Pourcy (Paris Basin, France): preliminary assessment of an early Eocene NW European tropical coastal environment from molluscs and vertebrate fossils

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We have studied the fossil fauna from the locality of Pourcy (Marne) in the northeast of the Paris Basin, France, housed in various collections, in order to assess the nature and diversity of the fauna and gain an insight into the nature of the conditions that could have produced this assemblage. The mollusc fauna is strongly indicative of varied tropical estuarine environments probably vegetated with mangroves, but may also contain material derived from underlying mangrove facies. Both coastal marine and terrestrial mollusc and vertebrate faunas are also represented. The terrestrial community contained indicators of subtropical rainforest lowland with broad river banks and lakes, but some reworking of materials seems likely. The early-middle Ypresian Falun de Pourcy probably reflected ongoing estuarine/mangrove conditions that characterised the late Sparnacian period. Preliminary species lists of mollusc and vertebrate fossils are given, together with a comparison of mollusc feeding guilds to those of a modern Indo-Pacific estuary system.

Key words: Ypresian, palaeoecology, biodiversity, mangrove, molluscs, vertebrates, NW Europe.

Résumé Français

Pourcy (Bassin de Paris, France, Marne): évaluation préliminaire d'un environnement tropical côtier nord-ouest européen de l'Éocène inférieur d'après les mollusques et les vertébrés fossiles

D'après différentes collections, nous avons étudié la faune fossile du site de Pourcy (Marne) localisé au nord-est du bassin de Paris, afin de présenter la diversité de la faune et de reconstituer les conditions qui ont déterminé cet assemblage. La faune de mollusques témoigne de différents environnements estuariens tropicaux probablement bordés de palétuviers mais pouvant aussi renfermer du matériel provenant du faciès de mangroves. On note la présence de mollusques marins côtiers et terrestres et une faune de vertébrés. L'association terrestre contient des indicateurs de forêts subtropicales de plaine avec des rivières à larges berges et des lacs fluviaux. Les faluns de l'Yprésien inférieur et moyen de Pourcy reflètent probablement le développement des conditions estuariennes et de mangroves qui ont caractérisé le Sparnacien supérieur. Une liste préliminaire d'espèces de mollusques et de vertébrés est donnée, et les guildes alimentaires des mollusques sont comparées à ceux d'un système actuel estuarien de l'Indo-Pacifique.

Mots-clés: Yprésien, paléoécologie, biodiversité, mangroves, mollusques, vertébrés, NW Europe.

Introduction

The classic locality of Pourcy is a small quarry located to the west of the village of Pourcy (49°9'33.28"N 3°54'33.68"E) in lower parts of the valley of the river Ardre on the southwestern side of the D386 road (Fig. 1). The relatively rich fossil lumachelle there was first noted by M. Pistat and recorded by Tuniot (1902) who listed 53 mollusc species and also noted the presence of fish, reptile and other vertebrate fossils. He gave a log of the section from a sketch by Lucien Bellevoye, noting five distinct beds below the topsoil. Fritel (1910, p. 267) later included a rough version of this log in his geological guide to the region and added two additional gastropod

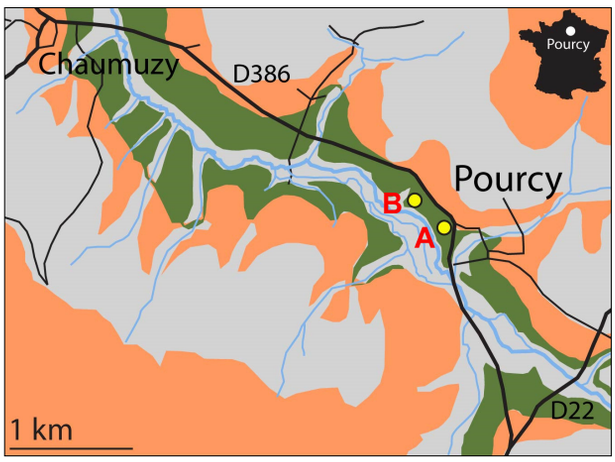


Figure 1. Location of the Pourcy localities: A. quarry, B. temporary exposure at the farm Le Moulin de l'Ardre; early Ypresian 'Falun de Pourcy' in green; unnamed late Ypresian deposits in orange; Lutetian and later deposits in grey.

records. Leriche (1912) gave a photograph of the quarry face indicating two distinct intervals and made some observations on the probable age of the deposit from the known distribution of various molluscs. Based on these accounts, together with field notes by the present authors and by J.J. Hooker (pers. comm.) we have made an estimated log of the overall stratigraphy (Fig. 2) which was seen to vary somewhat along the 16 m eastern face of the quarry. The dominant feature of the section was a 3-4 m 'falun' or bed of sand, the lower part packed with shells (bed 2), which appeared to be dipping northwards and perhaps channeling into the underlying horizontally bedded sands and clays (beds 3-5). The upper part of this bed comprised largely decalcified sand with intercalated clays containing fish teeth, otoliths and mammal remains (A. Lawson pers. comm. See Appendix 2). Recent authors (*e.g.* Duprat *et al*., 2010) have divided the falun into 'lower levels' placed in mammal zone MP8a and 'upper levels' in MP9.

The quarry existed until the end of the 20th century, but is now heavily overgrown and no longer accessible.

A temporary excavation in the eastern bank of the track to the farm 'Moulin de l'Ardre' was later made a few hundred metres to the west of the quarry, at 49°9'43.16"N 3°54'21.84"E (Jagt, 1982). This section showed approximately 2 m of homogenous yellow-brown fossiliferous sand covered by 2 m of barren sand (pers. obs., ES 1990). The fossil fauna was closely similar to that in the quarry and the two sections were considered to be continuous.

The fossil-bearing levels comprise the 'Falun de Pourcy' which is considered to represent a late stage of the early Eocene (basal Ypresian) Epernay Formation (Aubry *et al*., 2005). Based on microinvertebrates, Smith & Smith (2003) suggested a possible correlation with calcareous nannoplankton zone NP10 which would make it considerably older than the age of 53.27 ± 0.15 Ma calculated by

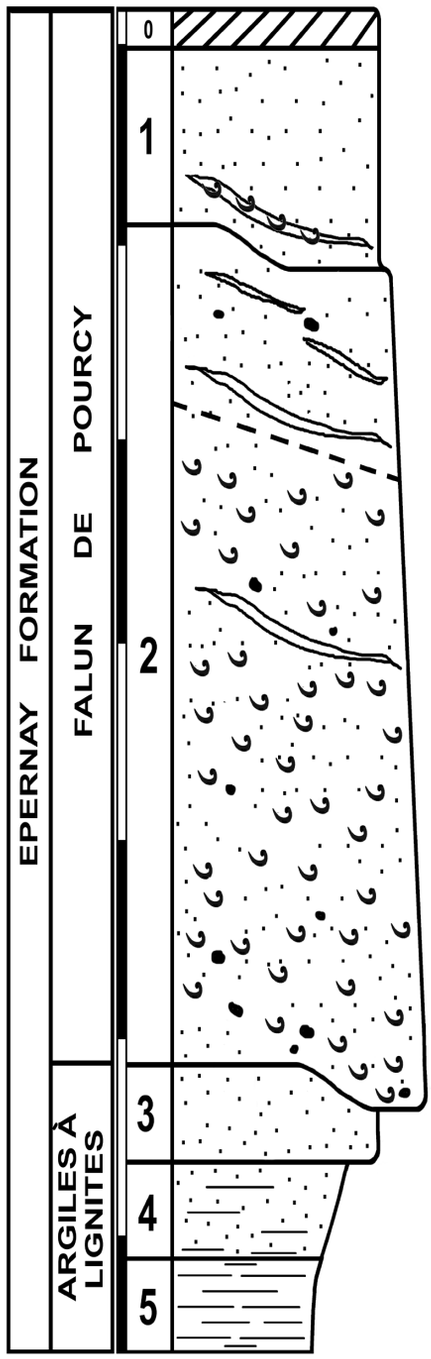


Figure 2. Averaged section in the quarry at Pourcy, based on a sketch of the eastern face by L. Bellevoye in Tuniot (1902) and various later field notes.

0. Thin topsoil.
1. Buff cross-bedded fine sand. A shelly lenticle several cm thick near the base 1-2 m.
2. Buff cross-bedded medium-fine sand, the upper part largely decalcified with clay lenticles but containing vertebrate fossils, the lower part packed with shells, mostly mesohaline species, and containing <5 mm glauconitic siliceous clasts, some resembling fragments of bioherms. Beds 1 and 2 have an apparent dip northwards 3-4 m.
3. Unfossiliferous fine sand 0.5 m.
4. Clayey sand ('terre sablonneuse) 0.5 m.
5. Clay seen to *c*. 0.5m. Beds 3, 4 and 5 horizontally bedded.

Escarguel (1999, p. 269). Conflicts in the dating of this shell bed are discussed below.
Permission to visit these sites should be sought from the landowners.

Geological setting

The Pourcy sites lie in the outer part of an Oligocene outlier to the northeast between Pourcy and Chamery. Overlying the Falun de Pourcy are later Ypresian (Cuisian) sands and clayey sands, the line of contact running close to the quarry, shortly to the south of the D386 as shown on the Carte Geologique de la France (à 1/50.000, BRGM, Fismes XXVII-12, 1987). These horizons were not recognised in the sections studied, but 80 m to the northeast of the quarry, a roadside exposure showed buff, fine calcareous sands with the gastropods *Bayania lactea* (Lamarck), *Sigmesalia* sp., *Sycostoma* sp. and *Keilostoma minus* (Deshayes) within this mapped zone, but the preservation indicated a Lutetian age . Within 1 km of the quarry to the northeast, excavations have shown the presence of middle Lutetian Calcaire Grossier Formation overlain by late Lutetian sands. The areas mapped as late Ypresian deposits were not specifically identified in the two sites investigated at Pourcy.

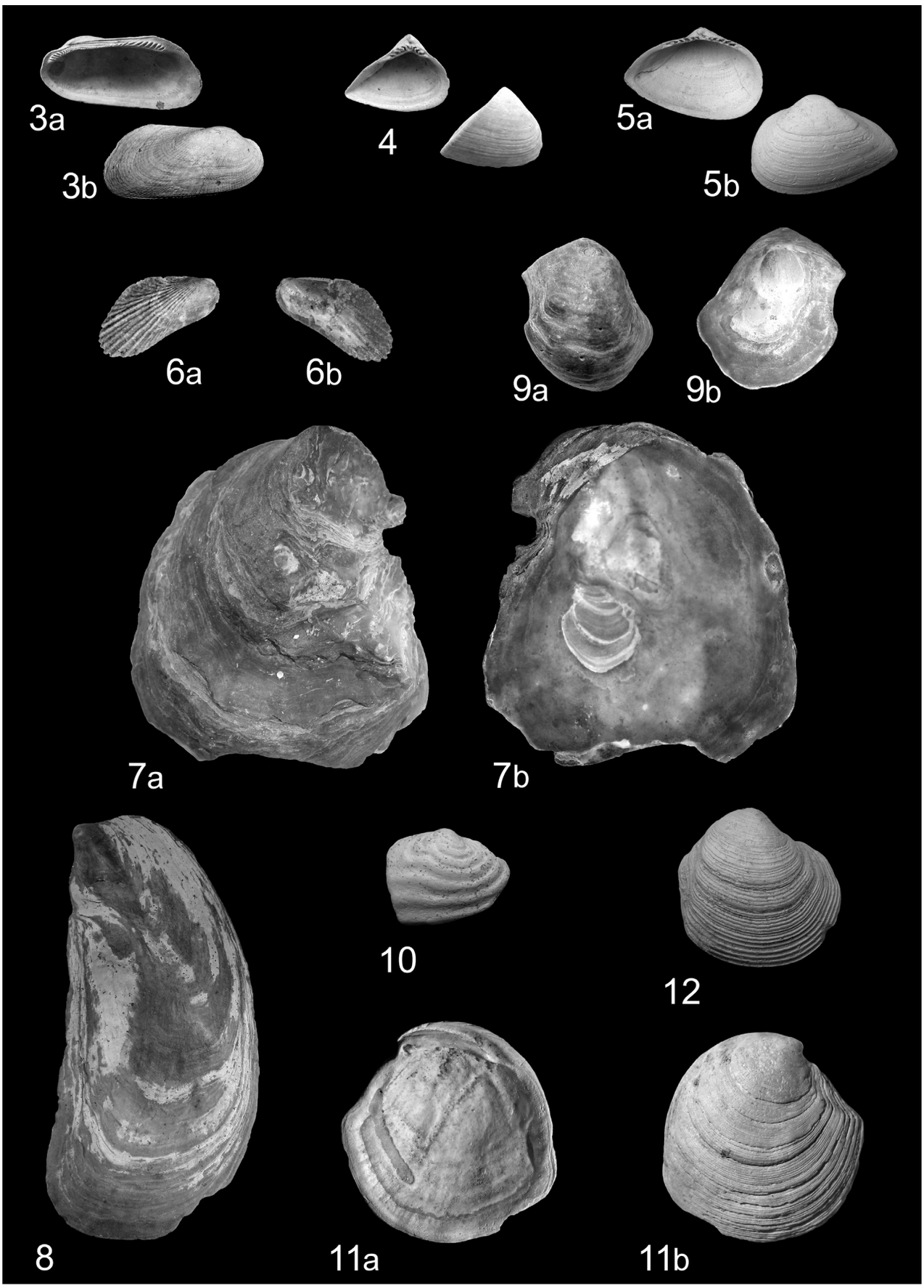
Material and methods

An inventory of the fossil collection of one of us (ES), recovered from the Pourcy sites over the last 30 years, has been supplemented with additional records from the present authors and other workers and material in the collections housed at Naturalis Biodiversity Center, Leiden, The Netherlands. The individual fossils found at Pourcy have been treated taxonomically in various publications but no recent assessment of the whole fauna has been attempted, which is one aim of this paper.
In mixed faunas such as that at Pourcy, containing euhaline, stenohaline/euryhaline as well as freshwater and terrestrial species, with a predominance of taxa from families today associated with tropical mangrove areas, it is traditionally assumed that the palaeoenvironment was a river estuary, thus explaining the means of transport of the various faunal elements.
Following the publication of a comprehensive account of the molluscs and flora of such a modern tropical river estuary by Lozouet & Plaziat (2010) we thought it useful to make an autecological assessment of the molluscs of Pourcy from a direct comparison of the overall faunal composition (including the feeding ecology) to investigate whether Pourcy could be matched to one or more subenvironments within a tropical estuarine system, and whether possible reworking of earlier deposits should be taken into consideration. We therefore compared the fauna from both sites at Pourcy (combined) with sample data from the Abatan (Bohol Island, Philippines) river estuary/open-mouth bay transect from which seven grab samples were assessed by Lozouet & Plaziat (2010). The results of the comparison are given in Figs 108, 109.
The following collections from the quarry have been studied for this paper: F.A.D. van Nieulande (Nieuw-en-St.-Joosland, The Netherlands, now in Naturalis Biodiversity Center, Leiden), J.J. de Vos (Terneuzen, The Netherlands; collection now in museum Het Warenhuis, Axel, The Netherlands) and material from the department of Fossil Mollusca of Naturalis Biodiversity Center (Leiden, The Netherlands). The latter collections include material donated by A. Haandrikman, H. van Haren, A.W. Janssen, D. van der Mark and L. Staadt. From excavations at Le Moulin de l'Ardre material was collected by E. Spijkerman (ES) of Krommenie, The Netherlands (including ex coll. C. Deerenberg), J. van der Voort (Osterncappeln, Germany) and from W. Groeneveld (now housed in the Naturalis Biodiversity Center collections). To maximise our coverage additional species in various private collections (A) have also been added to the lists where identifications could be verified, although these specimens were not included in the statistics.
Feeding guilds used in this study were herbivores/detritivores (H), predatory carnivores (CP; including scavengers and predators on foraminifers), parasites (P), suspension feeders (SU), deposit feeders (D) and chemosymbiontic deposit feeders (CD). Ecological information of molluscs was derived from the Neogene Marine Biota of Tropical America molluscan life habits database (Todd, 2001) and the comprehensive ecological information provided by Beesley *et al*. (1998).
Mollusc identifications follow Cossmann & Pissarro (1904-1906), Cossmann & Pissarro (1910-1913) and original descriptions where necessary, with nomenclature amended after Le Renard (1994, 1995), Le Renard & Pacaud (1994, 1995), Pacaud & Le Renard (1995), Reid *et al*. (2008), Pacaud & Harzhauser (2012) and Symonds & Pacaud (2010). Fish teeth were identified using Casier (1946), with reference to Leriche (1907) and Dutheil (1991), using the updated systematics and nomenclature of Cappetta & Nolf (2005) and Cappetta (2012). Turtle remains were identified from De Broin (1977) and mammal records and identifications using Louis & Michaux (1962), Michaux (1964, 1968), Russell *et al.* (1967), Rich (1971), Hartenberger (1971), Sudré *et al.* (1983), Baudry (1992), Hooker (1994, 1996, 2010), Escarguel (1999), Smith & Smith (2003), Tabuce *et al.* (2006), Solé *et al.* (2011) and Hand *et al*., 2015. Mammal systematics follow McKenna & Bell (1997).
One complication concerning the mammal faunas is that apparently several taxa were present during the early Eocene along the entire north coast of the Atlantic through the Thule land bridge (McKenna, 1972; Godinot, 1981, 1982; Hooker, 1994;). The occurrence of species on both American and European sides of the land bridge (Escarguel, 1999) may not be adequately reflected in their taxonomy (Simpson, 1929). For vertebrates recent taxonomic revisions have led to considerable changes in the characterization and number of taxa. Taxonomic revision of American vertebrates is beyond the scope of this paper. Therefore, the data presented here serve as a preliminary assessment of the faunal composition.

Figures 3-12. Mollusca from the Epernay Formation of Pourcy.

Sizes: W = width, L = length, H = height, D = diameter. Suggested environmental indicators: T = terrestrial; FW = freshwater; ME = normally associated with marine/open estuarine facies, although many of the species are also known from brackish facies of the underlying Argiles à Lignites; [unmarked] = brackish, which is likely to include a continuum of lowered salinity palaeoenvironments. RGM = Naturalis Biodiversity Center, Leiden. Most of the figured specimens are taken from private collections but will be deposited with the Natural History Museum, London in due course.

3a-b. *Barbatia modioliformis* (Deshayes, 1829), right valve, W 26.4 mm (ME).
4. *Trinacria inaequilateralis* (d'Orbigny, 1850), interior of left valve, W 6.5 mm; exterior of right valve, W 6.5 mm (ME).
5a-b. *Trigonodesma baudoni adelomorpha* Cossmann, 1913, left valve, W 2.3 mm (ME).
6a-b. *Brachidontes dutemplei* (Deshayes, 1858) RGM.794332, right valve, W 8.5 mm (ME).
7a-b. *Crassostrea* cf. *sparnacensis* (Defrance *in* Deshayes, 1832), right (lower) valve, W 38 mm. Ostreid species at Pourcy are frequently blackened and rolled and are not distinguishable on shell shape alone. This species somewhat resembles the gryphaeid *Pycnodonte* but lacks the vesicular shell structure that characterises that genus.
8. *Crassostrea sparnacensis* (Defrance *in* Deshayes, 1832), left (upper) valve exterior, W 25 x L 51.5 mm; typically elongate form.
9a-b. *Anomia casanovei* Deshayes, 1858, left valve, W 17.8 mm (ME).
10. *Palindonaia* sp., fragmentary juvenile right valve, W 3 mm (FW).
11a-b. *Saxolucina proxima sparnacensis* (Deshayes, 1857), right valve, W 16 mm (ME).
12. *Parvilucina nana* (Deshayes, 1857), exterior of right valve, W 2 mm (ME).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Figures 13-25. Mollusca from the Epernay Formation of Pourcy.

For abbreviations see caption of Figs 3-12.

13a-b. *Corbicula* (*s.l.*) *cardioides* (Deshayes, 1857), right valve, W 40.1 mm. A tumid smooth corbiculid intermediate between the Thanetian *C.* (*s.l.*) *veneriformis* (Deshayes) and the more angular *C.* (*s.l.*) *gravii* (Deshayes), under which name it is often recorded from Pourcy.

14. *Corbicula* (*s.l.*) *antiqua* Férussac, 1822, right valve W 35 mm. As noted by Tuniot (1902) this appears to be a large but stunted extreme morph of *C.* (*s.l.*) *cuneiformis* as found at Pourcy.

15a-b. *Corbicula* (*s.l.*) *cuneiformis* (Sowerby, 1817), RGM.794340, left valve, W 30.1 mm. Larger than the typical form from the Woolwich Formation of England, and separated with difficulty from *C.* (*s.l.*) *antiqua*.

16a-b. *Corbicula* (*s.l.*) *arnoudii* (Potiez & Michaud, 1839), left valve, W 10 mm.

17a-b. *Tellinocyclas tellinoides* (Férussac, 1822), right valve, W 17.2 mm. Much larger than the Thanetian *T. angusta* (Deshayes), *T. tellinoides* appears to be restricted to a narrow chronostratigraphic interval and is useful for correlation, as noted below.

18. *Eupera sublaevigata* (d'Orbigny, 1850), adult right valve, W 3.3 mm and juvenile left valve, W 1.1 mm (FW).

19. *Eupera denainvilliersi* (de Boissy, 1848), interior of left valve, W 2.1 mm; exterior of left valve of another specimen, W 2.1 mm (FW).

20. *Pisidium berellense* (de Laubrière & Carez, 1880), incomplete left valve, W 2.1 mm (FW).

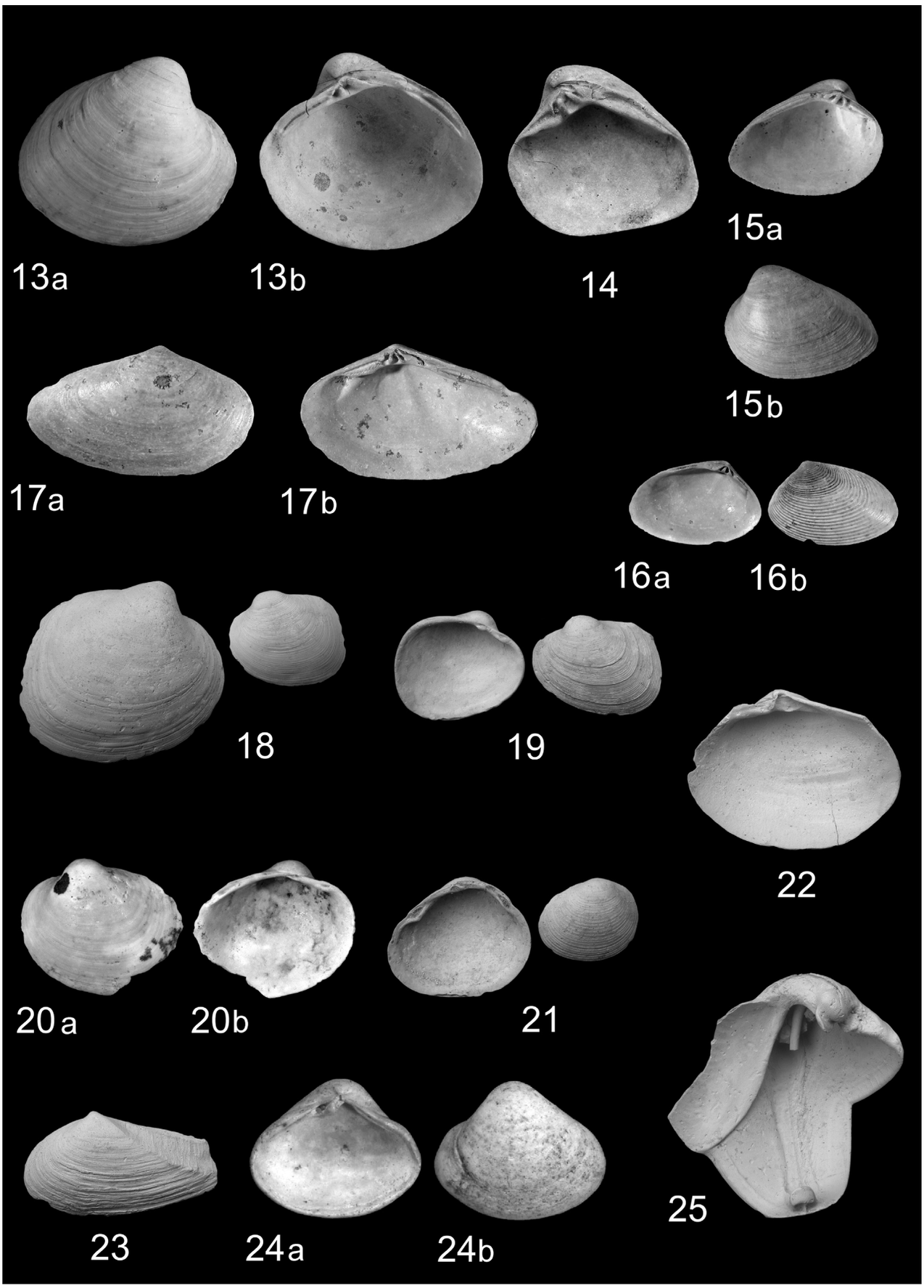
21. *Pisidium* cf. *gosseleti* (Leriche, 1899), interior of adult left valve, W 1.7 mm; exterior of juvenile right valve, W 1.2 mm (FW).

22. *Sphenia terquemi* Deshayes, 1857, right valve, W 5.1 mm (ME).

23. *Sphenia acuta* Staadt *in* Cossmann & Pissarro, 1913, left valve, W 2.3 mm (ME).

24a-b. *Varicorbula arnouldii* (Nyst, 1843), RGM.794336, right valve, W 6.9 mm (ME).

25. *Teredo* sp., interior of left valve, W 3.8 mm (ME).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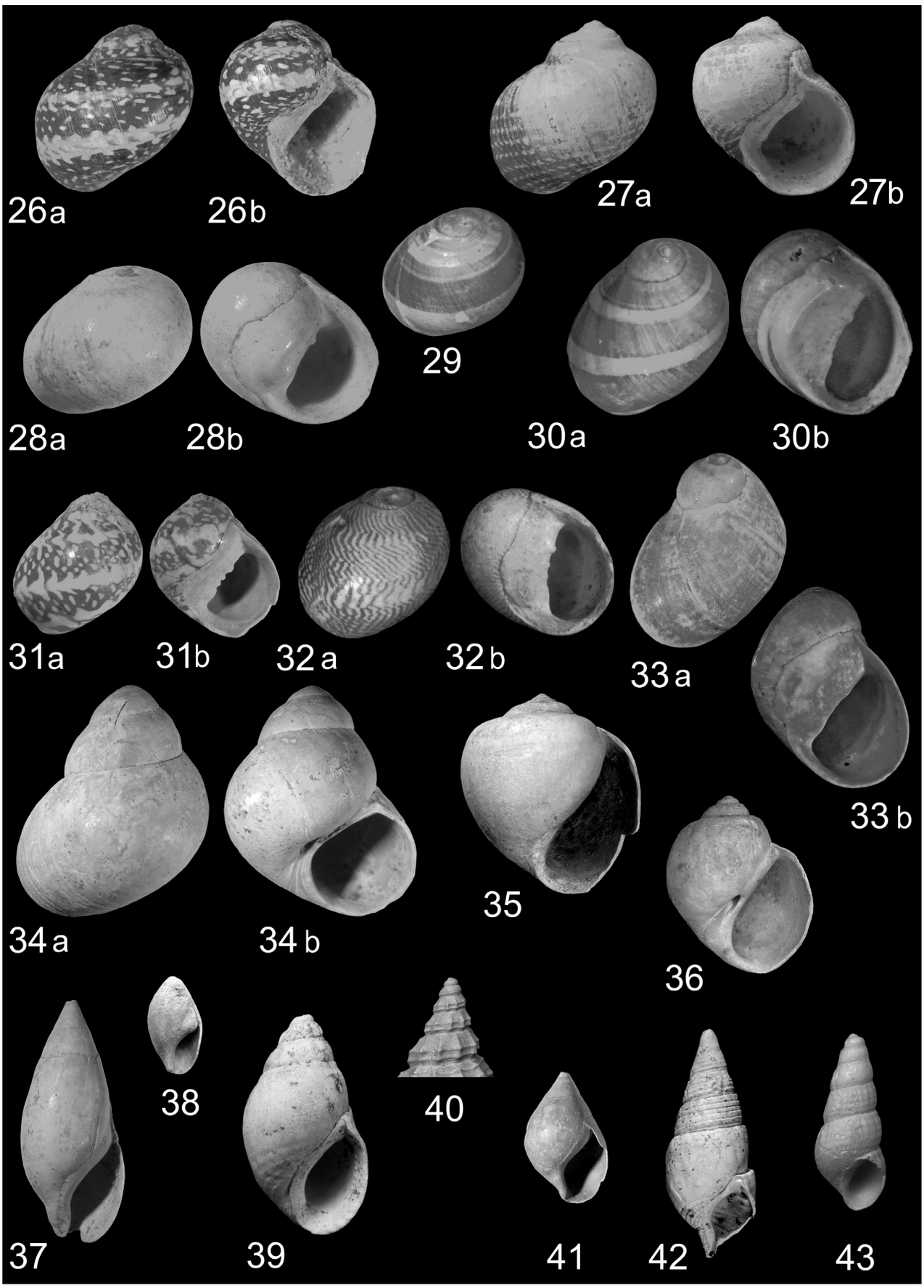
Figures 26-43. Mollusca from the Epernay Formation of Pourcy.

For abbreviations see caption of Figs 3-12.

26a-b. *Neritodryas dutemplei* (Deshayes, 1864), two views, H 15.8 mm.
27a-b. *Neritodryas guillioui* Symonds & Pacaud, 2010, two views, H 20 mm.
28a-b. *Neritoplica uniplicata* (Sowerby, 1823), two views, H 14 mm.
29. *Neritoplica uniplicata* (Sowerby, 1823), variety with colour banding, H 8.2 mm.
30a-b. *Clithon barbei* Symonds & Pacaud, 2010, two views, H 4.0 mm.
31a-b. *Clithon sobrinum* (Férussac, 1823), two views, H 9.9 mm.
32a-b. *Clithon pisiforme pisiforme* (Férussac, 1823), two views, H 4.5 mm.
33a-b. *Clithon pisiforme perlongum* (Cossmann & Pissarro, 1907), two views, H 6.5 mm.
34a-b. *Viviparus rimatus* (Michaud, 1837), two views, H 25.3 mm (FW). Recorded under various names, but there is no reason to suppose that more than one species is represented.
35. *Ampullina pistati* Cossmann, 1907, H 42 mm (M).
36. *Amaurellina lignitarum* (Deshayes, 1864), H 6.1 mm (M).
37. *Melanopsis antidiluviana* (Poiret, 1797), H 20 mm. Abundant (see Discussion and conclusions).
38. *Melanopsis* cf. *ovularis* Watelet, 1853, H 7.2,mm. Rare.
39. *Coptostylus pourcyensis* (Cossmann, 1907), H 20.8 mm.
40. *Coptostylus pourcyensis* (Cossmann, 1907), apex of juvenile shell, enlarged (protoconch D 150 μm).
41. *Coptostylus* cf. *albidus* (Lamarck, 1804), H 10.4 mm. Pourcy examples have shallower sutures and smoother spires than typical *C. albidus* from the Sables de Cuise. This species lacks the denticles inside the lip and basal cords usually developed in *C. pourcyensis*.
42. *Hemisinus pistati* (Cossmann, 1907), H 36 mm.
43. *Bayania* cf. *hordacea* (Lamarck, 1804), H 3.4 mm. Rare examples are somewhat waterworn (M).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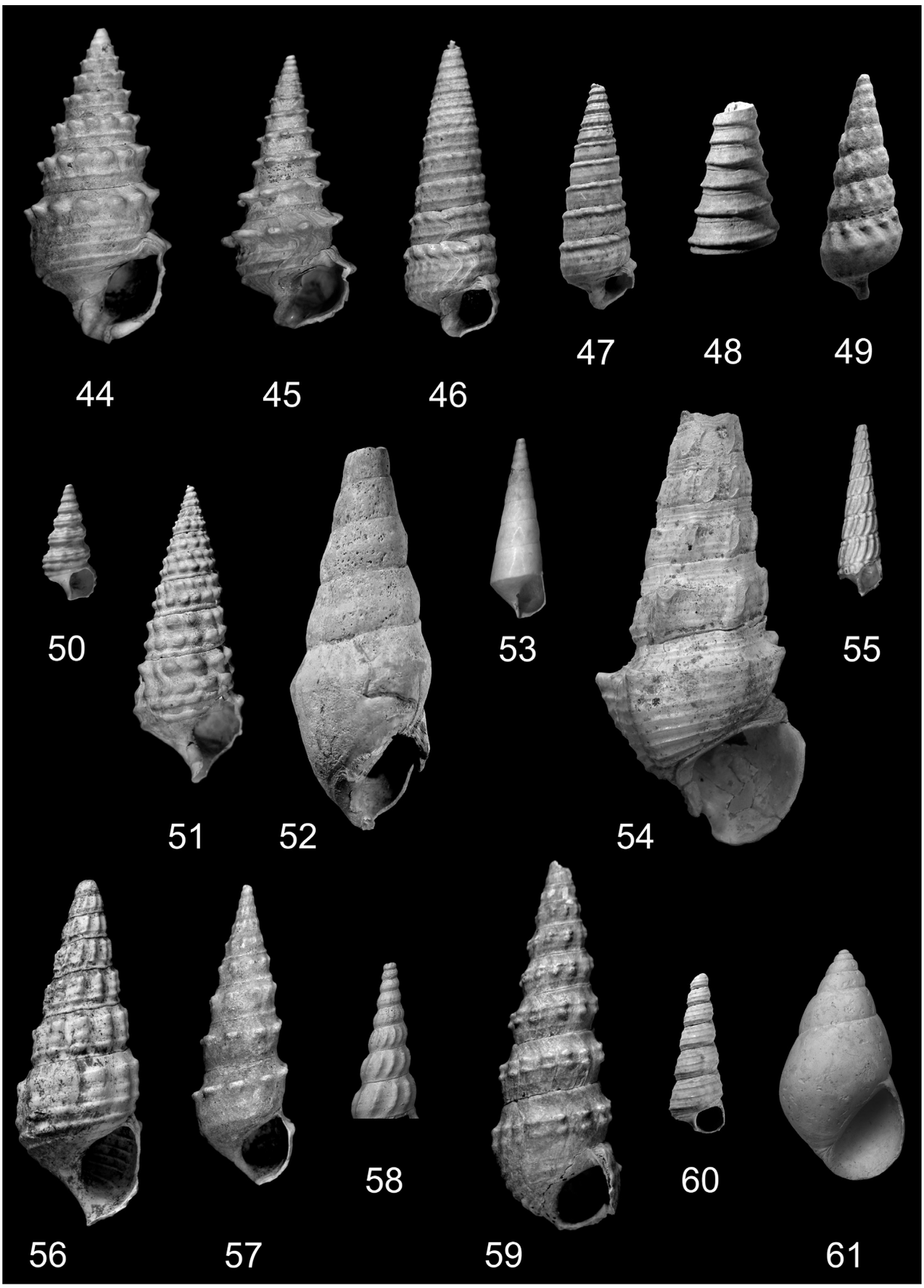
Figures 44-61. Mollusca from the Epernay Formation of Pourcy.

For abbreviations see caption of Figs 3-12.

44. *Potamides turris* (Deshayes, 1833), H 42 mm. Broad form resembling *P. papalis* (Lamarck, 1833) from the Sables de Cuise but differing in the apical ontogeny. Narrower examples show considerable variation.
45. *Potamides turris* (Deshayes, 1833), H 37.5 mm. Conical morph with irregular projecting flanges, that occurs throughout the Epernay Formation.
46. *Potamides funatus* (Sowerby, 1814), H 40 mm. Very variable at Pourcy and includes forms approaching var. *rillyensis* (Cossmann) and var. *cossmanni* (Cossmann & Pissarro). May be hard to distinguish from *P. turris* and *P. dimorphospira*, and the apical whorls, only present in juveniles, are often necessary to separate these species.
47. *Potamides dimorphospira* (Cossmann & Pissarro, 1913), H 27 mm. Characterised by the cyrtoconoid outline of the early whorls.
48. *Potamides pourcyensis* Cossmann & Pissarro, 1913, H 11.9 mm. Frequent in the Argiles à Lignites at Saran and Mutigny. The carinate juvenile develops adult ornament showing it belongs to the *P. funatus* complex.
49. *Vicinocerithium* cf. *biserialis* (Deshayes, 1833), H 24.5 mm. Usually rolled and damaged at Pourcy but common in the Sables de Cuise. Probably indicates a higher salinity than that of the potamidids.
50. *Vicinocerithium* cf. *biserialis* (Deshayes, 1833), juvenile, H 5.7 mm.
51. *Vicinocerithium* (*s.l.*) *fischeri* (Deshayes, 1864), H 48.2 mm. The broad tuberculate early whorls show that this does not belong in the lineage of *Vicinocerithium* (*s.str.*).
52. *Faunus cerithiformis* (Watelet, 1855), H 47 mm. Also occurs in the Argiles à Lignites at Mutigny.
53. *Faunus cerithiformis* (Watelet, 1855), juvenile, H 10.1 mm, showing smooth flattened early whorls.
54. *Jponsia cuvieri* (Deshayes, 1825), H 87 mm. The largest gastropod species at Pourcy, ranging up to the early Lutetian.
55. *Jponsia cuvieri* (Deshayes, 1825), juvenile, H 9.7 mm. Pacaud & Harzhauser (2012) described and figured a full growth-series of this species.
56. *Brotia praecessa* (Deshayes, 1861), H 30.6 mm. Known also from late Thanetian strata.
57. *Brotia melanioides melanioides* (Sowerby, 1816), H 40 mm. Abundant and commonly waterworn. Protoconch suggests a lecithotrophic larval life like many *Potamides* species, and probably a lagoonal habitat.
58. *Brotia melanioides melanioides* (Sowerby, 1816), apical whorls of young shell, H 2.8 mm. Juvenile whorls vary from convex (as shown) to subcylindrical with flattened sides.
59. *Brotia melanioides bicoronata* (Staadt *in* Cossmann, 1913), H 50 mm.
60. *Haustator* cf. *comptus* (Deshayes, 1861), juvenile, H 10 mm. Regarded as an indicator of shallow more euhaline conditions than most of the fauna (ME).
61. *Paludomus triticea* (Férussac *in* Deshayes, 1825), H 2.8 mm.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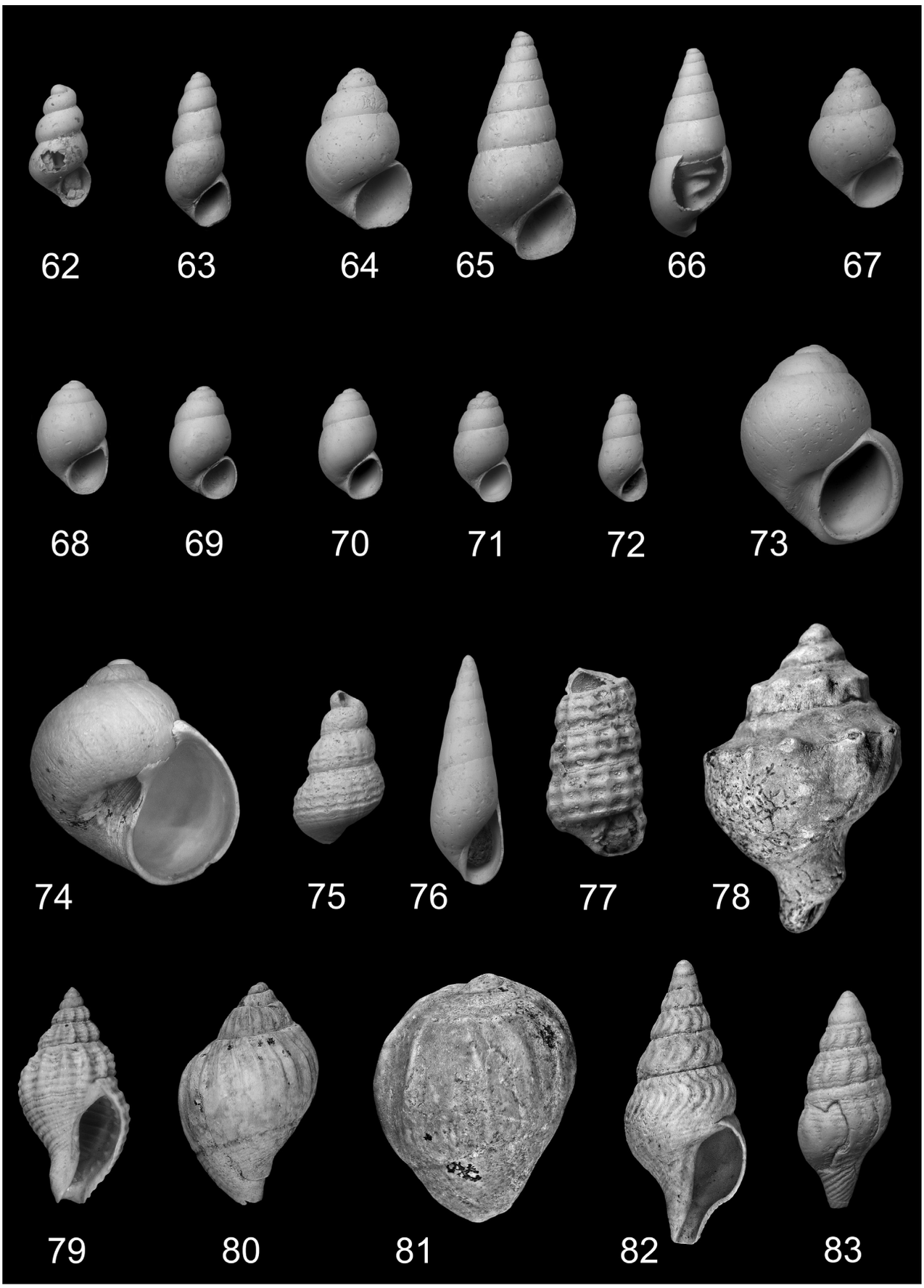
Figures 62-83. Mollusca from the Epernay Formation of Pourcy.

For abbreviations see caption of Figs 3-12.

62. *Hydrobia sparnacensis* (Deshayes, 1862), damaged juvenile shell, H 1.5 mm.
63. *Bythinella intermedia* (Melleville,1843), H 1.9 mm.
64. *Bythinella parkinsoni* (Morris, 1854), H 2.0 mm. Somewhat variable in shape but always with deep sutures [syn. *B. alta* (Deshayes)]. Also frequent in the slightly older Woolwich Formation in England.
65. *Lapparentia elatior* (Cossmann, 1907), H 3.8 mm. Also frequent in the slightly older Woolwich Formation in England
66. *Lapparentia elatior* (Cossmann, 1907), H 3.1 mm, with breakage exposing internal lamellae.
67. '*Stenothyra*' *chorista* (Cossmann, 1888), H 1.7 mm.
68. '*Stenothyra*' *miliola* (Melleville, 1840), H 1.4 mm.

69, 70. '*Stenothyra*' cf. *pulvis* (Deshayes, 1861), two examples both H 1.4 mm. Apparently a form intermediate between '*S*'. *miliola* and *'S'. pulvis*. While resembling the shape of some Stenothyridae, these Pourcy species lack the characteristic parietal ridge in the aperture that holds the operculum in living stenothyrids, and these seem likely to be convergent hydrobiids.

71. '*Stenothyra*' *pulvis* (Deshayes, 1861), H 1.3 mm.
72. *Pasithea pourcyensis* (Staadt *in* Cossmann & Pissarro, 1913), H 1.3 mm. Also frequent in the slightly older Woolwich Formation in England.
73. *Cirsomphalus tunioti* (Cossmann, 1902), H 2.4 mm. Introduced as *Bithynia tunioti* by Dollfus (*in* Tuniot, 1902) without figure or description. The first valid description was by Cossmann the same year.
74. *Euspira consobrina* (Deshayes, 1864), H 6.7 mm (ME).
75. *Acirsa subtenuistriata moloti* (Staadt *in* Cossmann & Pissarro, 1913), H 2.5 mm. Rare (ME).
76. *Margineulima suturalis* (Cossmann, 1907), H 2.5 mm. Rare (ME).
77. *Cerithiopsis* sp., H 2.8 mm. Rare (ME).
78. *Cornulina praecursor* (Cossmann, 1902),H 37.5 mm. Uncommon but probably over-represented in collections owing to bias. Some living Melongenidae inhabit the littoral zone in brackish environments (ME).
79. *Eocantharus latus* (Sowerby, 1813), H 6.4 mm. Often associated with brackish molluscs in lagoonal facies in France and England (ME).
80. *Pseudoliva fissurata* (Deshayes, 1835), H 8.3 mm. High-spired juveniles from Pourcy have been referred to *P. laudunensis* despite closely resembling the Thanetian *P. fissurata* (*e.g.* Pacaud & Tracey, 2000, pl. 1, fig. 5) (ME).
81. *Pseudoliva laudunensis* (Defrance, 1826), H 8.3 mm. This juvenile posesses the strong ribs and low spire that characterise *P. laudunensis*. Further research should show any differences that could reliably separate the convergent *P. fissurata* (ME).
82. *Eopleurotoma pourcyensis* (Cossmann, 1902), H 9.4 mm (ME).
83. *Domenginella* ? sp., H 3.6 mm (ME).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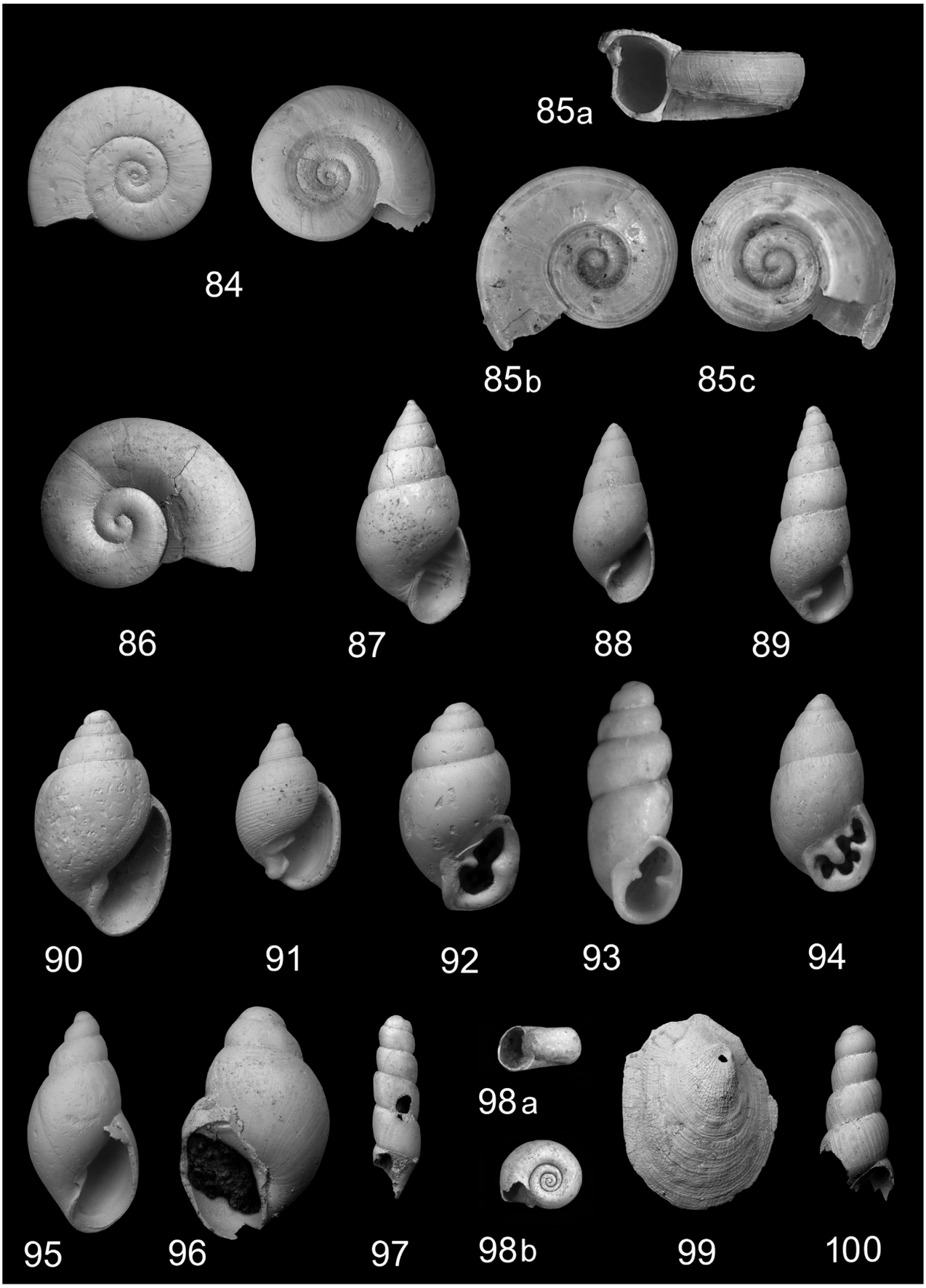
Figures 84-100. Mollusca from the Epernay Formation of Pourcy.

For abbreviations see caption of Figs 3-12.

84. *Anomalorbina hemistoma* (Sowerby, 1816), left-apical view showing flattened spire, D 1.3 mm; right-umbilical view of another shell, D 1.3 mm.
85a-c. *Anomalorbina* cf. *cuisensis* (Cossmann, 1885), RGM.1008190, three views showing biconcave angular profile and strong spiral ornament, D 1.0 mm. Usually with a few axial ribs on the early whorls. Arrangement of spiral threads varies and was not mentioned in the original description of the type from the Sables de Cuise. Uncommon.
86. *Valvata inflexa* Deshayes, 1862 ,apical view, D 1.6 mm (FW).
87. *Odostomia lignitarum* Deshayes, 1861, H 3.7 mm. Commonly associated with brackish molluscs in France and England (ME).
88. *Odostomia* cf. *primaeva* Deshayes, 1861, H 2.2 mm (ME).
89. *Odostomia* sp., H 3.6 mm (ME).
90. *Acteon sphaericulus granum* (Cossmann, 1907), H 4.1 mm (ME).
91. *Ringicula lignitarum* Cossmann, 1902, H 2.8 mm (ME).
92. *Carychium sparnacense* (Deshayes, 1863), H. 1.5 mm. Modern *Carychium* live in wet situations, often near freshwater (T).
93. *Carychium* aff. *cylindroides* Staadt *in* Cossmann & Pissarro, 1913, H 1.3 mm. The original figures (Cossmann & Pissarro, 1913, fig. 255-11) showed three shells which appear to represent two different species. The middle one of these most resembles our fig. 93 (T).
94. *Carychium* (*s.l.*) sp., H 1.4 mm. The size and half-ribbed ornament resembles some fossil species previously assigned to *Carychium*, although the complex apertural dentition suggests affinities to certain Ellobiidae (T?).
95. *Galba lignitarum* (Deshayes, 1863), H 4.0 mm (FW).
96. *Aplexa pulchella* (d'Orbigny, 1850), H. 2.2 mm (FW).
97. *Berellaia soluta* Staadt *in* Cossmann & Pissarro, 1903, H 1.8 mm (FW).
98a-b. *Biomphalaria subovata* (Deshayes, 1825), RGM.794333, two views, D 4.3 mm (FW).
99. *Acroloxus matheroni lemoinei* (Cossmann, 1889), D 1.4 mm (FW).
100. *Palaeostoa exarata* (Michaud, 1838), ? juvenile, H 1.7 mm. Ribbed fragments of adult *P. exarata* are also found at Pourcy. The fragility of many of the smaller freshwater and terrestrial species in the shell bed suggests that they were preserved in the interiors of larger gastropods (T).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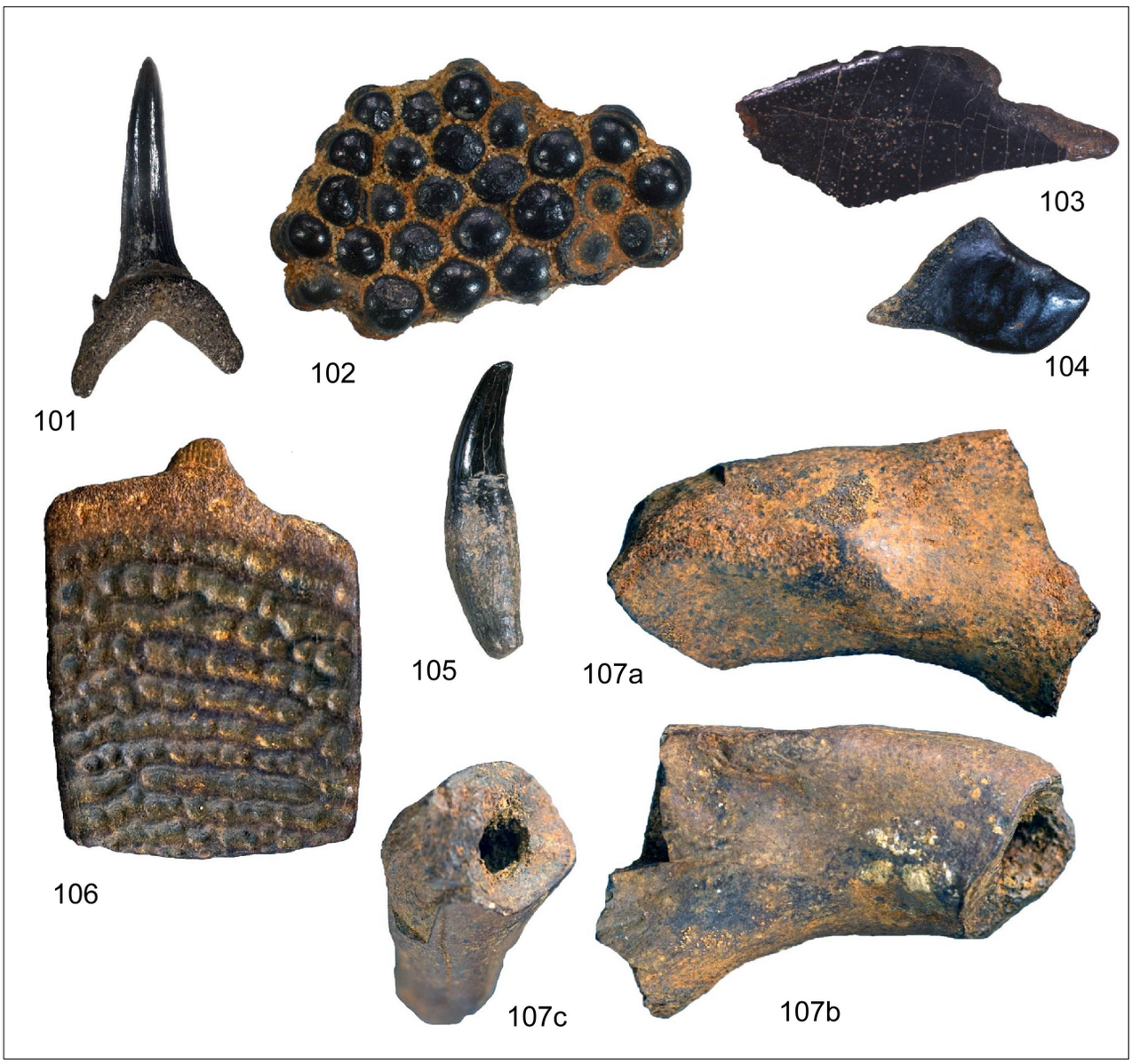

Figures 101-107. Some characteristic vertebrate taxa from Pourcy (coll. ES, except *Trionyx* sp.).

101. *Striatolamia macrota* (Agassiz, 1843); lower anterior tooth, lingual view, H 19 mm.
102. *Egertonia isodonta* Cocchi, 1866; pharyngeal plate, oral view, H 22 mm.
103-104. *Lepisosteus suessionensis* Gervais, 1852; external view of scales, 103: H 11 mm; 104: H 11 mm.
105. *Platychoerops daubrei* (Lemoine, 1879); incisor tooth, labial view, H 19 mm.
106. *Trionyx* sp.; RGM n.n.; pleural plate of carapax, dorsal view, W 30.6 mm.
107. *Gastornis parisiensis* Hebert, 1855; humerus, L 60 mm.

Statistical results

The composition of the mollusc and vertebrate faunas are provided in Tables 1 and 2. The mollusc fauna consisted of 30 bivalve and about 80 gastropod species (Table 1). The relative abundance of the common species in the studied collections, verified by the cursorary examination of an unsorted residue sample, was considered to provide an adequate reflection of actual frequency, although the percentages of rarer taxa were likely to be exaggerated owing to collecting bias. The bivalve fauna was dominated by Corbiculidae (57%) and Corbulidae (24%), the gastropod fauna by Neritidae (20%), Melanopsidae (18%) and Potamididae (18%). In mollusc species numbers, slightly more than half of the Pourcy fauna was dominated by herbivores/detritivores. Suspension feeders made up about one third and the combined groups of predators and parasites 14%. In abundance, suspension feeders (mostly bivalves) made up almost half; carnivores were rare (4%).

	Q	M
Class Bivalvia		
Family Arcidae		
3 *Barbatia modioliformis* (Deshayes, 1829)	6	7
Family Noetiidae		
4 *Trinacria inaequilateralis* (d'Orbigny, 1850)	61	23
5 *Trigonodesma baudoni adelomorpha* Cossmann, 1913	7	5
Family Mytilidae		
6 *Brachidontes dutemplei* (Deshayes, 1858)	120	19
Family Ostreidae		
Ostrea cf. *bellovacina* (Lamarck, 1806)	15	12
7,8 *Crassostrea sparnacensis* (Defrance *in* Deshayes, 1832)	86	155
Family Anomiidae		
9 *Anomia casanovei* Deshayes, 1858	12	75
Family Unionidae		
10 *Palindonaia* sp.	-	A
Family Lucinidae		
11 *Saxolucina proxima sparnacensis* (Deshayes, 1857)	25	17
12 *Parvilucina nana* (Deshayes, 1857)	-	A
Family Leptonidae		
Anomalokellia pourcyensis (Cossmann & Pissarro, 1906) [(a)]	-	-
Family Cardiidae		
Orthocardium moloti (Staadt *in* Cossmann & Pissarro, 1913) [(a)]	-	A
Family Psammobiidae		
Gari staadti (Cossmann & Pissarro, 1913)	-	2
Family Corbiculidae		
13 *Corbicula* (*s.l.*) *cardioides* (Deshayes, 1857)	31	24
14 *Corbicula* (*s.l.*) *antiqua* Férussac, 1822	314	876
15 *Corbicula* (*s.l.*) *arnoudii* (Pot. & Mich., 1839)	226	96
16 *Corbicula* (*s.l.*) *cuneiformis* (Sowerby, 1817)	100	230
17 *Tellinocyclas tellinoides* (Férussac, 1822)	32	13
Donacopsis heberti (Deshayes, 1857)[(x)]	1	-
Familie Sphaeriidae		
20 *Pisidium berellense* (de Laubrière & Carez, 1880)	-	1
21 *Pisidium* cf. *gosseleti* (Leriche, 1899)	-	A
18 *Eupera sublaevigata* (d'Orbigny, 1850)	-	A
19 *Eupera denainvilliersi* (de Boissy, 1848)	-	A
Familie Veneridae		
Pitar lamberti (Deshayes, 1857)	18	1
Family Myidae		
23 *Sphenia acuta* Staadt *in* Cossmann & Pissarro, 1913	7	-
22 *Sphenia terquemi* Deshayes, 1857	11	6
Family Corbulidae		
24 *Varicorbula arnouldii* (Nyst, 1843)	435	420
Family Pholadidae		
Cyrtopleura orbignyana (Lévesque *in* Graves, 1847)[(a)]	-	A
Teredina personata Lamarck, 1806	5	8
25 *Teredo* sp.	-	A
Class Gastropoda		
Family Neritidae		
26 *Neritodryas dutemplei* (Deshayes, 1864)	27	4
27 *Neritodryas guillioui* Symonds & Pacaud, 2010	-	1
28,29 *Neritoplica uniplicata* (Sowerby, 1823)	88	175
30 *Clithon barbei* Symonds & Pacaud, 2010	-	A
31 *Clithon sobrinum* (Férussac, 1823)	251	236
32 *Clithon pisiforme pisiforme* (Férussac, 1823)	-	19
33 *Clithon pisiforme perlongum* (Cossmann & Pissarro, 1907)	32	11
Family Viviparidae		
34 *Viviparus rimatus* (Michaud, 1837)	2	-
Family Ampullinidae		
35 *Ampullina pistati* Cossmann, 1907	10	20
36 *Amaurellina lignitarum* (Deshayes, 1864)	44	36
Family Potamididae		
44,45 *Potamides turris* (Deshayes, 1833)	246	237
46 *Potamides funatus* (Sowerby, 1814)	112	101
47 *Potamides dimorphospira* (Cossmann & Pissarro, 1913) [(b)]	-	A
48 *Potamides pourcyensis* Cossmann & Pissarro, 1913	62	39
Family Batillariidae		
49,50 *Vicinocerithium* cf. *biserialis* (Deshayes, 1833)	-	A
51 *Vicinocerithium* (*s.l.*) *fischeri* (Deshayes, 1864)	27	5
Family Pachychilidae		
57,58 *Brotia melanioides melanioides* (Sowerby, 1816)	150	143
59 *Brotia melanioides bicoronata* (Staadt *in* Cossmann, 1913)	23	25
56 *Brotia praecessa* (Deshayes, 1861)	1	-
54,55 *Jponsia cuvieri* (Deshayes, 1825)	44	24
53 *Faunus cerithiformis* (Watelet, 1855)	27	23
Family Melanopsidae		
37 *Melanopsis antidiluviana* (Poiret, 1797)	325	428
38 *Melanopsis* cf. *ovularis* Watelet, 1853	-	A
39,40 *Coptostylus pourcyensis* (Cossmann, 1907)	40	36
41 *Coptostylus* cf. *albidus* (Lamarck, 1804)	5	-
Family Thiaridae		
42 *Hemisinus pistati* (Cossmann, 1907)	8	3
Family Pseudomelaniidae		
43 *Bayania* cf. *hordacea* (Lamarck, 1804)	-	A
Family Paludomidae		
61 *Paludomus triticea* (Férussac *in* Deshayes, 1825)	10	-
Family Turritellidae		
Haustator cf. *circumdatus* (Deshayes, 1861)[(x)]	28	-
60 *Haustator* cf. *comptus* (Deshayes, 1861)	14	5
Ispharina cf. *hybrida* (Deshayes, 1835) [(x)]	-	2
Family Hydrobiidae (*s.l.*)		
62 *Hydrobia sparnacensis* (Deshayes, 1862)	208	64
Peringia glandinensis (De Laubrière & Carez, 1880) [(x)]	1	2
Peringia sp. [(x)]	7	2
Pseudamnicola pistati (Cossmann, 1907) [(x)]	1	-
63 *Bythinella intermedia* (Melleville,1843) [(x)]	-	19
64 *Bythinella parkinsoni* (Morris, 1854)	22	53
65,66 *Lapparentia elatior* (Cossmann, 1907)	16	3
Lapparentia stenochora (Cossmann, 1888)[(x)]	6	7
Staliopsis bouryi (Cossmann, 1888) [(x)]	23	1
73 *Cirsomphalus tunioti* (Cossmann, 1902)	17	4
67 '*Stenothyra*' aff. *chorista* (Cossmann, 1888)	76	11
68 '*Stenothyra*' aff. *miliola* (Melleville, 1840)	-	14
69-71 '*Stenothyra*' aff. *pulvis* (Deshayes, 1861)	14	1
Paladilhia plicistria (Cossmann, 1888)	A	-

Table 1, continued next page

Table 1, continued

	Q	M
Family Iravadiidae		
72 *Pasithea pourcyensis* (Staadt *in* Cossmann & Pissarro, 1913)[(b)]	-	A
Family Naticidae		
74 *Euspira consobrina* (Deshayes, 1864)	42	71
Family Epitoniidae		
75 *Acirsa subtenuistriata moloti* (Staadt in Cossmann & Pissarro, 1913)[(b)]	-	A
Cirsotrema stueri (De Boury, 1890) [(x)]	1	1
Family Eulimidae		
76 *Margineulima suturalis* (Cossmann, 1907)[(b)]	-	A
Family Cerithiopsidae		
77 *Cerithiopsis* sp.	-	A
Family Muricidae		
Nucellopsis sarroniensis (Carez, 1879)	-	A
Family Turbinellidae		
78 *Cornulina praecursor* (Cossmann, 1902)	2	9
Family Buccinidae		
79 *Eocantharus latus* (Sowerby, 1813)	18	35
Family Pseudolividae		
80 *Pseudoliva fissurata* (Deshayes, 1835)	-	A
81 *Pseudoliva laudunensis* (Defrance, 1826)	15	6
Family Turridae		
82 *Eopleurotoma pourcyensis* (Cossmann, 1902)	5	5
Family Borsoniidae?		
83 *Domenginella* ? sp.	-	A
Family Cornirostridae		
84 *Anomalorbina hemistoma* (Sowerby, 1816)	61	101
85 *Anomalorbina* cf. *cuisensis* (Cossmann, 1885)	1	A
Family Valvatidae		
86 *Valvata inflexa* Deshayes, 1862	-	A
Family Pyramidellidae		
88 *Odostomia primaeva* Deshayes, 1861[(x)]	1	-
Odostomia asthenoptyxis (Cossmann, 1907) [(b)]	-	-
87 *Odostomia lignitarum* Deshayes, 1861	44	25
Odostomia gravesi Deshayes, 1861[(x)]	8	4
Odostomia microscopica (Cossmann, 1907)	-	A
89 *Odostomia* sp.	-	A
Syrnola sp.	1	1
Family Acteonidae		
90 *Acteon sphaericulus granum* (Cossmann, 1907)[(b)]	-	A
Crenilabium pourcyense (Cossmann, 1907) [(b)]	-	-
Family Ringiculidae		
91 *Ringicula lignitarum* Cossmann, 1902	3	-
Family Retusidae		
Retusa lignitarum (Cossmann, 1907)	2	-
Family Ellobiidae		
Stolidoma pistati Cossmann, 1907[(b)]	-	-
Family Carychiidae		
92 *Carychium sparnacense* (Deshayes, 1863)	1	-
93 *Carychium cylindroides* Staadt *in* Cossmann & Pissarro, 1913[(b)]	1	-
94 *Carychium* sp.	-	A
Family Lymnaeidae		
95 *Galba lignitarum* (Deshayes,1863)	-	A
Family Physidae		
96 *Aplexa pulchella* (d'Orbigny, 1850)	1	-
Berellaia bonneti Cossmann, 1907[(b)]	-	-
97 *Berellaia soluta* Staadt *in* Cossmann & Pissarro, 1903[(b)]	1	A
Family Planorbidae		
98 *Biomphalaria subovata* (Deshayes, 1825)	23	10
Family Acroloxidae		
99 *Acroloxus matheroni lemoinei* (Cossmann, 1889)	-	A
Family Megaspiridae		
100 *Palaeostoa exarata* (Michaud, 1838)	-	A

Table 1. Molluscs from Pourcy. For bivalves the number of valves is indicated. First column (Q): Quarry. Second column (M): outcrop 'Le Moulin de l'Ardre'. Records from the literature: [(a)] Cossmann & Pissarro (1906); [(b)] Cossmann & Pissarro (1913); [(c)] Symonds & Pacaud (2010); [(x)] (record not verified). A= additional material noted in private collections. Bold numbers in front of species refer to figures.

The vertebrate fauna consisted of 4 shark, 4 batoid, 7 bony fish, 5 turtle, 2 crocodilian, 1 bird and 34 mammal species (Table 2). Some characteristic species are shown in Figs 101-107.

The shark and batoid fauna was dominated by Odontaspididae/Mitsukurinidae (46%; the shark teeth were predominately of juvenile animals) and Myliobatidae (46%). The bony fish fauna (represented by teeth and scales) was dominated by Lepisosteidae (47%) and Phylodontidae (29%). Otoliths were rather rare and those recorded are listed in Appendix 2. The reptiles comprised crocodilians (50%) and turtles (50%). Only a few remains of birds and mammals have been recorded.

Discussion and conclusions

Sedimentation

Harzhauser *et al*. (2015) gave a simplified estimate of origin of various lithologies resulting from deltaic/estuarine environments. The closest match to the Falun de Pourcy was 'Medium- to fine-grained sandstones with bioclasts and small mudclasts. Cross-bedding, normal grading; traction carpets, HCS. Large foraminifera, mollusks. Densely packed and well-sorted beds and pavements. [interpreted as] Transported (sedimentologic) distal delta front (shelfal lobes)'. Large foraminifera were, however, not common at Pourcy.

Vegetation

Following Ellison *et al*. (1999), Plaziat *et al*. (2001) examined the history of mangroves in detail and concluded they had existed at least since earliest Paleocene times, and that the early Tertiary was a period of pan-tropical/subtropical homogeneity of the mangrove ecosystem. Pollen and spores of the extant mangrove plants *Nypa*, *Bruguiera* and *Acrostichum aureum* have been found in samples of the uppermost Argiles à Lignites d'Epernay

	Q	M
Phylum Chordata		
Class Chondrichthyes		
Family Mitsukurinidae		
Striatolamia macrota (Agassiz, 1843)[a,b,e]	-	38
Family Odontaspididae		
Brachycarcharias lerichei (Casier, 1946)[a,b,e]	-	14
Hypotodus verticalis (Agassiz, 1843)[a,b,e]	-	40
Family Carcharhinidae		
Physogaleus secundus (Winkler, 1876)[a,b]	-	14
Family Pristidae		
Pristis sp.[a]	-	-
Family Myliobatidae		
Myliobatis sp.[a]	-	92
Aetobatus irregularis Agassiz, 1843[f]	-	-
Family Mobulidae		
Burnhamia daviesi (Woodward, 1889) [b]	-	-
Class Osteichthyes		
Family Lepisosteidae		
Lepisosteus suessionensis Gervais, 1852[a] (29 scales, 20 teeth)	-	49
Family Amiidae		
Amia (Pappicthys) barroisi Leriche, 1905[a]	-	-
Family Phylodontidae		
Egertonia isodonta Cocchi, 1866[a] (7 jaws, 1 scale, 21 teeth)	-	29
Phyllodus toliapicus Agassiz, 1844[a,f] (1 tooth)	-	1
Family Ariidae		
Arius egertoni Dixon, 1850 (1 jaw, 1 scale, 12 spines)	-	14
Family Sparidae		
Sparidae indet. (otoliths)	1	1
Family Labridae		
Labrodon trapezoidalis Leriche, 1905[a] (jaws)	-	9
Class Reptilia		
Family Petomedusidae		
Neochelys sp. [c]	-	-
Family Trionychidae		
Palaeotrionyx vittatus (Pomel, 1847) [c]	-	3
Trionyx sp. [c]	-	32
Family Carettochelyidae		
Allaeochelys sp. [c]	-	3
Family Testudinidae		
Palaeochelys sp. [c]	-	-
Family Crocodylidae		
Diplocynodon sp.	-	36
Family Alligatoridae		
Allognathosuchus sp.	-	2
Class Aves		
Family Gastornithidae		
Gastornis parisiensis Hebert, 1855	-	2
Class Mammalia		
Family Herpetotheriidae		
Amphiperatherium maximum Crochet, 1979[d]	-	-
Peratherium sp.[g]	-	-
Family Paramyidae		
Ailuravus michauxi Hartenberger, 1975[h]	-	-
Euromys thaleri (Michaux, 1964)[h,i]	-	-
Pseudoparamys teilhardi (Wood, 1962)[h,i]	-	-
Pantrogna russelli (Michaux, 1964) [h,i,j]	-	-
'*Paramys' woodi* Michaux, 1964[h]	-	-
Sparnacomys chandoni (Hartenberger, 1971)[d,k]	-	-
Family Apatemyidae		
Apatemys sigogneaui Russell *et al*., 1979[d,m]	-	-
Apatemys mutiniacus Russell *et al*, 1979[d]	-	-
Family Esthonychidae		
Plesiesthonyx minimus (Baudry, 1992)[n][t]	-	-
Plesiesthonyx luciae (Baudry, 1992)[n][t]	-	-
Family Coryphodontidae		
Coryphodon (?) *eocaenus* Owen, 1846[d,g]	-	-
Family Paroxyclaenidae		
Paroxyclaenidae indet.[o]	-	-
Family Oxyaenidae		
Palaeonictis gigantea de Blainville, 1842[p]	-	-
Family Amphilemuridae		
Placentidens latus Russell *et al*., 1973[d]	-	-
Neomatronella luciannae (Russell *et al*.1975) [d]	-	-
Family Onychonycteridae		
Marnenycteris michauxi Hand *et al.*, 2015 [f]	-	1
Family Plesiadapidae		
Platychoerops daubrei (Lemoine, 1879) [d,l]	-	1
Plesiadapis cf. *remensis* Lemoine, 1887[g,l]	-	-
Family Paromomyidae		
Phenacolemur fuscus (Russell *et al*, 1967) [d]	-	1
Family Adapidae		
Protoadapis curvicuspidens (Lemoine, 1878)[g]	-	1
Cantius eppsi (Cooper, 1932) [d,l]	-	1
Family Arctocyonidae		
Landenodon woutersi Quinet, 1966[d,h]	-	3
Family Louisinidae[u]		
Paschatherium dolloi (Teilhard de Chardin, 1927) [d]	-	2
Teilhardimys musculus (Teilhard de Chardin, 1927) [d,g]	-	-
Family Phenacodontidae		
Phenacodus teilhardi Simpson, 1929[g]	-	-
Family Dichobunidae		
Diacodexis varleti Sudré *et al*., 1983[d,q]	-	-
Protodichobune oweni Lemoine, 1878[g]	-	-
Bunophorus cappetai Sudré *et al.*, 1983[d,q]	-	-
Family uncertain		
Hallensia louisi Hooker, 1994[r]	-	-
Superfamily Equoidea		
Pliolophus vulpiceps Owen, 1858[d,r,s]	-	-
Hyracotherium aff. *leporinum* Owen, 1841[d,g,r]	-	1
'Propachynolophus' sp.[r]	-	-

Table 2. Vertebrate fossils from Pourcy. First row (Q): Quarry. Second row (M): Outcrop 'Le Moulin de l'Ardre'. References: [a] Leriche, 1907; [b]Dutheil, 1991; [c]De Broin, 1977; [d]Hooker, 1996; [e]Casier, 1946; [f]Hand *et al*., 2015; [g]Louis *et al*., 1962; [h] Escarguel, 1999; [i]Michaux, 1964; [j]Michaux, 1968; [k]Hartenberger, 1971; [l]Russell *et al*., 1967; [m, n)]Baudry, 1992; [o]Rich *et al*., 1971; [p]Solé *et al*., 2011; [q]Sudré *et al*., 1983; [r]Hooker, 1994; [s]Smith & Smith, 2003; [t]Hooker, 2010 ; [u]Hooker & Russell, 2012.

at Verzenay, about 16 km east of Pourcy and at localities near Epernay, southeast of Pourcy (Gruas-Cavagnetto *et al*., 1980a, 1980b). From these, and from the lithology at Verzenay, the authors deduced the existence of a mangrove soil in this interval. Although not proven, the Falun de Pourcy must be either laterally equivalent to this palaeosol or later in date, perhaps channeling into penecontemporaneous beds. Mangroves today are restricted to the tropical/subtropical regions of the world and their presence in the Epernay Formation suggests similar climatic conditions at the time of the Pourcy deposits.

Dominant molluscs

The most abundant molluscs in the Pourcy fauna comprised Corbiculidae, Corbulidae, Neritidae, Melanopsidae, Potamididae and Hydrobiidae.

Corbiculidae[1]

Among the extant Corbiculidae the genus *Corbicula* (*s.s*.) is characterised by a thick, rounded equilateral shell with strong concentric folds. It lives in rivers and is restricted to freshwater, tolerating only the lowest salinity of tidal reaches, however this genus is not represented in the early Cenozoic. With the exception of the concentrically ridged but elongate and thin-shelled *Corbicula* (*s.l*.) *arnoudii*, all the Pourcy corbiculids have more or less smooth shells and are convergent with the living genera *Polymesoda* and *Geloina* which inhabit estuarine swamps and tropical/subtropical mangroves and lagoons respectively. This is taken as an indication that these smooth Cenozoic corbiculids were brackish water species, some of which might require new genera. Here we assign these species to *Corbicula s.l.* The fragile but well-preserved shells of *Corbicula* (*s.l*.) *arnoudii* were frequent at Pourcy although the relationships of this species are not fully known. It bears some resemblance to the genus *Batissa* which today lives in low salinities of the upper estuarine channel of the Abatan River (Lozouet & Plaziat, 2010). All corbiculid species at Pourcy were represented by abundant growth series from the smallest juveniles upwards. Shells of the relatively uncommon *Tellinocyclas tellinoides* were mostly rather waterworn. This species appears to have a limited stratigraphic range, occurring in the Sables de Sinceny and also in the Blackheath Formation in England which may be considered more or less coeval with Pourcy on the basis of molluscs, although mammal-based correlation is not yet certain.

[1] Bieler *et al*. (2010) thought the available senior name, Cyrenidae (Gray, 1840), had been used and so could not be considered a *nomen oblitum*, but Article 40.2 of the ICZN Code states 'If, however, a family-group name was replaced before 1961 because of the synonymy of the type genus, the substitute name is to be maintained if it is in prevailing usage.' We regard the family name Corbiculidae Gray, 1847 to have been in prevailing usage throughout most of the 20th century, and that it would be confusing to revert to a disused family name based on a junior synonym, so we therefore prefer to conserve Corbiculidae (ICZN 1999).

Corbulidae

The single *Varicorbula* species, occurring in large numbers at Pourcy, approaches the Paleocene-Recent genus *Lentidium* in morphology, and is presumed to have had a similar ecology. This in turn resembles *Potamocorbula*, in the Abatan River as noted by Lozouet & Plaziat (2010) who recorded large colonies of *Potamocorbula* living superficially buried in marginal sandbanks of the estuarine channel in divergent salinities of between 5 and 34‰. More strongly ornamented *Varicorbula* species were characteristic of euhaline environments in the Eocene.

Neritidae

Two extant genera are represented at Pourcy. *Neritodryas* today lives on the trunks of waterside trees in the lower (freshwater) reaches of tropical rivers and streams. The *Clithon* species at Pourcy are all referred to the subgenus *Pictoneritina* which typically lives intertidally in lagoons and estuaries, although other species of *Clithon* may extend some distance upstream to freshwater. The species diversity at Pourcy is comparable with that occurring at Abatan and in other island streams in the Indo-Pacific region, and the Pourcy species could all have been contemporaneous. However it is notable that the rare *C. barbei* also occurs exclusively with *Potamides funatus* in the underlying Argiles à Lignites d'Epernay at Saran near Epernay while the common *Neritoplica uniplicata* and *Clithon sobrinum* are found in other beds of the same formation at Mont Bernon, Epernay (Laurain *et al*., 1983) and at Mutigny to the east of Pourcy (pers. obs. ST).

Melanopsis

Although species of *Melanopsis* in Europe today are restricted to freshwater streams and lakes, their morphologically similar relatives in the Indo-west Pacific (New Caledonia, New Zealand) are often abundant in the brackish tidal estuaries of streams and rivers, sometimes in close association with mangroves (Franc, 1956; pers. obs. ST).

Tympanotonos/*Potamides*

Living *Tympanotonos* occurs only in West Africa where it inhabits estuarine mudflats and mangrove areas both distally and proximally. We follow Reid *et al*. (2008, p.692) who considered that all Cenozoic *Tympanotonos* species should be referred to *Potamides* (type species: *Cerithium lamarckii* Brongniart, 1810; Oligocene, France). This has not been widely accepted, perhaps owing to the fact that several other genus-level taxa have been proposed within this group, mostly poorly defined. For this reason we use *Potamides* pending a full phylogeny of the group taking account of their ontogeny (work in progress). This is also pragmatic as the name *Potamides* Brongniart, 1810 would replace *Tympanotonos* Schumacher, 1817 if the two were considered synonymous. Although Cenozoic Potamididae were clearly not restricted to mangrove settings, their constant presence in the underlying early Ypresian laminated clays suggests a similar palaeoenvironment to

that of the morphologically analogous living *Tympanotonos*. Other modern potamidids are always associated with sheltered habitats of reduced salinity, particularly in areas with mangroves (Reid *et al*., 2008).

Hydrobiidae

The abundant small, mostly smooth species are here referred to the Hydrobiidae *s.l.* pending an in-depth taxonomic assessment. The intraspecific variation is better judged from populations found at specific horizons in the underlying clays.

Molluscan feeding guilds

Overall, there is a good resemblance between the feeding guild compositions of the Eocene Pourcy and the modern Abatan mollusc faunas, with the caveat that no standardised collecting has been undertaken (Figs 108, 109). About half of each fauna is composed (both in species diversity and in abundance) of herbivores/detritivores. Carnivores are more common in the Abatan fauna at the expense of suspension feeders. In both Pourcy and Abatan samples the diversity of carnivores is greater, but they are not abundant.

The seven samples from the Abatan river taken by Lozouet & Plaziat (2010) spanned a transect from the river channel to the open bay mouth. Predatory carnivores were absent in the riverine and upper estuarine samples (Fig. 109). In species numbers the herbivores dwindled at the expense of carnivores towards the marine end of the transect. The abundance data did not show a clear trend.

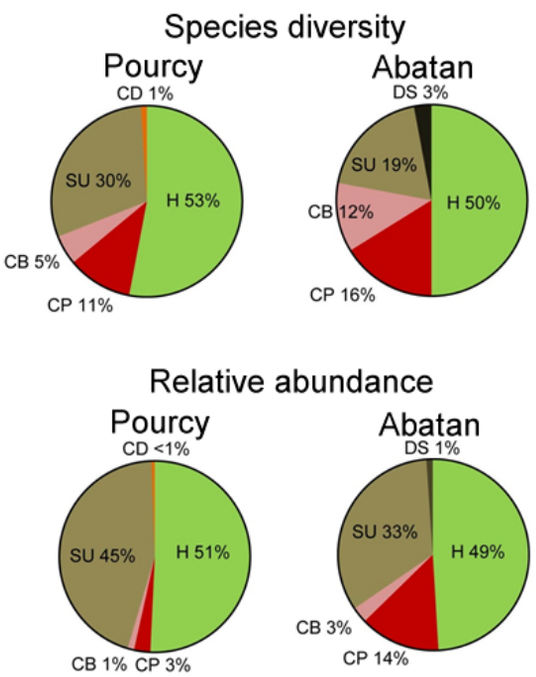

Figure 108. Mollusc feeding guilds of Pourcy and Abatan. H: herbivores/detritivores, CP: predatory carnivores, CB: browsing carnivores, SU: suspension feeders, DS: deposit feeders, CD: chemosymbiontic feeders.

The feeding guild composition of the Pourcy fauna showed the highest resemblance to middle, and lower estuarine and mouth bay faunas of Abatan. However, the much better resemblance of the feeding guilds of the Pourcy fauna with the entire Abatan data set suggests that Pourcy represents an environmentally (time) averaged fauna. This is also shown by the admixture of apparently ecologically incompatible species at Pourcy, such as freshwater-oligohaline taxa, (*e.g.* sphaeriid bivalves and viviparid and pulmonate snails) with mesohaline-polyhaline taxa, (*e.g.* oysters, mussels and turritellid snails).

Laurain *et al*. (1983) listed the molluscs from the fossiliferous sands and clays of beds 16-32 of the Epernay Formation at Mont Bernon (Marne). These beds occupy the lower two-thirds of the formation. Significantly 20 of the 23 species recorded also occur at Pourcy. Tuniot (1902) gave other occurrences of the species he listed from Pourcy. Significantly, none of the species listed were unequivocally indicators of a Cuisian date except perhaps *Barbatia modioliformis* (also at Sinceny and Cuise-la-Motte and higher strata) which was also one of the few species usually regarded as indicating euhaline conditions (although Tuniot, 1902 also recorded it from 'Les Lignites'). *Cyrtopleura orbignyana*, occurring at Sinceny and Cuise-la-Motte, was also identified from a

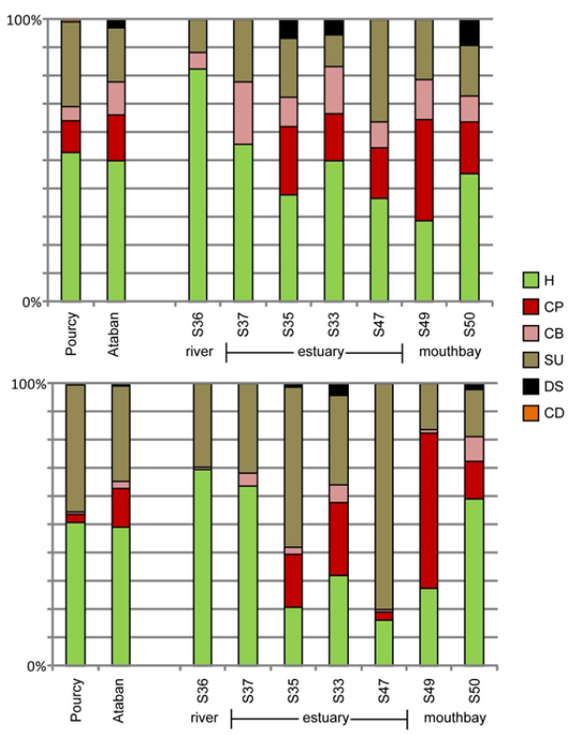

Figure 109. Feeding guilds of the Pourcy and the entire Abatan faunas, and those of the seven sample stations from Abatan that represent riverine to marine settings. Abatan data from Lozouet & Plaziat (2010). H: herbivores/detritivores, CP: predatory carnivores, CB: browsing carnivores, SU: suspension feeders, DS: deposit feeders, CD: chemosymbiontic feeders. The feeding guild is given for species diversity (upper graph) and relative abundance (lower graph) data.

few fragments at Pourcy and is regarded as a marine indicator. *Eopleurotoma pourcyensis*, which would normally be considered a fully marine species, was also recorded from the Argiles à Lignites at Mailly-Champagne and Rilly by Bellevoye (1907) who remarked that it was truly a Sparnacian species. In the lower beds of the Epernay Formation examined at Saran (Marne) to the southeast of Pourcy it was found that *Potamides funatus* almost exclusively occupied one stratum of the 'lignites' while the flanged morph of *Potamides turris* (Fig. 45) was similarly abundant at a lower horizon. This adds support to the theory that the Falun de Pourcy with its confusing intraspecific variation among the Potamididae is in fact a mixture that includes material reworked from underlying levels. The clays of Mutigny to the east of Pourcy contained an impoverished but similar mix of subspecific variants to those at Pourcy. Duprat *et al*. (2010) placed Mutigny between the 'upper and lower levels' at Pourcy.

The Pourcy fauna has a dissimilar feeding composition from those of other fossil coastal tropical associations studied so far. A Miocene Indo-Pacific sea grass fauna (Reich *et al*., 2014) shows a much higher abundance of the herbivore/detritivore guild. Instead, a coral-carpet associated fauna from the same region shows dominance of carnivores (A. Kusworo, pers. comm., 2013). A Pleistocene fluviolacustrine to high estuarine environment from Trinil, Java (Joordens *et al*., 2009) is dominated (>90% in abundance) by thiarid snails (grazers/detritivores). The accompanying mollusc fauna included *Corbicula* (*s.str.*) and indicated the upper reaches of a river or stream although neritid snails were lacking in the Trinil fauna. Overall the composition of molluscan feeding guilds at Pourcy was broadly most similar to that of the modern Indo-Pacific mangrove-estuarine setting of Abatan.

Vertebrates

The shark teeth were predominantely of juvenile animals, which indicates a possible mangrove setting (T. Bor, pers. comm.) The bony fish genera *Amia* and *Lepisosteus* are compatible with a tropical or subtropical, brackish to freshwater environment with shallow lakes and swamps (V.W.M. van Hinsbergh, pers. comm., 2013; Wilson, 1982; Winkler, 1983). The turtles too, indicate a tropical environment with estuarine and terrestrial taxa represented in the material (De Broin, 1977; Buffetaut *et al*., 1982; Davenport, 2011; Jimenez-Fuentes *et al*., 1994). The alligatorid crocodile species implies brackish conditions and the crocodyliid species implies a freshwater environment (Davenport, 2011). The presence of the bird genus *Gastornis* suggests a warm to subtropical coastal lowland with alluvial floodplains, well-vegetated swamps and open savannas (Andors, 1991; Mustoe *et al*., 2012).

Among the mammals, the relatively large number of primates is remarkable, with seven genera. This is a strong indication of a warm, relatively aseasonal climate resulting in the availability of seeds and fruits during the entire year (van den Hoek Ostende, pers. comm.). Genera found at Pourcy were mainly fruit- and seed-eaters, just like the eight genera of rodents of this locality. The hoofed animals were represented by Condylarthra and primitive Artiodactyla and Perissodactyla. These were usually small forms adapted to live in or among trees. Some representatives belonged to groups that are now extinct, such as the Tillotheriidae and the Coryphodontidae. The tillothere *Franchaius* is considered to have been a root and tuber eater (Agusti & Anton, 2002) and the semi-aquatic *Coryphodon* had a similar diet. The only carnivore in the assemblage, the creodont *Palaeonictis*, hunted in trees. Overall the mammals represent a relatively humid, forest environment.

This assessment of the palaeoecology of the mammal fauna raises the question of their relation to an estuarine mangrove environment as deduced from the other fossils, and whether they might be derived from earlier terrestrial deposits. Hooker (1996) originated a series of Paleocene-Eocene mammal zones defined by first and last appearances of various taxa. Zone PEI was dated as latest Paleocene defined by the last appearances of various species including *Landenodon woutersi, Paschatherium dolloi*, *Microhyus musculus* and *Phenacodus teilhardi.* Zone PEII included the first appearance of *Neomatronella luciannae* and was dated as early Eocene. These species all occur together in the Falun de Pourcy which has caused problems with dating the deposit (see Hand *et al.,* 2015). Cavelier (1987) also commented on this phenomenon and cited earlier similar observations. Mammals of zone PEI would not be expected to occur in the Epernay Formation, except perhaps in reworked material at the base, so their presence at Pourcy in the upper part of the formation is enigmatic.

Other fossils found at Pourcy confirm the general palaeoecology as deduced from molluscs and vertebrates. Four species of ostracods, *Cytheridea* sp., *Clitrocytheridea canceratica* Apostrolescu, 1956, *Vetustocytheridea guitrancourtensis* Apostrolescu, 1956 and *Hemicyprideis* sp. (identifications by C.M. Pirkenseer, Fribourg, Switzerland) suggest a brackish coastal, lagoonal or estuarine environment (C.M. Pirkenseer, pers. comm., 2012). Rare occurrences of serpulid worms (*Ditrupa plana* (Sowerby, 1815) and *Rotularia bognoriensis* (Mantell, 1822) indicate lagoonal to open marine settings (Morton & Harper, 2009; Morton & Salvador, 2009). In England *Ditrupa plana* first appears in the Tilehurst Member of the Harwich Formation while *Rotularia bognoriensis* appears in the lower part of the London Clay Formation, both in fully marine facies. The echinoid *Scutellina lenticularis* (Lamarck, 1816), is characteristic of marine environments (J. Eberson, Utrecht, pers. comm. 2008). In addition a few poorly preserved freshwater charophytes and a single small example of the foraminifer *Nummulites planulatus* were found. This species reached its acme in the mid-late Ypresian (Cuisian) which is usually regarded as its first appearance, although it is also recorded from Sinceny (Aisne) (MNHN-GG-GG2004-77213 Coll. Abrard, Soyer; MNHN-GG-GG2004-77221 Collection Bonnet) which may be tentatively correlated with the Falun de Pourcy on the basis of molluscs, although mammal records are equivocal (Hooker, 2015).

In conclusion, the invertebrate faunas from Pourcy represent early Eocene tropical coastal settings probably with mangroves. They contain indicators for full marine, euryhaline and freshwater as well as terrestrial settings. The forest environment, which may have been the source of the mammals, suggests a degree of transport and certainly some reworking. The same is probably true of the molluscs as the intraspecific variation seen in the common brackish water groups, mentioned above, is far greater than would be expected among living populations in any one locality today.

A landscape reconstruction made for the North Sea Basin Eocene provided in Fig. 110 shows a palaeoenvironment probably similar to that of Pourcy.

Figure 110. Reconstructed mangrove landscape in the Ypresian of the southern North Sea Basin that at the time included also the Paris Basin. Drawing by E.J. Bosch (Naturalis Biodiversity Center, Leiden).

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Appendix 1

Information about abundance (number of specimens in the studied collections), feeding-behaviour and salinity preferences of the mollusc families. Only material from the studied collections is included (not taxa recorded in literature only or additional material in private collections). Salinity preferences are estimated and only an approximation.

Abbreviations for feeding ecology:

SU = suspension feeder; D = deposit feeder; CD = chemosymbiontic deposit feeder; H = herbivore/detritivores; P = parasite; CP = predatory carnivore. Salinity: F = freshwater; B = brackish (stenohaline/euryhaline); M = marine (euhaline); T = terrestrial.

	Abundance (n)	Feeding behaviour	Salinity preference
Class Bivalvia			
Family Arcidae	13	SU	M
Family Noetiidae	96	SU	M
Family Mytilidae	139	SU	M/B
Family Ostreidae	268	SU	M
Family Anomiidae	87	SU	M
Family Lucinidae	42	CD	M
Family Psammobiidae	2	D	M
Family Corbiculidae	1943	SU	B/(F)
Family Pisidiidae	1	SU	F
Family Veneridae	19	SU	M
Family Myidae	24	SU	M
Family Corbulidae	855	SU	M/B
Family Pholadidae	13	SU	M/B/(F)
Class Gastropoda			
Family Neritidae	844	H	B/F/(M)
Family Viviparidae	2	H	F
Family Ampullinidae	110	H	M
Family Potamididae	797	H	B/M
Family Batillariidae	32	H	B/M
Family Pachychilidae	460	H	B/F
Family Melanopsidae	834	H	B/F
Family Thiaridae	11	H	B/F
Family Turritellidae	49	SU	M
Family Hydrobiidae (s.l.)	572	H	B/F
Family Naticidae	113	CP	M
Family Epitoniidae	2	CP	M
Family Turbinellidae	11	CP	M
Family Buccinidae	53	CP	M
Family Pseudolividae	21	CP	M
Family Turridae	10	CP	M
Family Cornirostridae	163	H	M
Family Pyramidellidae	85	P	M/(B)
Family Ringiculidae	3	CP	M
Family Cylichnidae	2	CP	M
Family Carychiidae	2	CP	T/(F)
Family Physidae	2	H	F
Family Planorbidae	33	H	F

Appendix 2

Additional records of fish remains from the two sites at Pourcy in the Allan Lawson collection (Mill Hill, London, England), which are not included in the statistics.

Synechodontidae	
Synechodus sp.	1 tooth (rolled)
Heterodontidae	
Heterodontus sp.	1 tooth (rolled)
Carcharhinidae	
Physogaleus secundus (Winkler, 1874)	6 teeth
Odontaspididae	
Striatolamia macrota (Agassiz, 1843)	1 tooth
Jaekelotodontidae	
Palaeohypotodus rutoti (Winkler, 1874)	1 basal fragment
Scyliorhinidae	
Scyliorhinus gilberti (Casier, 1946)	1 tooth
Scyliorhinus sp.	1 tooth
Rhinobatidae	
Rhinobatos bruxelliensis (Jaekel, 1894)	1 tooth
Dasyatidae	
Dasyatis jaekeli Leriche, 1905	7 teeth
Jaquhermania duponti (Winkler, 1874)	1 tooth
Hypolophidae	
Hypolophodon sylvestris (White, 1931)	1 tooth (crown)
Lepisosteidae	
Lepisosteus suessionensis Gervais, 1852	34 teeth, 20 scales
Amiidae	
Amia sp.	1 tooth
Albulidae	
Pterothrissus tardinensis (Leriche, 1908)	17 otoliths
Synodontidae	
Argentina abbatiae Stinton, 1965	4 otoliths
Serranidae	
Polyperca serranoides Stinton, 1965	10 otoliths
serranid sp. 1	2 otoliths
PERCOIDEI	
Anthracoperca cf. *siebergi* Voigt, 1934	4 otoliths
LABROIDEI	
Diaphyodus sauvagei (Leriche, 1900)	6 palate fragments