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New species of Neritidae (Neritimorpha) from the Ypresian and Bartonian of the Paris and Basse-Loire Basins, France

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Abstract

Five gastropod taxa of the family Neritidae in the Ypresian and Bartonian (Eocene) of the Paris and Basse-Loire Basins, are introduced: *Cuisenerita* **gen. nov**., *Tomostoma angusta* **sp. nov**., *Nerita gouetensis* **sp. nov**., *Clithon barbei* **sp. nov**., *Neritodryas guillioui* **sp. nov**. and *Cuisenerita tuberosa* **sp. nov**. New combinations introduced are: *Neritodryas dutemplei* (Deshayes, 1864) and *Neritodryas globosa* (J. de C. Sowerby, 1823). This is the earliest record of *Neritodryas* and the first record for this genus from Europe.

Key words: Mollusca, Gastropoda, Eocene, France

Introduction

Both the Paris and Basse-Loire Basins in France are species rich in Mollusca from the Eocene. Many gastropods have been described and figured by authors in the past but new taxa are still being discovered (see Le Renard 1995 and Le Renard & Pacaud 1995 for a comprehensive list of primary references). Taxonomic observations regarding Neritidae from France were made by the senior author and a neotype designated for the taxon *Neritopsis parisiensis* Deshayes, 1864 (Symonds 2009). The purpose of this paper is to describe five new species in the family Neritidae, the type material of which is held in the Muséum National d'Histoire Naturelle, Paris, France (MNHN) and The Natural History Museum, London, England (NHM).

Systematic palaeontology

Family Neritidae Rafinesque, 1815

Genus *Tomostoma* Deshayes, 1824

Type species. By subsequent designation, Fischer (1885: 803): *Pileolus neritoides*, Deshayes, 1824. Eocene, Europe.

Diagnosis. Capuliform, smooth, apex not terminal, aperture trapezoidal, inner lip with sinus, type species 7 to 9 mm in length. (Amended after Keen 1960).

Tomostoma differs from most other genera in Neritidae in being capuliform. For the differences from the other Tertiary capuliform genus see *Cuisenerita* gen. nov. below.

Remarks. Cossmann (1925) and Keen (1960) regarded *Tomostoma* as a subgenus of *Pileolus* G. B. Sowerby, 1823. Bandel *et al.* (2000) erected a new family Pileolidae based on the genus *Pileolus* but did not comment on whether they regarded *Tomostoma* as a subgenus of *Pileolus*. They placed Pileolidae within Neritoidea Rafinesque, 1815 for which they gave the diagnosis: "In these cycloneritimorphs the internal shell

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walls are resorbed" (2000: 85). However Sowerby (1823: 443) stated that *Pileolus* has an "internal spire". This is clearly shown by Pană (1998: Pl. 2, Fig. 13) in a section through the teleoconch of *Pileolus*. On this basis Pileolidae should not be included within Neritoidea. Symonds (2009) did not see a close similarity between *Pileolus* and *Tomostoma* as the protoconch of *Pileolus* is spherical and rather large in relation to the rest of the shell while the protoconch of *Tomostoma* is obovate and typical of those genera within the Neritidae that have a planktotrophic larval stage. The teleoconch of the former is distinctly patelliform unlike that of the latter, which is capuliform. The aperture of *Pileolus* is rather narrow and semilunar whilst in *Tomostoma* the aperture is much broader. *Pileolus* has a straight or slightly convex septum edge, which is smooth or regularly crenulated; in *Tomostoma* the septum edge is concave and the dentition distinct but very irregular. Additionally in *Pileolus* the septum is thickened to form a prominent basal plate, a feature not present in *Tomostoma*. Finally, as mentioned above, *Pileolus* has a columella while the internal walls of *Tomostoma* are entirely reabsorbed. As the morphology of both the protoconch and the teleoconch corresponds to Neritidae, Symonds (2009) regarded *Tomostoma* as being in Neritidae rather than Pileolidae and this is followed here. Woods & Saul (1986: 650) commented that "Deshayes is usually credited with proposing *Tomostoma* in 1824; but he did not do so." They considered that it was not until 1864 that he validly proposed *Tomostoma* and that as a result *Culana* Gray, 1842 (type species *Pileolus altavillensis* Defrance, 1818) should have priority. Deshayes (1824a; 1824b) made it clear that he had intended to propose the name *Tomostoma*, but he did not do so at the time as he considered that it was synonymous with *Pileolus*, which had just been proposed by Sowerby (Sowerby, 1823). Later, Deshayes (1864: 25) considered that there were two distinct forms of *Pileolus*: those from the Mesozoic with a circular base and central apex and those from the Tertiary with an elliptical base and an apex towards the posterior end; to the latter group could be attached the name *Tomostoma* "que nous avons proposé autrefois". Article 11.6.1 of the International Code of Zoological Nomenclature (the Code) provides that if a name first published as a junior synonym is subsequently used as a valid name before 1961, it dates from its first publication as a synonym. Accordingly *Tomostoma* was published in 1824 and *Culana* is here considered a subjective junior synonym.

***Tomostoma angusta* sp. nov.**
(Fig. 1a–d)

Type material. Holotype MNHN A31487 (Pacaud leg., Fig. 1a–d); 6 paratypes MNHN A31488 (Pacaud leg.), 30 paratypes (Pons coll.). All from type locality.

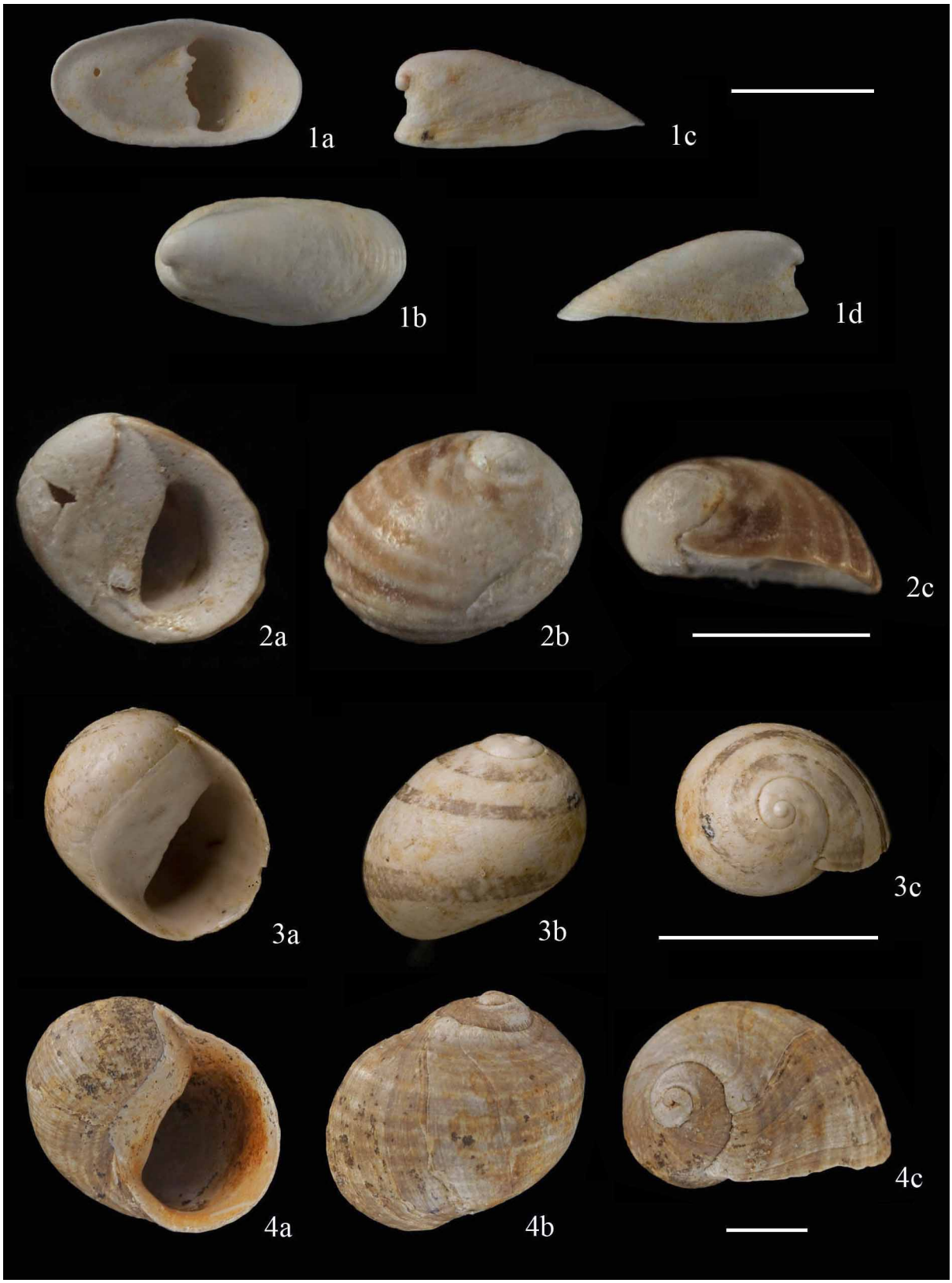
Stratum typicum. Late Eocene, Bartonian, "Marinesian".

Locus typicus. Le Quoniam, Haravilliers, Val d'Oise, France. 49˚11′2.68″ N 2˚2′17.53″ E.

Derivatio nominis. The name is derived from Latin *angustus*, referring to the narrow shape of the shell.

Diagnosis. A rather small, narrow *Tomostoma*, capuliform, posterior and anterior margins of teleoconch ovate, not pointed, septum edge strongly concave in centre.

Description. Protoconch, though rather worn in specimens available, prominent, approximately 0.2 mm wide, smooth, obovate. Teleoconch capuliform, apex above posterior end in holotype, slightly anterior to it in most paratypes. Anterior and posterior margins ovate with posterior usually slightly narrower than anterior. Dorsal surface strongly convex, sloping steeply upwards to elevated posterior end, smooth apart from fine growth lines. No colour pattern visible on only known specimens. Aperture relatively large, semicircular. Inner lip protruded as broad septum covering more than half of base of shell, surface slightly concave, usually smooth but holotype has 3 faint grooves about 0.2 mm long perpendicular to septum edge coinciding with spaces between teeth on central part of septum. Septum edge strongly concave in centre with 1 to 5 small, prominent or indistinct teeth bordered on adapical side by larger tooth, which continues for short distance within aperture as low ridge on inner side of septum, followed by further concavity, short but quite deep. On abapical side of central concavity one broad, rather rounded tooth. Outer lip broad, smooth with very slight ridge running from one end of septum, in arc on inside of outer lip, to other end of septum. Small ridge below each end of septum, adapical larger, below septum edge, abapical narrower, lower, set further back.



FIGURES 1–4. 1. *Tomostoma angusta* **sp. nov.**, holotype, a. apertural, b. abapertural, c-d. side views. Length 5.2 mm, width 2.8 mm. Bartonian, Le Quoniam, Haravilliers, Val d'Oise, France. MNHN A31487 (J-M Pacaud leg.). **2.** *Nerita gouetensis* **sp. nov.**, holotype, a. apertural, b. abapertural, c. apical views. Height 4 mm, width 4 mm. Bartonian, Bois-Gouët, Saffré, Loire-Atlantique, France. MNHN A31489 (J-M Pacaud leg.). **3.** *Clithon barbei* **sp. nov.**, holotype, a. apertural, b. abapertural, c. apical views. Height 3.2 mm, width 3.2 mm. Ypresian, Pourcy, Marne, France. NHM PI TG 26448 (M. F. Symonds coll.). **4.** *Neritodryas guillioui* **sp. nov.**, holotype, a. apertural, b. abapertural, c. apical views. Height 15 mm, width 16 mm. Ypresian, Pourcy, Marne, France. MNHN A31490 (Faullummel coll.).

Size. The holotype is 5.2 mm long and 2.8 mm wide.

Remarks. Three somewhat similar taxa occur in the Eocene of the Paris Basin and Cotentin: *Tomostoma altavillensis altavillensis* (Defrance, 1818), *Tomostoma altavillensis neritoides* (Deshayes, 1824) and *Tomostoma altavillensis rostratum* Cossmann, 1888 (Le Renard & Pacaud, 1995). Of the three, *T. altavillensis neritoides* is closest in appearance to *T. angusta* with its anterior and posterior margins oval, not pointed as in the other two taxa. *Tomostoma angusta* can be distinguished from *T. altavillensis neritoides* by the concave centre to its septum edge, the smaller, more regular teeth in the centre and its narrower form. The average length to width ratio for *T. angusta* is 2.3:1 (from the 37 specimens in the Pacaud and Pons collections) compared with 1.6:1 for *T. altavillensis neritoides* (from 30 specimens from the Lutetian of Chaussy, Val d'Oise, France). A t-test applied to the length to width ratio of these specimens results in a probability of <0.0001.

Range and distribution. *Tomostoma angusta* is known only from the type locality.

Genus *Nerita* Linné, 1758

Type species. By subsequent designation, Montfort (1810: 347): *Nerita peloronta* Linné, 1758. Recent, marine, Caribbean.

Diagnosis. Sturdy shells, smooth to spirally ribbed; inner lip septum well developed, its surface commonly pustulose or irregularly ribbed (Keen 1960).

Nerita (*Amphinerita*) *gouetensis* sp. nov.

(Fig. 2a–c)

Type material. Holotype MNHN A31489 (Pacaud leg., Fig. 2a–c).

Stratum typicum. Late Eocene, Bartonian, "Sands of Bois-Gouët".

Locus typicus. Bois-Gouët, Saffré, Loire-Atlantique, France. 47˚29′9.25″ N 1˚36′45.55″ E.

Derivatio nominis. Named after Bois-Gouët, the type locality and the only locality at which this species has, as yet, been found.

Diagnosis. A small *Nerita* with prominent, rounded, spiral ribs and a smooth, edentate septum.

Description. Protoconch badly worn in only known specimen. Teleoconch of just over two whorls increasing rapidly in size, earlier rather worn in holotype. Last whorl bears nine prominent, smooth, rounded, spiral ribs, mostly evenly spaced; 6th and 7th below suture closer together. Apart from spiral ribs, surface of teleoconch smooth, lacking any collabral ornamentation other than some fine, rather faint growth lines. No colour pattern discernable but brown colour remains between ribs where shell relatively unworn. Slightly worn septum smooth, edge slightly concave, edentate. Outer lip thickened within, smooth apart from small protuberance about 1 mm from adapical end of septum. Gutter at junction of adapical end of septum and outer lip. Apertural tooth prominent, below abapical end of septum, in form of apostrophe with thicker end inward, higher, sloping to tail of apostrophe.

Size. The holotype is approximately 4 mm high, and 4 mm wide.

Remarks. *Nerita* (*Amphinerita*) *gouetensis* does not fit precisely within any of the generally accepted subgenera of *Nerita*. Those that share diagnostic characteristics with *Na.* (*A.*) *gouetensis* are:

Lisanerita Krinjen, 2002 (Type species by original designation: *Nerita lirellata* Rehder, 1980);

Heminerita Martens, 1887 (type species by monotypy: *Nerita pica* Gould, 1859 = *Nerita japonica* Dunker, 1861);

Amphinerita Martens, 1887 (type species by subsequent designation Crosse, 1892: 98: *Nerita umlaasiana* Krauss, 1848);

Cymostyla Martens, 1887 (type species by subsequent designation Crosse, 1892: 98: *Nerita undata* Linné, 1758);

Theliostyla Mörch, 1852 (type species by subsequent designation Kobelt, 1879: 147: *Nerita albicilla* Linné, 1758);

Subgenus	Septum	Septum edge	Teleoconch
Lisanerita	Smooth	Edentate or with very small teeth	Smooth or with finely incised lines
Heminerita	Smooth	Edentate or with 1 or 2 obscure low broad projections	Smooth or with low spiral lirae
Amphinerita	Smooth	Edentate or with small, obscure or well defined teeth	Smooth or with spiral ribs
Cymostyla	Rugose	Prominent teeth	Prominent spiral ribs
Theliostyla	Tuberculate	Prominent teeth	Low, rounded spiral ribs
Na.(*Amphinerita*) *gouetensis*	Smooth	Edentate	Prominent spiral ribs

In his subgenus *Amphinerita,* Martens (1887) included *Na. umlaasiana* and *Na. georgina* Récluz, 1841. The former has an almost smooth shell but the latter has numerous well developed spiral ribs. *Amphinerita* is recorded in Europe from as early as the Thanetian [*Na.* (*A.*) *semilugubris* Deshayes, 1864, Le Renard & Pacaud 1995]. Although *Na.* (*A.*) *gouetensis* has fewer and broader ribs than *Na.* (*A.*) *georgina*, we consider that it can nevertheless be placed within *Amphinerita.*

Nerita (*A.*) *gouetensis* is superficially similar to some juvenile specimens of *Nerita* (?) *plutonis* Basterot, 1825 from the Miocene of the south of France but its septum is normally neither smooth nor edentate but has granules on the surface and several well defined teeth on the edge.

Range and distribution. Only known from type locality.

Genus *Clithon* Montfort, 1810

Type species. By original designation: *Nerita corona* Linné, 1758.

Recent, fresh to brackish water, eastern Indian Ocean to the southwestern Pacific.

Diagnosis. Small spire, large body whorl, some species with one subsutural row of spines, labial area smooth with one or more teeth on margin, operculum smooth or bearing minute granules on exterior surface, inner side with two apophyses connected by calcareous callus.

Subgenus *Pictoneritina* Iredale, 1936

Type species. By original designation, *Neritina oualaniensis* Lesson, 1831.

Recent, in estuaries and brackish lagoons, Indo-Pacific.

Diagnosis. Shell small, 3 to 15 mm in height, smooth; septum weekly arched with one large, several small teeth.

Remarks. In the absence of a detailed description by Iredale (1936) the above diagnosis has been based on that given by Keen (1960). In the type species, the large tooth is about a third of the distance from the apical end of the septum with up to 5 small teeth abapical to it. The shell is glossy and the colour patterns are very variable.

Clithon (Pictoneritina) barbei sp. nov.

(Fig. 3a–c)

Type material. Holotype NHM PI TG 26448 (M. Symonds coll., Fig. 3a–c). One paratype NHM PI TG 26449 (M. Symonds coll.), one paratype MNHN A33473 (Ledon coll.). All from type locality.

Stratum typicum. Early Eocene, Ypresian (Sparnacian), “Sands of Pourcy”.

Locus typicus. Pourcy, Marne, France. 49˚09′43″ N 3˚54′21″ E.

Derivatio nominis. Named after Gérard Barbe of Champillon, Marne, France, a palaeontologist, who is familiar with the fossils of Pourcy, and who assisted the senior author with the collection of material from there, in which the types of this taxon were found.

Diagnosis. A small semiglobose *Pictoneritina*; spire depressed, septum with poorly defined teeth, colour pattern of three dark spiral bands on light background.

Description. Shell small for subgenus, consisting of about 2.25 whorls, semiglobose with spire depressed. Protoconch small, approximately 0.2 mm wide, smooth, almost spherical. Teleoconch about 2.25 whorls, evenly convex, increasing rapidly in size; surface glossy, smooth. Suture sharp, well defined. Colour pattern of 3 dark spiral bands on light background, highest immediately below suture, varying in width but usually narrower than spaces between them. Aperture oblique, semicircular. Septum convex, smooth. Septum edge slightly concave in centre; teeth consist of one rather broad, rounded, indistinct tooth at about one third of distance from adapical end of septum, 1 to 3 denticulations abapical to it, also indistinct. Outer lip evenly rounded, thin, smooth within. Apertural tooth low, curved ridge below abapical end of septum.

Size. Holotype: height 3.2 mm, width 3.2 mm.

Remarks. *Clithon* (*P.*) *barbei* is similar in size and shape to *Clithon* (*P.*) *nucleus* Deshayes, 1825 from the Cuisian of Cuise-la-Motte, Oise, France, although in that species the spire is usually wholly or partially covered by the following whorl. The colour pattern in *C.* (*P.*) *nucleus* consists of dark, wavy, transverse lines on a light background, in some specimens the transverse lines are interrupted by two or three pale spiral bands, while *C.* (*P.*) *barbei* has a colour pattern of 3 dark spiral bands on a light background.

Range and distribution. Only known from type locality.

Genus *Neritodryas* Martens, 1869

Type species. By subsequent designation, Baker (1923: 153): *Nerita cornea* Linné 1758. Recent, freshwater, Indopacific.

Diagnosis. Moderately large, up to 40 mm in height, spire blunt, labial area smooth, a blunt tooth below, often with small teeth on septum edge, operculum ribbed. (Amended after Keen 1960).

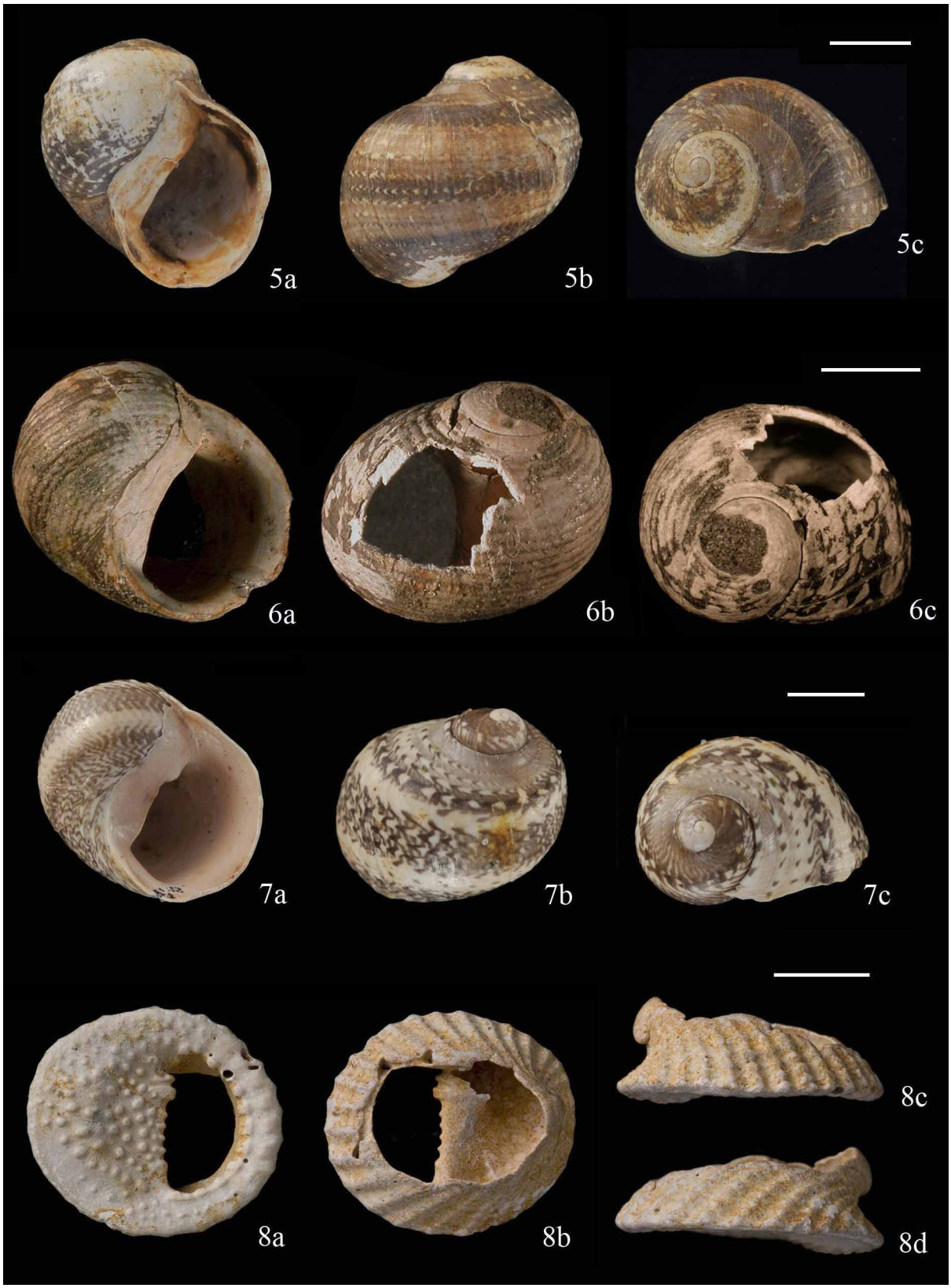
Remarks. Martens (1869), when erecting *Neritodryas*, placed within it the two Recent species *N. cornea* (Linné, 1758) and *N. dubia* (Gmelin, 1791). Subsequently (Martens 1879) he covered *Neritodryas* in greater detail and included two additional species *N. chimmoi* (Reeve, 1856) and *N. subsulcata* (Sowerby, 1836). He described the columellar edge of *Neritodryas* as being without teeth but specimens of all four of these species commonly have small columellar teeth (pers. obs.). Accordingly Marten's diagnosis is incorrect in this respect and we have amended the above diagnosis to include a reference to small teeth on the septum edge. All the Recent species have spiral ridges on the teleoconch except for *N. dubia*, which is smooth, apart from fine collabral growth lines. The genus is unusual within Neritidae in that the Recent species live mainly on trees and bushes beside freshwater and in mangrove swamps (Cowie & Smith 2000). The ontogeny of *Neritodryas* is not fully known. Kano (2006) considered that the considerable intraspecific variation in the size of the opercular nucleus might suggest nonplanktotrophic development. Holthuis (1995) took the view that *Neritodryas* species have short-lived, possibly non-feeding (lecithotrophic) pelagic larvae as, firstly, the protoconch size is intermediate between planktotrophic veligers of *Neritina* and *Clithon* and those of benthic *Fluvinerita* and, secondly, their geographic distribution is extensive enough to imply pelagic larvae even though more limited than ranges of typical *Neritina* and *Clithon*.

Neritodryas guillioui sp. nov.

(Figs 4–5)

Type material. Holotype MNHN A31490 (Faullummel coll., Fig. 4a–c); one paratype MNHN A31491 (Pacaud leg., Fig. 5a–c), 4 paratypes MNHN A32900 (Pacaud leg.) 5 paratypes MNHN A31492 (Faullummel coll.). All from type locality.

Stratum typicum. Early Eocene, Ypresian (Sparnacian), "Sands of Pourcy".



FIGURES 5–8. 5. *Neritodryas guillioui* **sp. nov.**, paratype, a. apertural, b. abapertural, c. apical views. Height 14.5 mm, width 15 mm. Ypresian, Pourcy, Marne, France. MNHN A31491 (Faullummel coll.). **6.** *Neritodryas globosa* (J. de C. Sowerby, 1823), neotype, a. apertural, b. abapertural, c. apical views. Height 18.2 mm, width 13.8 mm. Bartonian, Highcliff, Hampshire, U.K. NHM GG 22558 (A. G. Davis coll.). **7.** *Neritodryas dutemplei* (Deshayes, 1864), a. apertural, b. abapertural, c. apical views. Height 9 mm, width 9.1 mm. Ypresian, Pourcy, Marne, France. MNHN A31493 (Faullummel coll.). **8.** *Cuisenerita tuberosa* **sp. nov.**, holotype, a. apertural, b. abapertural, c. & d. side views. Length 14 mm, width 12.5 mm., Ypresian, Trosly-Breuil, Oise, France. NHM PI TG 26450 (S. Tracey coll.).

Locus typicus. Pourcy, Marne, France. 49˚09′33″ N 3˚54′33″ E.

Derivatio nominis. Named after Maurice Guilliou of Étoges, Marne, France, who has studied the fossils of the Paris Basin for many years and who first brought this taxon to the attention of the senior author.

Diagnosis. A rather small, globose *Neritodryas* with 14 to 18 low, spiral ridges; septum edentate or with poorly defined teeth.

Description. Protoconch, worn in all known specimens, appears ovate, about 0.4 mm wide. Teleoconch consisting of about 2.5 whorls, globose with rather low but well-defined spire, large, rounded last whorl. Whorls convex, shouldered with short concavity immediately below impressed suture. On last whorl 14 to 18 low, flat or slightly rounded, spiral ridges with spaces between them approximately equal to width of ridges; ridges wider apart and broader at periphery. Fine, distinct, sinuous, collabral growth lines, opisthocyrt below suture. Aperture broad, septum smooth or with few slight curved ridges oblique to columellar edge; edge with slight, rounded swelling approximately one third of distance from adapical end, otherwise edentate or occasionally with up to 3 poorly defined teeth below it. Gutter between adapical end of the septum and outer lip. Outer lip thin, smooth within. Prominent ridge, slightly curved, below abapical end of septum. Holotype, though well preserved, without colour pattern, but yellowish grey colour apparent between ribs. Paratype illustrated in Figure 5 has colour pattern of pale chevrons on dark brown background arranged in spiral lines, pointing in direction of growth.

Size. Holotype: height 15 mm, width 16 mm.

Remarks. *Neritodryas guillioui* is very similar to *Neritodryas globosa* (J. de C. Sowerby, 1823) (Fig. 6a–c), assigned here to *Neritodryas* rather than *Nerita*, from the Bartonian of the Hampshire Basin, England, however *Ns. globosa* has a larger number [25 in the neotype designated by Symonds (2002)] of more prominent and more closely spaced ribs than *Ns. guillioui*. Symonds (2002) noted the similarity of *Ns. globosa* to *Neritodryas* but, with only the neotype available for study, did not move it to that genus. It is now clear, in view of the great similarity to *Ns. guillioui*, that *Ns. globosa* should be assigned to *Neritodryas*. *Neritodryas guillioui* is also very similar to *Ns. dutemplei* (Deshayes, 1864) (Fig. 7a–c), again assigned here to *Neritodryas* rather than *Nerita*, which occurs with it in the Ypresian deposits at Pourcy. *Neritodryas dutemplei* can be distinguished from *Ns. guillioui* by the absence of conspicuous ribs in the former.

The operculum of *Neritodryas* has longitudinal ribbing on one of the apophyses, which forms an important characteristic of this genus but, unfortunately, no operculum has yet been found for any of the three fossil species referred to above.

Range and distribution. Only known from type locality and one other site in the Ypresian (Sparnacian) at Pourcy, Marne, France.

Genus *Cuisenerita* gen. nov.

Type species. *Cuisenerita tuberosa* **sp. nov.**

Derivatio nominis. The only known species within this genus is from the Cuisian of Trosly-Breuil near Cuise-la-Motte and it has many of the characters of a *Nerita* and so the name is a free combination of Cuise and *Nerita*.

Diagnosis. Capuliform, apex not terminal, radially ribbed, septum well developed, tuberculate, margin dentate, outer lip thickened, lirate.

Remarks. *Cuisenerita* is similar in some respects to *Velatella* Meek, 1873 from the Upper Cretaceous of North America. In describing *Neritina* (*Dostia?*) *carditoides*, Meek (1873: 499) commented: "In several respects it agrees with *Velates*, and possibly might, without impropriety, be called *Velates carditoides*. I suspect, however, that when better specimens can be examined, it will be found typical of an undescribed section, including also the little species *N. bellatula*. If so I would propose for the group the name *Velatella*." Article 11.5.1 of the Code provides that a name proposed conditionally for a taxon before 1961 is not to be excluded on that account alone. Article 11.9.3.6 provides that a species-group name first published before 1961 in combination with a previously available generic name, but accompanied by a new nominal genus

conditionally proposed to contain the new species, is deemed to have been made available in combination with the previously available generic name. The example of Lowe (1843), given in the Code, covers essentially the same situation as that of Meek and *Velatella*. Accordingly, although Meek only proposed *Velatella* conditionally, *Velatella* Meek, 1873 is valid. Between his descriptions of *N. bellatula* and *N. carditoides* Meek (1873) also described *Neritina* (*Dostia?*) *patelliformis.* In his description he commented that *N. patelliformis* is evidently very close to *N. bellatula* and may possibly be a more robust variety of the same. Presumably, therefore, Meek intended to include *N. patelliformis* with *N. bellatula* and *N. carditoides* in the group for which he proposed the name *Velatella*. No diagnosis or description is given by Meek for *Velatella* but the three species within the group are described in detail, although not figured. White (1883) considered *N. carditoides* to be identical with *N. bellatula*. Both were figured by him [*N. bellatula*: White 1883: pl. 5, figs 8–9, *N. carditoides*: White 1883: pl. 5, fig. 10]. White's figures of *N. bellatula* and *N. carditoides* show a dorsal morphology very similar to *Cuisenerita*, except that the apex is more strongly involute and curved to one side, and this is supported by Meek's descriptions. White's figures do not give an apertural view but Meek (1873: 497–498) described *N. bellatula* as having an "inner lip very broad, or shelf like and occupying more than half of the underside, convex and more or less thickened, with the inner margin concave in the middle, and provided with a slight projection on each side, but not properly crenate or dentate". White also figured a third species, *Neritina (Velatella) baptista* White, 1878 (White 1883: pl. 23, figs 16–20), and included an apertural view, which shows a smooth, edentate septum. This accords with Meek's description but is in contrast to *Cuisenerita*, which is strongly dentate on the septum edge and lirate on the outer lip; *Cuisenerita* is also characterised by its tuberculate septum, a feature that is lacking in *Velatella.*

Cuisenerita also resembles *Gargania* Guiscardi, 1857 from the Upper Cretaceous of Italy, which is also radially ribbed and has an apex that is not strongly involute. However the septum is smooth and edentate (Keen 1960) while in *Cuisenerita* it is tuberculate and strongly dentate. Keen treated both *Velatella* and *Gargania* as subgenera of *Pileolus.* As mentioned above, *Pileolus* has a culumella and has now been placed in the family Pileolidae. In *Cuisenerita* the internal whorls have been reabsorbed and we have no doubt that *Cuisenerita* belongs in Neritidae not Pileolidae. The base of *Cuisenerita* is similar to that of some species of *Nerita* but it differs from that genus in being capuliform with radial ribs. *Tomostoma* is also capuliform but the dorsum is smooth, without radial ribs, and the base lacks the tubercles, which are a conspicuous feature of *Cuisenerita*.

***Cuisenerita tuberosa* sp. nov.**
(Fig. 8a–d)

Derivatio nominis. The name is derived from Latin *tuberosus*, referring to the protuberances on the base of the shell.

Type material. Holotype NHM PI TG 26450 (S. Tracey coll., Fig. 8a–d).

Stratum typicum. Middle Eocene, Ypresian, Cuisian.

Locus typicus. Trosly-Breuil, near Cuise-la-Motte, Oise, France. 49˚24′05″ N 2˚59′25″ E.

Diagnosis. Capuliform, apex not terminal, slightly involute, radial ribs with ornament of tubercles, septum well developed, tuberculate, margin prominently dentate, outer lip thickened, lirate, tuberculate.

Description. Protoconch worn in the only known specimen. Teleoconch capuliform with raised apex anterior to posterior end, slightly involute, curved to left. Anterior, posterior margins rounded with posterior slightly narrower than anterior. On dorsal surface approximately 30 ribs radiate from apex to margin. Ribs fairly evenly spaced, increasing in width from apex towards margin, each bearing single row of prominent, closely spaced tubercles throughout length, also increasing in size towards margin. Although surface rather worn, prominent, closely spaced growth lines clearly seen between ribs. Inner whorls reabsorbed. No colour pattern visible. Aperture relatively large, semicircular. Inner lip protruded as broad septum that covers rather more than half of base of shell, surface more or less flat near septum edge becoming slightly convex towards posterior end, covered with prominent tubercles. Septum edge slightly concave in centre, 4 narrow,

prominent, evenly spaced teeth bordered on abapical side by larger, rounded tooth, on adapical side by larger cubed tooth adjacent to which is narrower tooth, both continue for short distance as ridges on outer surface of septum. Outer lip considerably thickened, 12 prominent lirae on inner side, row of tubercles on surface.

Size. The holotype is 14 mm long and 12.5 mm wide.

Remarks. The above description is based on the holotype, which is the only known example of *C. tuberosa*, and accordingly takes no account of any variation that may occur within this species.

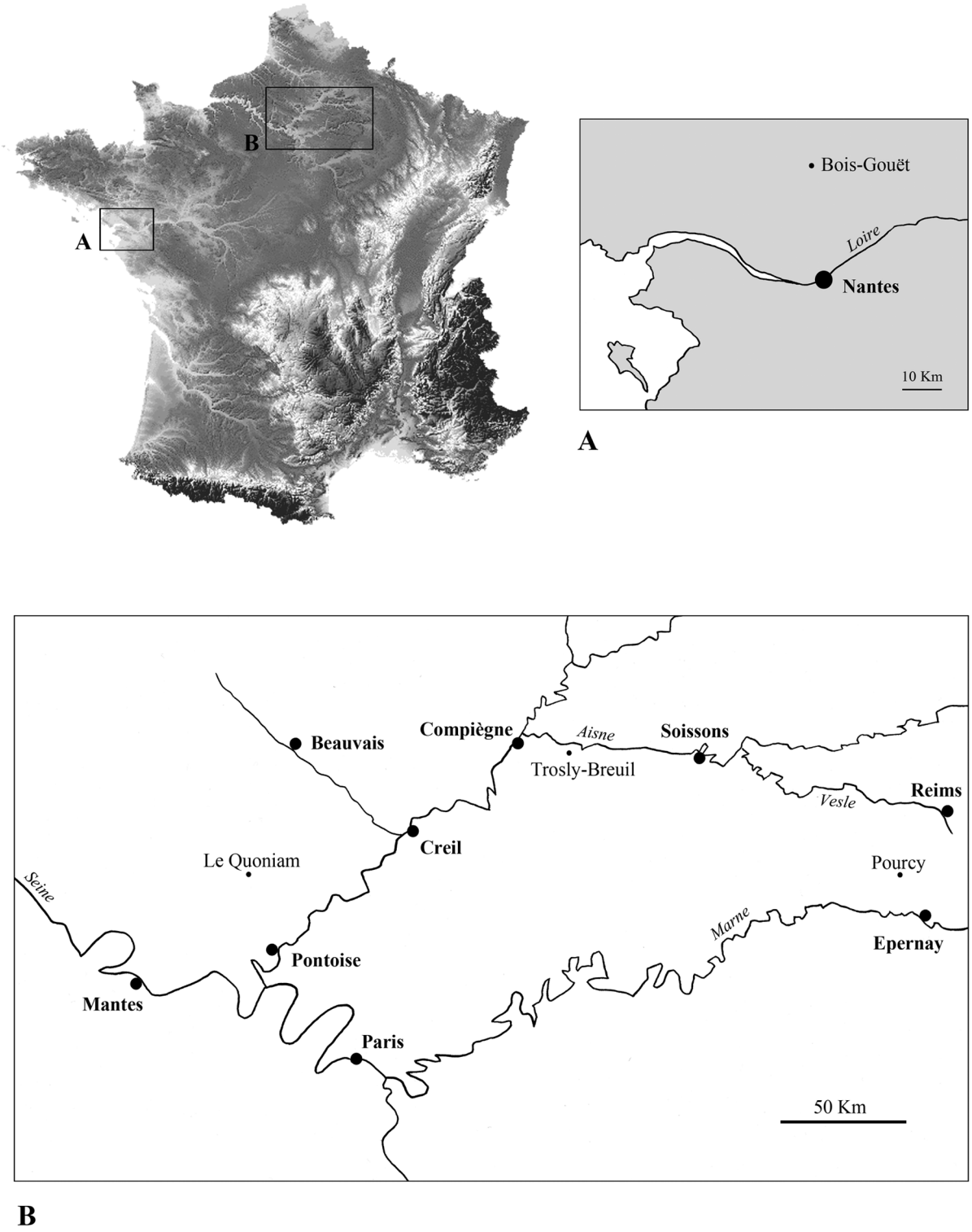


FIGURE 9. Map of France showing the approximate positions of the type localities of the new species herein described

No other species of *Cuisenerita* is known and *C. tuberosa* is quite unlike any other Caenozoic taxon. The differences between *Cuisenerita* and *Tomostoma* are outlined above. Of the other gastropods of capuliform shape, *Calyptronerita* Le Renard, 1980 lacks prominent ribs on the dorsum and has a smooth, edentate septum. In Crepidulidae the septum, if present, is smooth and edentate.

The coordinates for the type locality are only approximate as there were several Cuisian sites around Trosly-Breuil and it is not known from which one the holotype originated.

Range and distribution. Only known from type locality.

Discussion

The fossil fauna of a locality can give important indications as to the palaeohabitat. The molluscan assemblage at Pourcy consists mainly of brackish water genera with some marine elements and occasional fresh water genera and probably represents an estuarine or inshore shell-bank. The type species of *Pictoneritina, C.* (*P.*) *oualaniensis*, is an euryhaline species commonly living intertidally in areas with periodically lowered salinity. *Clithon* (*P.*) *barbei* is an addition to several other *Pictoneritina* species, which together form a significant part of the Pourcy brackish water fauna. Recent *Neritodryas* are at least partly arboreal and it is perhaps reasonable to assume that the fossil species occupied a similar habitat. On this basis, *N. guillioui* and *N. dutemplei* represent an interesting addition to the Pourcy fauna and support the suggestion that molluscs swept downstream by one or more rivers took their part in the formation of the shell-bank.

As *Tomostoma* is an extinct genus, the environment in which it lived can only be inferred from the deposits in which it is found. *Tomostoma* occurs in some middle Lutetian deposits in the Paris basin where the fauna indicates a shallow water marine environment and, since the shells of *Tomostoma* are fairly common and well preserved, it can be assumed that they formed part of this community. The narrow, capuliform shape of *Tomostoma* is unusual among fossil and Recent gastropods and probably indicates adaptation to a specialised habitat. The Recent neritoidean genus *Septaria* de Férussac, 1807 has a shell of rather similar shape but all species are much larger than *Tomostoma* and generally broader. However there are two distinct forms of *S. tesselata* (Lamarck, 1816); a broad form found attached to stones in fast flowing rivers and a narrow form adapted to living on plant material such as grass stalks in quiet water (Haynes 2001). It is possible that *Tomostoma* showed a similar adaptation, within a marine environment, and lived on the leaves of *Zostera* spp. The fauna of Bed S10 of the Bracklesham Group at Selsey, West Sussex, England, which contains frequent *T. altavillensis*, has been interpreted as a sea-grass fauna (Curry *et al*. 1977; Tracey *et al*. 1996). The discovery of *T. angusta* extends the range of the genus in the Paris Basin from the Middle Eocene, Lutetian to the Late Eocene, Bartonian.

The molluscan assemblage from Le Quoniam (Pacaud 2003) indisputably represents an accumulation of organisms coming from different environments. In the pebble-bearing sandy strata, the littorinids *Echinolittorina* Habe, 1956, *Littoraria* Griffith & Pidgeon, 1834, *Melarhaphe* Menke, 1828 and *Peasiella* Nevill, 1884, the planaxids *Leioplanaxis* Lozouet & Maestrati, 1994 and *Hinea* Gray, 1847 as well as numerous other genera that are very abundant at Le Quoniam, indicate a mediolittoral community living on hard substrates (Lozouet & Maestrati 1994; Dolin & Pacaud 2000). Some terrestrial and lagoonal species have also been transported to the area. The fauna of Le Quoniam is mainly marine but the proximity of brackish water is indicated by a few euryhaline species such as *Clithon* (*Pictoneritina*) *passyanus* (Deshayes, 1864).

The Cuisian of Trosly-Breuil contains a mixture of shallow marine and brackish water molluscs. Even though extensive collections of the fauna have been made over many years the holotype is the only known specimen of *C. tuberosa*, despite it being a relatively large and distinctive taxon. The extreme rarity of this species at Trosly-Breuil, in conjunction with its rather poor preservation, probably means that it was not actually living in the area but that the holotype had been transported from its natural habitat, which may have been a considerable distance away. The rather solid, strongly ribbed and tuberculate shell of *C. tuberosa* is unlike that of most freshwater gastropods and it appears to have been more suited to a marine environment. Recent capuliform molluscs live on hard surfaces where the smooth edge to the lip provides good contact,

important in a high-energy environment or to prevent desiccation on exposure to the air. However the pustules on the underside of *C. tuberosa* would have prevented such contact with a hard surface. More material is required to cast light on the probable origins and mode of life of this interesting neritid.

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