Cuisian; Cuise-la-Motte (Oise). Vrinat collection.
5 Height 5.0 mm. Cuisian; Cuise-la-Motte (Oise). Vrinat collection.
6 Height 8.0 mm. Cuisian; Saint-Gobain (Aisne). Leroy collection.

Plate 8

Clithon (Pictoneritina) pisiformis (de Férussac, 1823). Ypresian (Lower Eocene).

1 Original illustration of de Férussac.
2a Height 5.7 mm. Sparnacian; Aÿ Mont Bernon (Marne). Deshayes collection, UCBL-EM32161a.
2b Label from the Deshayes collection.
3 Height 2.5 mm. Sparnacian; Aÿ Mont Bernon (Marne). Deshayes collection, UCBL-EM32161b.
4 Height 3.0 mm. Lower Cuisian; Pourcy (Marne). Faullummel collection, MNHN.F.A29402.
5 Height 4.0 mm. Lower Cuisian; Pourcy (Marne). Faullummel collection, MNHN.F.A29402.
6 Height 4.5 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection.
7 Height 6.0 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection.

Plate 9

Clithon (Pictoneritina) saincenyensis (Deshayes, 1864). Ypresian (Lower Eocene).

1a **Syntype**. Height 12.1 mm. Sparnacian; Sinceny (Aisne). Deshayes collection, UCBL-EM32672a.
1b Label from the Deshayes collection.
2 Height 5.0 mm. Mont Bernon, Epernay (Marne). Deshayes collection, UCBL-EM32170c. This specimen was selected by Deshayes to figure *Clithon (Pictoneritina) sobrinus* de Férussac, 1823.
3 Height 6.0 mm. Sparnacian; Sinceny (Aisne). Leroy collection.
4 Height 8.5 mm. Sparnacian; Sinceny (Aisne). Leroy collection.
5 Height 5.0 mm. Sparnacian; Sinceny (Aisne). Leroy collection. Rather atypical specimen with stronger teeth. The columellar callus is slightly narrower. The ornamentation is covered by a reddish brown coating, looking like a periostracum (which normally does not fossilise).
6 Height 6.0 mm. Sparnacian; Sarron (Oise). Coll. Cossmann, MNHN.F.J09801.

Plate 10

Clithon (Pictoneritina) sobrinus (de Férussac, 1823). Ypresian (Lower Eocene).

1a Original illustration of de Férussac.
1b Label from the Cossmann collection.
1c Label from the Deshayes collection.
2 **Figured specimen**. Height 6.0 mm. Lower Cuisian; Pourcy (Marne). Cossmann collection, MNHN.F.J02078.
3a **Figured specimen**. Height 7.0 mm. Sparnacian; Rilly (Marne). Deshayes collection, UCBL-EM32170a.
3b Operculum. Longueur:5.0 mm. Rilly (Marne). Deshayes collection, UCBL-EM32170d.
4 Height 8.5 mm. Sparnacian; Rilly (Marne). Deshayes collection, UCBL-EM32170b.
5 Height 8.0 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection.
6 Height 4.0 mm. Lower Cuisian; Pourcy (Marne). Laporte collection.

Plate 11

Clithon (Pictoneritina) sobrinus (de Férussac, 1823). Ypresian (Lower Eocene).

1 Height 6.5 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection.
2 Height 3.0 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection. Juvenile specimen, with hardly developed columellar callus.
3 Height 7.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection.
4a Height 5.0 mm. Sparnacian; Mont-Bernon, Epernay (Marne). Deshayes collection; UCBL-EM30642a.
4b Label from the Deshayes collection, batch UCBL-EM30642.
5 Height 5.0 mm. Sparnacian; Mont-Bernon, Epernay (Marne). Deshayes collection; UCBL-EM30642b.
6 Height 9.0 mm. Sparnacian; Soissons (Aisne). Leroy collection.

Plate 12

Clithon (Pictoneritina) tigrinus nov. sp. Cuisian, Ypresian (Lower Eocene); Cuise-la-Motte (Oise).

1 **Holotype**. Height 3.0 mm. Vrinat collection, MNHN.F.A71148.
2 **Paratype**. Height 5.0 mm. Deshayes collection, UCBL-EM30644a.
3 **Paratype**. Height 2.0 mm. MNHN.F.A71153.
4 **Paratype**. Height 2.0 mm. Vrinat collection, MNHN.F.A71149.
5 **Paratype**. Height 4.0 mm. Vrinat collection, MNHN.F.A71150. Specimen having lost its ornamentation, but identifiable by the shape of its columella.
6 **Paratype** (figured in Cossmann, 1888). Height 2.5 mm. De Boury collection, UCBL-EM31894, with original labels and label from the UCBL collection.

Plate 13

Clithon (Pictoneritina) zonarius (Deshayes, 1832). Cuisian, Ypresian (Lower Eocene).

1a **Syntype** (probably the figured specimen). Height 8.53 mm. Cuise-la-Motte (Oise). Deshayes collection, UCBL-EM32197a.
1b Label from the Deshayes collection.
2 **Syntype**. Height 11.3 mm. Cuise-la-Motte (Oise). Deshayes collection, UCBL-EM32197b.
3 **Syntype**. Height 8.5 mm. Cuise-la-Motte (Oise). Deshayes collection, UCBL-EM32197c.
4 Height 3.0 mm. Cuise-la-Motte (Oise). UCBL-EM30643. A doubtful specimen with very elongated shape and almost no ornamentation, *Clithon (Pictoneritina) cf. zonarius*.
5 Height 7.0 mm. Brasles (Aisne). Leroy collection.
6 Height 7.0 mm. Brasles (Aisne). Leroy collection.

Plate 14

Clithon (Pictoneritina) zonarius (Deshayes, 1832). Cuisian, Ypresian (Lower Eocene)

1a Height 8.0 mm. Mons-en-Laonnois (Aisne). Lhomme collection. MNHN.F.B57240. Specimen identified as *Clithon (Pictoneritina) inequidentata* (Récluz, 1850) (=*Neritina lineolata* Desh.) in the MHNH collection.
1b Label from the Lhomme collection.
2 Height 7.0 mm. Trosly-Breuil (Oise). Faullummel collection, MNHN.F.A29399.
3 Height 4.0 mm. Brasles (Aisne). Leroy collection.

Neritodryas laubrierei (Cossmann, 1888). Thanetian (Palaeocene).

4 Height 6.0 mm. Chalons-sur-Vesle (Marne). Cossmann collection, MNHN.F.J02075.
5 Height 6.5 mm. Prouilly (Marne). Leroy collection.
6 Height 8.5 mm. Prouilly (Marne). Leroy collection.

Plate 15

Neritodryas dutemplei (Deshayes, 1864). Ypresian (Lower Eocene).

1a **Syntype** (figured under numbers 21 and 22). Height 15.4 mm. Aÿ (Marne). Deshayes collection, UCBL-EM32670.
1b Label from the Deshayes collection for specimen UCBL-EM32670
2a **Syntype** (figured under numbers 23 and 24). Height 18.2 mm. Aÿ (Marne). Deshayes collection, UCBL-EM32671.
2b Label from the Deshayes collection for specimen UCBL-EM32671.
3 Height 13.0 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection.
4 Height 22.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection. Gerontic specimen.
5 Height 6.0 mm. Lower Cuisian; Pourcy (Marne). Leroy collection. This specimen has an ornamentation which is very different from the typical one, and a rather marked tooth. However, it is close to the ornamentation which can be observed on the spire of the syntype UCBL-EM32671. It is thus considered as a juvenile form of *N. dutemplei*.

Clithon (Pictoneritina) saincenyensis (Deshayes, 1864)

6 Height 7.0 mm. Lower Cuisian, Ypresian, (Lower Eocene); Pourcy (Marne). Vrinat collection.

Plate 16

Neritoplica uniplicata (J. de C. Sowerby, 1823). Ypresian (Lower Eocene).

1 Original illustration of Sowerby.
2 Original illustration of de Férussac.
3 **Syntype**. Height 6.0 mm. Blackheath Formation; Charlton or Woolwich, Greater London (England). J. de C. Sowerby collection, NHMUK PI TG 26818.
4a *Neritina globulus*. Height 13.9 mm. Disy-Cumières (Marne). Deshayes collection, UCBL-EM32160b.
4b Labels from the Deshayes collection.
5 *Neritina globulus*. Height 12.8 mm. Disy-Cumières (Marne). Deshayes collection, UCBL-EM32160c.
6 Height 11.0 mm. Sparnacian; Mont Bernon, Epernay (Marne). Douvillé collection, UCBL-EM30641.
7 Height 12.0 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection.
8 Height 11.0 mm. Lower Cuisian; Pourcy (Marne). Vrinat collection. Worn specimen, showing the usually concealed spire.

Plate 1. Some particular distinguishing characteristics.

Plate 2. *Neritina elegans* (1), *Neritina lineolata* (2-3), *Neritoplica subornata* (4), *Clithon (Pictoneritina) barbei* (5) *and Clithon (Pictoneritina)* sp. (6).

Plate 3. *Clithon (Pictoneritina) coeuvrensis* (1) and *Clithon (Pictoneritina) bouryi* (2-6).

Plate 4. *Clithon (Pictoneritina) nucleus.*

Plate 5. *Clithon (Pictoneritina) nucleus.*

Plate 6. *Clithon (Pictoneritina) occultatus*.

Plate 7. *Clithon (Pictoneritina) occultatus*.

Plate 8. *Clithon (Pictoneritina) pisiformis.*

Plate 9. *Clithon (Pictoneritina) saincenyensis.*

Plate 10. *Clithon (Pictoneritina) sobrinus.*

Plate 11. *Clithon (Pictoneritina) sobrinus.*

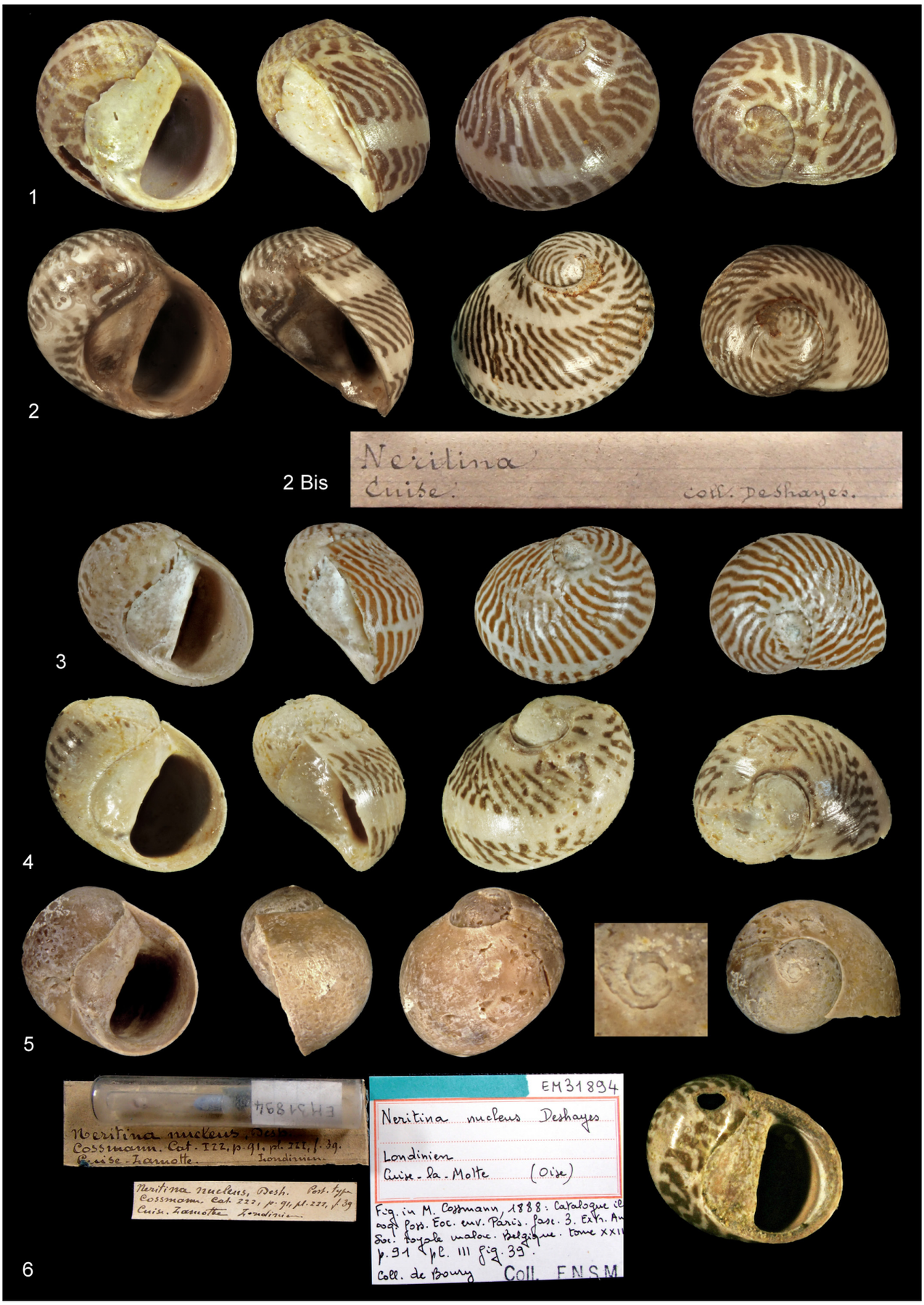

Plate 12. *Clithon (Pictoneritina) tigrinus*.

Plate 13. *Clithon (Pictoneritina) zonarius.*

Plate 14. *Clithon (Pictoneritina) zonarius* (1-3) and *Neritodryas laubrierei* (4-6)

Plate 15. *Neritodryas dutemplei* (1-5) and *Clithon (Pictoneritina) saincenyensis* (6)

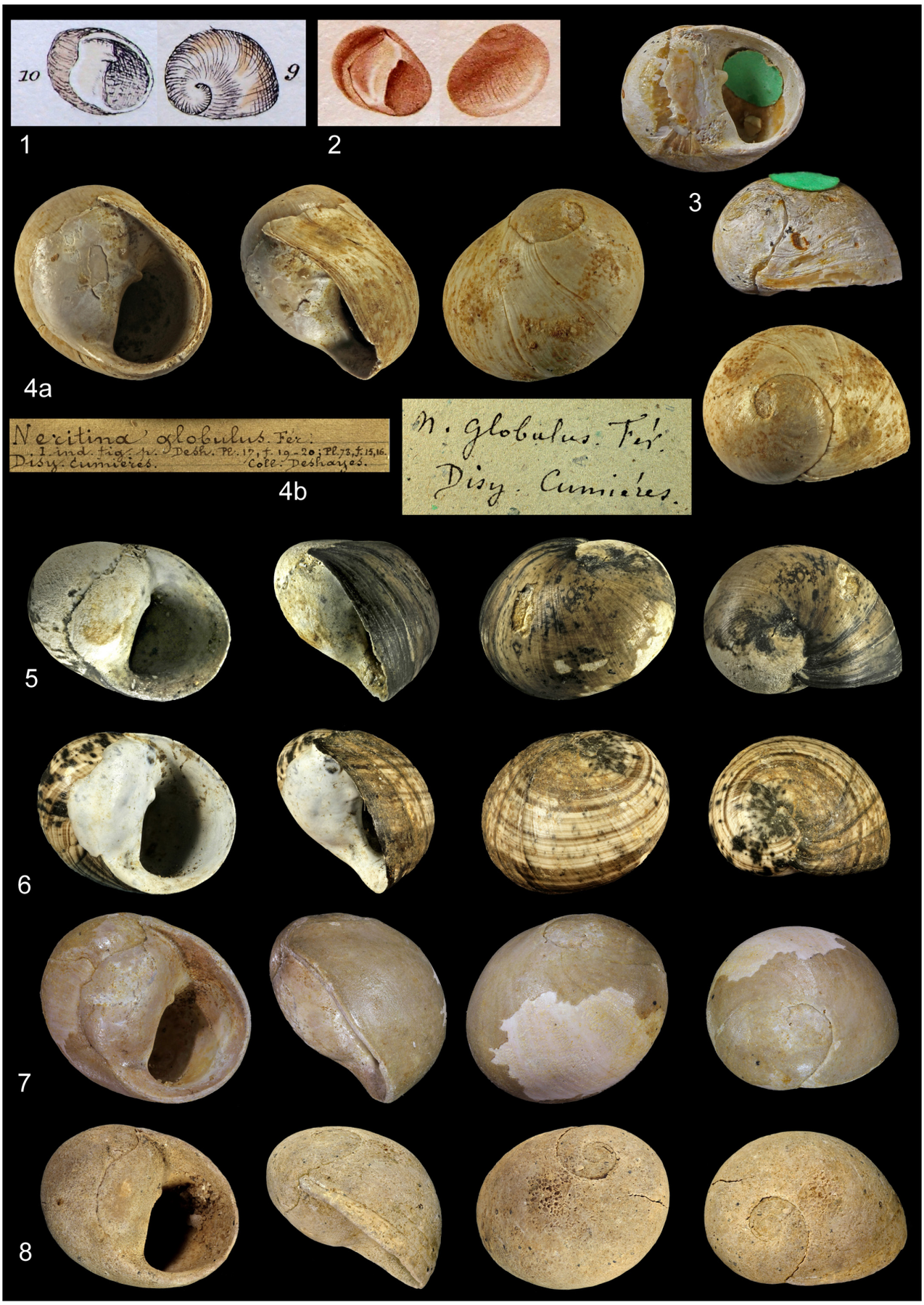

Plate 16. *Neritoplica uniplicata*.